
INTERNATIONAL SOCIETY FOR BEHAVIORAL ECOLOGY

ISBE NEWSLETTER

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From the president

I wish to report on two recent actions, one by ISBE and the other by the U.S. National Science Foundation, that should further the cause of behavioral ecology.

First, ISBE will soon begin requesting a “*lay summary*” from authors who publish their work in our journal, *Behavioral Ecology*. The purpose of this new initiative is to increase awareness of the work being done in our discipline by making the results of our research easily accessible to a wider audience of interested readers.

Here is the way it will work. Authors of papers accepted for publication in *Behavioral Ecology* will be asked to submit both a lay summary and the traditional scientific abstract of their work. The lay summary will place the findings in a broad context and explain their importance in terms that are understandable to non-specialists. Each lay summary will then be posted on our journal’s home page on the World Wide Web. Oxford University Press (OUP), which maintains our home page as part of its website, is enthusiastic about the project and has agreed to make these summaries freely available, as they currently do for our scientific abstracts and table of contents. When this new initiative goes into effect, any internet browser will be able to search, read and download easy-to-understand summations of work being done in behavioral ecology.

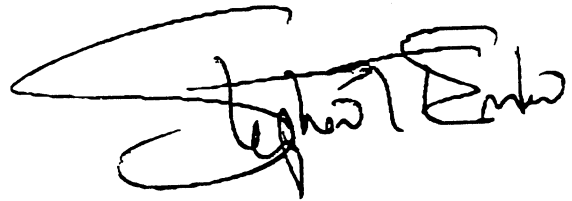
The posting of non-technical summaries on the Web will constitute a major advance in our ability to communicate both the excitement and the significance of our work to others. It will provide an easy means for a wide variety of readers - be they science writers, administrators and government officials, high school teachers and their students, or interested members of the public - to learn more about behavioral ecology.

It will also make it easier for those of us in the discipline to obtain information of the sort we need to argue the case for behavioral ecology to deans, directors or other public officials. I thank David Prosser, Commissioning Editor at OUP, for his support of the idea and ISBE's editors for their willingness to work with the Executive Committee to implement it. Details for the preparation of the new lay summaries will be announced in future instructions to authors.

Second, the U.S. National Science Foundation recently announced an increase in funding for its Animal Behavior Program by 25% - from 4.8 to 6 million dollars for the Fiscal Year 1999. This large increase was the result of many factors, one of which was the successful lobbying effort last fall by officers of the Animal Behavior Society, ISBE, and the animal behavior division of the Society for Integrative and Comparative Biology. Meredith West, Steve Nowicki and I met with Drs. Mary Clutter, James Edwards and Bruce Umminger at NSF to emphasize the increased impact that evolutionary studies of behavior are having on numerous disciplines ranging from genetic engineering to cognitive studies and from medicine to conservation. We also stressed the central role of animal behavior in science education. Our advance letter to NSF, in which we develop these arguments, is reprinted in the November 1998 Newsletter of the Animal Behavior Society. The funding increase reaffirms NSF's recognition of the importance of our discipline.

We all know that the continued health of behavioral ecology depends, in part, upon our success in communicating what we do, and why it is worth doing, to others. Oxford University

Press is giving us the platform to make such information freely accessible to those who wish to learn more about us. The lay summary initiative will require some time and effort from all of us. I believe, however, that the benefits associated with an increased public awareness of our science will far outweigh these costs.



Stephen T. Emlen

Editorial

Several members have written me that they did not receive a copy of the (last) Newsletter with their issue of *Behav Ecol*. The distribution of the Newsletter is done by OUP in the US, so please, contact OUP directly to get your copy (Gloria Bruno: gbs@oup-usa.org).

I'd like to thank all who contributed to this issue, and in particular the authors of the Forum piece and the book reviewers for their excellent efforts.

Please, note that there is a ballot hidden in this issue (pages 4 and 5). Please, take a few moments and send your answer to the Secretary. The next issue of the Newsletter will come out with the November/December issue of *Behavioral Ecology*, so copy that reaches me **before 15 October** can be included.

Bart Kempenaers
Newsletter Editor

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Society News

Nominations for new Officers

A nominating committee, which consists of Anders Berglund, Janis Dickinson and myself, seek suggestions from the membership for the following posts:

President-Elect
Treasurer
Councillors (two positions)

We will draw up a short-list of two nominees each for President-Elect and Treasurer, and four nominations for the two councillor positions. There will then be a ballot printed in the November/December 1999 Newsletter.

Please send suggestions for the short-list to me by 31 July 1999. There's no need to contact your potential nominees at this stage. We will confirm that short-listed candidates are willing to stand for election.

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Ballot

The following amended versions of articles 1 and 9 of the constitution and articles 4 and 5 of the By-Laws of the ISBE were submitted to council by the treasurer and approved by the majority of Council.

In accordance with article 7 of the constitution these proposed versions need the approval of the membership before they can be adopted. Please could you therefore take the time to vote by mailing or faxing the following signed declaration to the Secretary of the ISBE as soon as possible.

CONSTITUTION

Article 1: NAME AND OBJECT. The society shall be called "The International Society for Behavioral Ecology," hereafter referred to as "The Society". The object of the society shall be to sponsor periodic scientific meetings for behavioral ecologists, to promote scientific research in behavioral ecology, and to foster the integration of various related disciplines with behavioral ecology.

(This article is the same as in the original constitution except the final sentence "The Society shall be incorporated under the laws of the United States of America" has been removed)

Article 9: ORGANIZATIONAL STATUS. The International Society for Behavioral Ecology is organized exclusively for charitable, educational and scientific purposes, including, for such purposes, the making of distributions to organizations that qualify as exempt organizations under section 501(c)(3) of the Internal Revenue Code, or corresponding section of any future federal tax code.

(This is an additional article to the original constitution)

By-Laws

Article 4: DISSOLUTION: Upon the dissolution of The Society, title to and all assets shall be distributed for one or more exempt purposes within the meaning of section 501(c)(3) of the Internal Revenue Code, or corresponding feature of any future federal tax code. In practice, the society shall identify an exempt organization or organizations as the membership of the society shall deem best qualified to carry on the functions of The Society. The membership of The Society shall make this determination by a simple majority vote conducted by mail ballot on proposals formulated by the Council. The voting shall be administered by the Secretary.

(This article replaces “In the event of dissolution or termination of The Society, title to and possession of all property of the Society shall pass forthwith to such organization as the membership of the Society shall deem best qualified to carry on the functions of The Society. The membership of The Society shall make this determination by a simple majority vote conducted by mail ballot on proposals formulated by the Council. The voting shall be administered by the Secretary.”)

Article 5: GENERAL PROHIBITIONS

a) The International Society for Behavioral Ecology shall be organized exclusively for scientific, charitable and educational purposes within the meaning of Section 501(c)(3) of The Internal Revenue Code or corresponding section of any future federal tax code;

b) The International Society for Behavioral Ecology shall be operated exclusively for scientific, charitable and educational purposes within the meaning of Section 501(c)(3) of The Internal Revenue Code or corresponding section of any future federal tax code;

(These replace “a) The International Society for Behavioral Ecology shall be organized exclusively for scientific and educational purposes; b) The International Society for Behavioral Ecology shall be operated exclusively for scientific and educational purposes;”)

This exact language was required by the Internal Revenue Service of the United States in order that the Society can claim tax-exempt status. If the Treasury should move to another country, then further modifications would likely be required to meet that country’s tax laws.

Please delete as appropriate:

I am in favour / not in favour of the ammended versions of articles 1 and 9 of the Constitution and articles 4 and 5 of the By-Laws.

Signed

Name in full

Date

Please mail / fax to:

Dr. Marion Petrie, Evolution and Behaviour Research Group, Department of Psychology, University of Newcastle, Newcastle-upon-Tyne, NE1 7RU, UK

Fax: +44 (0)191 222 5622

Address List for Members

PLEASE SEND DETAILS

I am trying to compile a complete contact list for members of the ISBE. I have received from OUP a current mailing list but, this is not in an electronic format, nor does it include e-mail addresses or phone numbers for any of the current membership. I would therefore be grateful if all members could e-mail me with all these details. The completed list will only be made available to members of the ISBE.

Please e-mail your details in the following form *name/mail address/e-mail address/phone number/fax number* to:

Marion.Petrie@ncl.ac.uk
Secretary ISBE

8th ISBE CONGRESS

University of Zürich, 8-12th August 2000

The 8th ISBE Conference will take place in August, 2000 in Zürich, Switzerland. The main organiser is Paul Ward: pward@zoolmus.unizh.ch. The rest of the local committee are Wolf Blanckenhorn, Barbara König and Paul Schmid-Hempel. The traditional football match will be organised by Innes Cuthill and Mark Elgar will referee. Other sports facilities will also be available for delegates.

Located in the centre of Europe, Zürich has direct air connections to all major international airports. The airport at Kloten has excellent public

transport connections to the city centre. A train or taxi journey to the main station takes about 15 minutes. The city is located on both banks of the River Limmat, the outflow from Lake Zürich. The Alps are about 50 km to the south. There is a modern zoo, a major art gallery, Switzerland's national museum and a wealth of other cultural attractions.

The Irchel campus of the University of Zürich will be the site of all highly-intellectual events and is about 15 minutes by tram from the city centre. The tram and bus system is outstanding and you are never more than about 200m from a stop. The campus is an excellent modern complex in its own park at the edge of a wooded hill - the Züriberg. 'Walks in the woods' are within ten minutes of the campus.

The lecture theatres are all on one level and close together in the centre of the campus. The two main theatres together sit 1023 (577 and 446) and have a complete video link. Three other theatres each seat 283 and a small theatre will be available for talk preparation. There is plenty of space for posters. We anticipate abstract submission to be in January or February 2000; a later flyer will have the details.

Accommodation will mainly be in hotels. The room rate for a shared twin room will be about SFr 140 per night for bed and breakfast. We are looking for cheaper options for students. Meals will be catered at the campus but there are lots of other restaurants in the city. We expect that social events will include a boat trip on the lake and a bus trip to the mountains.

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 newest issues of our journal Behavioral Ecology.

Spousal Membership

For \$5 per year spouses of full members can become members of ISBE. Spousal members receive the annual newsletter and information concerning biannual meetings, but do not receive a subscription to the journal. Please see information in any issue of Behavioral Ecology.

Conferences

ANIMAL BEHAVIOR SOCIETY MEETING

The Animal Behavior Society Annual Meeting will be held 26 June - 1 July 1999 at Bucknell University in Lewisburg, Pennsylvania. Plenary speakers include Gail Michener, Lynne Houck, and Steve Nowicki. Symposia include "Educating About Animal Behavior: A Broader Perspective." For further information see: <http://www.cisab.indiana.edu/ABS/index.html> or contact the local host, Michael Pereira: mpereira@bucknell.edu, +1-717-524-1430.

Grants and Jobs

POSITIONS IN ANIMAL BEHAVIOUR

Applications are invited for a **Research Position** and a **Postdoctoral Fellowship** in behavioural sciences at the Konrad Lorenz-Institut für Vergleichende Verhaltensforschung in Vienna. PhD and pertinent professional experience needed in either behavioural ecology or behavioural physiology or ethology.

The Konrad Lorenz-Institut für Vergleichende Verhaltensforschung (KLIVV) is part of the Austrian Academy of Sciences and investigates mainly reproductive systems (co-operation, brood parasitism, sexual selection and sperm competition), foraging and habitat use (sensory ecology, ecomorphology), and cognitive behaviour (exploration, tool use). Applicants should be experienced in either of these or in closely related fields. For the **Research Position** practice and good working knowledge of molecular methods are particularly welcome.

The **Research Position** is offered for 4 years starting with October 1999, tenure possible. The **Postdoctoral Fellowship** is offered for 1 year starting with October 1999. Send CV, statement of current research interests, copies of significant publications and at least two letters of recommendation before **1st July 1999** to

Prof. Dr. H. Winkler
 KLIVV, Savoyenstr. 1a, A-1160 Wien, Austria.
 E-mail: h.winkler@klivv.oeaw.ac.at

Forum

An early and previously unappreciated application of the quantitative analysis of diet choice

Lawrence M. Dill¹, Alex Fraser¹, and Helgi Thorarensen²

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In his 1997 book “Cod”, author Mark Kurlansky makes reference to a 1914 essay by the Icelandic banker Tryggvi Gunnarsson, concerning the value of dried cod heads (a staple in the local diet at that time) relative to their various costs. With the assistance of Prof. J. Th. Thor, of the Icelandic Centre for Fisheries History Research, we managed to track down the original essay, which was in Icelandic. A translation prepared by one of us (guess which) follows:

“The Cod Heads”

When I came to Reykjavik in the spring of 1893, the fishing season was good; there were often around 70-80 large cod in the daily share of each fisherman. The cod head sale kept pace. Large caravans of pack horses were leaving Reykjavik and the south coast of Faxaflói Bay daily, heading east to Arnes and Rangarvellir counties. I was appalled at how short sighted people were and told them that these purchases and travels were not worth their while, but still they continued.

To find more out about this trade, I bought 120 dried cod heads - I was told that was about what one horse could carry - and hired an

experienced man to tear the edible parts from the heads. He worked for 1.5 days. The edible parts from 120 heads weighed only a little more than 16 pounds. I didn't think that this was much and had another person repeat the experiment, but with the same results.

The food from one horse load was little, but worse still was that it was barely edible; I saw how the heads were dried. The heads were barely washed and then put directly onto stone walls, which then were common around farms. When the weather was dry and windy, dirt and other nice things from the road were blown on the heads, but when it rained for a long time they got soggy; so one can just imagine how the horse loads looked after a long rainy journey along muddy roads.

If we assume that the trip takes four days from the far corners of Arnes and Rangarvellir counties to Reykjavik or the fishing posts on the south side of Faxaflói Bay with one person and a horse for riding, then the trip will cost for five horses 6.25 kronur each day or 25 kronur for four days and the cost of hiring the man for the same time will be 10 kronur. The price for the heads was 2.40 kronur. In total, this is 37.40 kronur when we do not count the work involved in tearing the edible parts off the heads for which I paid 4.50 kronur. The food from these four horse loads was 64 pounds.

It is apparent that much of what we think of as modern optimal foraging theory is embodied in Gunnarsson's argument, namely:

- an experimentally derived measure of handling time (1.5 days for 120 cod heads)
- an estimate of the useable food value of this many cod heads (16 pounds, although it is “hardly edible”)
- a calculation of the travel time required to “capture” these heads and return them to the central place, and

- an attempt to express all costs in a common currency (kronur).

From these data, one can calculate the profitability of cod heads as a diet item for Icelanders:

- 4 horse loads (1 trip) produced 64 lbs of meat (evidently, 480 heads)
- the heads cost 2.40 kronur, but to this must be added the 25 kr for the horses, 10 kr for the man to accompany them to the fishing villages, and 18 kr for stripping the meat (4 x 4.5 kr, since there are 4 times as many heads as in the experiment).

Thus, the “profitability” of cod heads is 64 lbs of meat/55.4 kr, or 1.16 lb/kr (the travel and handling times do not appear in this calculation, having been converted to kr at the prevailing wage rates, namely 2.5 kr/day for the rider, and 3 kr/day for the “head tearer”).

Taking the inverse of this results in the effective cost of dry cod flesh, namely 0.86 kr/lb, and if dry cod meat weighs 1/13 that of fresh fish (Gunnar Karlsson, pers. comm.) then this is equivalent to 0.066 kr per lb. of fresh cod. By comparison, a pound of lamb in Iceland in 1895 (the closest date for which we could obtain the data) cost 0.36 kr per kilogram, or about 0.16 kr/lb (Gudmundur Jonsson, pers. comm.). However, dried cod could be purchased in shops at that time for only 0.17 kr/lb. So Gunnarsson’s claim that Icelanders were short-sighted is well founded; they certainly don’t seem to have been foraging optimally. We therefore propose that Tryggvi Gunnarsson be considered the father of modern foraging theory, rather than Eric (The Red?) Charnov. Sadly, Gunnarsson missed out on this accolade in his lifetime and had to be content with being a member of the Icelandic Parliament (the world’s oldest) and Chairman of the Icelandic National Bank, and having his picture at one time on the 100 kronur bill.

References

- Gunnarsson, T. 1914. Calendar of the Icelandic Patriotic Society, 1915 (*Almanak Hins islenzka thjodvinafelags*, 1915), pp 97-98.
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Book Reviews

Game Theory and Animal Behavior.

Edited by L.A. Dugatkin & H.K. Reeve.
Oxford University Press, 1998. 334 pp.
ISBN 0-19-509692-4

This edited volume consists of fourteen chapters, starting with “What is evolutionary game theory” (Hammerstein) and ending with “Why we need evolutionary game theory” (Reeve & Dugatkin). The chapters are quite different in style: some are reviews while others are essentially research papers. This variety is not necessarily a bad thing. Although a lot of ground is covered, there is nothing on parental care (though Mock, Parker & Schwagmeyer refer to a recent review of theirs), sperm competition or dynamic games.

Analysis of game-theoretic models can get rather technical, but although most of the chapters are concerned with theoretical issues, they are not cluttered with maths (the chapter by Gomulkiewicz on the relationship between game theory and quantitative genetics is probably the toughest). The development of game theory in evolutionary biology has resulted in the formalisation of verbal arguments. Both Mock, Parker & Schwagmeyer (in the context of parent-offspring conflict) and Johnstone (in the context of the handicap principle) discuss the limits of

verbal arguments and the improvement in our understanding that has resulted from the construction of mathematical models. By giving an equation-free account of communication, Johnstone shows that although theory is a necessary foundation, the key issues can be described verbally.

Dugatkin attempts the difficult task of reviewing work on co-operation. The evolution of co-operation in the context of the Prisoner's Dilemma has received considerable attention. Dugatkin summarises the theoretical work in a table that takes up nearly three pages. He then discusses various examples, the first of which is egg trading in the black hamlet, a fish that is a simultaneous hermaphrodite. Following the work of Fischer (1988) he develops an account based on viewing egg trading as an iterated Prisoner's Dilemma and discusses the stability of Tit for Tat. Although Dugatkin mentions that Connor (1992) has given an alternative view, the work of Friedman & Hammerstein (1991) is not mentioned. Not only do Friedman & Hammerstein develop a model of egg trading, but they also discuss the limitations of modeling egg trading as an iterated Prisoner's Dilemma. In their model, the time required to find a mate and to display (which is not considered by Dugatkin) is important in discouraging cheating. Biologists have probably overused the Prisoner's Dilemma as a framework for the analysis of co-operation. Egg trading could have been used as a case study to bring out the limitations of this approach.

Ideal free theory is covered from different perspectives by Brown and by Sih. Sih concentrates on games involving three trophic levels: a resource, consumers that eat the resource, and predators that eat the consumers. When both the consumers and the predators distribute themselves adaptively, we have what Sih calls a double Ideal Free Distribution. Brown looks at habitat selection when only animals on

one trophic level make a choice. In his analysis of Ideal Free Distributions with predation, Brown proves that the ESS in such circumstances cannot involve each animal staying in one habitat (pp. 200-202). In contrast, Moody et al. (1996) obtain solutions of this form. I suspect that this apparent conflict is the result of a difference in assumptions. Moody et al. are considering instantaneous decisions, whereas Brown is concerned with decisions over a finite time interval. This suggests to me that we may be in need of a review of habitat choice under predation risk that unifies these results on Ideal Free Distributions (and perhaps relates it to work on vigilance).

I found many of the chapters stimulating. I particularly enjoyed Reeve's chapter which in addition to reviewing previous work on reproductive skew also presents lots of new models. In conclusion, despite the fact that this book does not provide an overview of all aspects of evolutionary game theory, it presents lots of interesting perspectives.

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References

- Connor, R.C. 1992. Egg-trading in simultaneous hermaphrodites: an alternative to Tit-for-Tat. *J Evol Biol* 5:523-528.
- Fischer, E. 1988. Simultaneous hermaphroditism, Tit-for-Tat, and the evolutionary stability of social systems. *Ethol Sociobiol* 9: 119-136.
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Moody, A.L., Houston, A.I., McNamara, J.M.
1996. Ideal free distributions under
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131-143.

The Social Regulation of Competition and Aggression in Animals.

M.H. Moynihan. Smithsonian Institution
Press, 1998. 158 pp.

With a memorable personal style the late Martin H. Moynihan conveys a powerful message in this book. The message is not supported by fancy mathematical models; it is simply presented with the energetic insight of the careful observer of animal behavior. The main message is clearly stated in the title. This book is about the regulation of aggression in the face of competition. A topic that is certainly not new to some areas of ethology but is much neglected in behavioral ecology.

There is another message that grows in importance through the book. It is about the richness of detailed descriptions of animal behavior. These descriptions hold the special wealth that has been at the basis of many great discoveries. Theoretical advances often start with detailed observations that lead to testable hypotheses. Moynihan's emphasis on behavioral descriptions also hints to a more balanced approach to the study of animal behavior, an approach that should not ignore the proximate mechanisms.

In the first page of the editors' preface, the book is presented as the first to focus on the forms and evolution of the mechanisms to control aggression. This is not true. Frans de Waal started to present an alternative view of aggression and its regulating mechanisms two decades ago. His original intuition was based on earlier accounts of temporal relations between aggressive and friendly

interactions in various species and on his own detailed observations of chimpanzees. Most of his work, and that of many other scientists following his steps, has been carried out on primates. This taxonomic selection has not facilitated the diffusion of the new view to the larger audience of behavioral ecologists probably because students of primates sadly occupy a "special niche" within the scientific community. Hence, even though Moynihan's book is not the first to deal with the mechanisms for the regulation of aggression (de Waal's *Peacemaking among Primates*, published in 1989, is actually cited in Moynihan's book), it is a pioneering work because it is directed to an audience not much exposed to this topic.

The book presents five major sections along with an introduction, two appendixes, and a glossary. The "Partial Recapitulation with Comments" toward the end captures the essence of the book. After presenting the case for the control of competition and aggression (unfortunately without mentioning the costs of aggression related to the disturbance to cooperative relationships), Moynihan describes various tactics from subtle signals to complex interactions which may regulate conflict between conspecifics. As the list of tactics progresses, the link with the control of aggressive expression becomes looser. The "complicated devices", such as allopreening, allogrooming, or altruism in general, are presented without explicitly reminding the reader of their role in controlling aggression. The fact that they are "friendly" in nature appears sufficient for them to have a deterrent function. Following this theme, "gregariousness" is basically presented as a synonymous of "friendliness", but we know that it is also a source of competition. The descriptions of animal signaling are fascinating but a closer focus on how the various mechanisms may actually work in reducing aggressive competition would have better capitalized on the wealth of the behavioral observations presented.

The book will undoubtedly bring the view of social regulation of aggression where it has not been successfully delivered yet. As the editors stated in the preface Moynihan left us a gift. I believe that this gift is a strong reminder of the importance of detailed behavioral observations of animals in action.

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Behavioral Ecology and Conservation Biology. Edited by T. Caro. Oxford University Press, New York, 1998. 582 pp. ISBN: 0-19-510489-7; 0-19-510490-0 (pbk.).

Conservation is hot! That is the case for political reasons, both as personal engagement, but also at local, national and global scales. Conservation is also hot because research funding for conservation biology is relatively more plentiful than for other areas. Hence, an increasing interest has emerged in a number of biological fields for this subject including the behavioral sciences. The volume "Behavioral Ecology and Conservation Biology", edited by Tim Caro, presents a broad view of the usefulness of behavioral perspectives in conservation biology ranging from modeling, and empirical and comparative approaches to more political issues.

The flag is raised high from the very beginning, although the usefulness of a behavioral ecological approach ranges from the almost tragicomic to the most serious. My favorite example among the first category derives from the reintroduction program of Asiatic wild asses as one of several biblical (!) animals being released into

Judea and Samaria by the Israeli government! The first introduction contained only males (!) that not surprisingly quickly dispersed. Dan Rubenstein writes: "That only males were initially introduced underscores the need to pay attention to detail." However, anybody with a minimum knowledge of animal breeding would realize that both males and females are needed. Obviously, behavioral ecologists would do as well as shepherds, farmers or vets! The harder issues are treated in six different parts of the book: baseline data and conservation, baseline data and conservation intervention, mating systems and conservation, mating systems and intervention, dispersal and inbreeding, and human behavioral ecology. The most interesting part is the last section: It is the understanding of why humans behave in the way they do that will help the most to resolve conservation issues. These insights range from Michael Alvard's puncture of the myth of the noble savage born as a conservationist to the evolutionary human psychology of environmental problems. The latter chapter by Margo Wilson, Martin Daly and Stephen Gordon addresses the determinants of risk taking, resource use and environmental degradation by humans. Perhaps not surprisingly, men, in particular young men, competing most intensely for social success are the main culprits; or is the women that prefer such men as partners? This conclusion, albeit based on preliminary investigations, has potentially many different implications for management of resources, conservation, education and not least political decision-making.

Sexual selection also enters in a chapter on the effects of hunting in relation to mating system by Correigh Greene et al. and a chapter on the importance of mate choice for maintenance of viable captive populations by Mats Grahn et al. It seems surprising that the ghost of zoos from the past with individuals being divided into "monogamous pairs" independent of mating system still hovers over much captive propagation. Is it better to equalize individual

contributions to the future breeding populations, or should females be allowed to “decide”? Do humans know better or do animals? Grahn et al. provide a thought-provoking overview that seriously questions current practice. This issue about breeding or lack thereof re-appears repeatedly in several chapters. The so-called Allee effect, which refers to negative frequency-dependent reproductive success, is repeatedly used as an “explanation”, although the basis for this remains obscure.

Conservation genetics have successfully managed to grab a disproportionate share of funding for conservation biology. However, the determinants of genetic variation as influenced by inbreeding, dispersal and mating system remain far from clear, and the same applies to their influence on conservation status. There is a strange lack of information on the importance of the behavior of individuals for population processes, and this becomes even more remarkable given the level of sophistication of genetic analyses. Some chapters attempt to bridge this gap between individual behavior and population processes using a modeling approach. However, this is still the weak point of behavioral ecology, but potentially also its strength given that the study of individual behavior potentially can lead to an understanding of how this translates into population phenomena. Scientists working at the population level traditionally neglect individual differences, and thereby completely the mechanisms generating the observed population patterns.

The book is generally interesting, well-written and thought-provoking. However, it is about behavioral ecology and conservation biology as seen from a US and British perspective. The 31 authors are distributed with 15 from USA, 4 from U. K., 4 from Canada (two chapters), 3 from Sweden (one chapter), two from New Zealand, and one each from Germany, Hong Kong, and Kenya. This makes the book read

along the traditional lines of research in the Anglo-Saxon tradition. A broader perspective would have been interesting. What would scientists from the tropical countries with most of the biodiversity have to say? One can wonder.

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Unto Others: The Evolution and Psychology of Unselfish Behavior.

E. Sober & D.S. Wilson. Harvard University Press, 1998. 394 pp. ISBN 0-674-93046-0 (hardcover).

This excellent book represents a very complete and readable account of the group selectionist approach that Elliott Sober and David Sloan Wilson have been promoting for some time now in the scientific literature. It is very much a book of two halves, possibly reflecting the contrasting backgrounds of the two authors. The first half deals with Evolutionary Altruism, reviewing the history of group selection in evolutionary biology, before introducing their ‘multi-level selectionist’ approach and its application in the evolution of altruistic behavior in human groups. The second half is altogether different and examines Psychological Altruism, providing a philosophical treatment of the proximate mechanisms by which humans are motivated to engage in unselfish behavior.

As a good behavioral ecologist, brought up on and inspired by Dawkins, I had always viewed the Sober and Wilson revival of group

selection theory as somewhat perverse, dismissing their arguments as 'trait group selection' - a much less threatening variety of group selection which only works because it contains elements of kin selection, or so the mathematicians tell us. I was therefore keen to see how these authors would deal with the monolith of kin selection when discussing evolutionary altruism. Well, they meet it head-on, arguing very persuasively that kin selection only works because it actually is group selection, and that clever guys like W.D. Hamilton have known this all along! Sober & Wilson carefully explain the background to the group selection controversy and succeed in demonstrating that 'The debate about group selection has been repeatedly short-circuited by a confusion - different ways of viewing the same process have often been confused with different processes.' (p. 330). With a minimum of mathematics, the authors use the space that such a book affords to make a very convincing case for their multi-level selectionist approach as an alternative to the current mixture of kin selection, reciprocal altruism and selfish gene theories. They view individuals as 'groups' of genes, social and kin relationships as 'groups' of individuals, and species as 'groups' of populations, etc. Natural selection can be viewed as occurring at all levels, acting both within and between the 'groups' in this hierarchy. Multi-level selection theory thereby provides a neat unified evolutionary framework, which may be especially appropriate for explaining altruism.

The majority of the book is, however, concerned with the specific details of human altruism. As a result this is a very interdisciplinary volume, using an anthropological survey of human cultures to confirm predictions derived from evolutionary biology, and matching experimental evidence from social psychology with detailed philosophical arguments concerning the human motives underlying apparently altruistic acts.

Interesting parallels are drawn between the 'individualism' that presently dominates evolutionary biology and the supremacy of 'egoism' (the idea that the only ultimate goals an individual has are self-directed) within the fields of social psychology and philosophy. Sober and Wilson conclude that 'pluralism' should be the approach of choice in both cases, be it the evolutionary pluralism of multi-level selection or the motivational pluralism of psychological egoism and altruism. The result is an informed and stimulating challenge to current modes of thought in both subject areas.

Overall, I felt that the second half of the book never quite matched the clear and persuasive arguments about evolutionary altruism contained in the first half. The two halves of this volume are also never reconciled, despite a very full discussion of proximate psychological mechanisms in human evolution. As a result, the concluding chapter is less integrated and hence less satisfying than one might have hoped. Nevertheless, this is probably the most important book on the evolution of altruism since *The Selfish Gene*, and the section on multi-level selection theory should be required reading for all behavioral ecologists. Hopefully, through this book the authors will succeed in their aim of re-introducing group selection theory to the behavioral sciences.

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Parasites in Social Insects. P. Schmid-Hempel. *Monographs in Behavior and Ecology* (J.R. Krebs and T. Clutton-Brock, eds). Princeton University Press, Princeton, New Jersey, 1998. 409 pp. Paperback \$ 35.00, ISBN 0691059241
Hardcover \$ 85.00, ISBN 0691059233

Parasites are knocking on the colony's door

Parasitism and sociality are both derived life history strategies that have at least two common characteristics, their extreme ecological success, and the fascination they exert for ecologists and evolutionary biologists. This interest is well illustrated by the recent publication of several important monographs on either parasites or social insects. Now Schmid-Hempel goes one step further by discussing the interplay between parasitism and social life in insects. The major themes of this book are how parasites have influenced social organization of insects and how variation in social organization influences parasite load. Throughout the book it becomes clear that addressing these questions requires competence in many fields, including behavioral ecology, population genetics, epidemiology, immunology, life history and kin selection theory.

The first chapters present the large number of actors in this coevolutionary theatre play, with numerous examples of the strategies by which parasites such as viruses, fungi, nematodes and flies manage to break into the social fortresses of bees, wasps, ants and termites. The diversity is simply astonishing. One intriguing example of convergent evolution comes from the ability of fungi and trematodes to manipulate the behavior of their host in order to improve their chances of

transmission. Wood ants infected with fungi of the group Entomophthorales can be seen climbing to the top of grasses where they fix themselves with their mandibles. At the same time fungal hyphae grow and fasten the ant to the straw. Soon the ant dies and spores of the parasite are spread by the wind. The symptoms of this "summit disease" are similar to those of wood ants infected with the liver fluke. By forcing its host to climb to the top of grasses the parasite increases the probability that the ant will be eaten by a grazing vertebrate, the primary host of the parasite.

In the subsequent chapters the author discusses how parasite load should covary with variation in social organization (e.g., breeding system, colony size, colony genetic structure and demographic parameters). He conducts several comparative analyses on the basis of an extensive review of the parasites that have been recorded in species of social insects (all compiled data are provided in a comprehensive and very useful appendix). However, the scattered nature of the existing records sets limits for such comparative analyses. Thus, the load of parasites in any particular social insect is quantified as the number of parasite species reported in the literature weighted by the number of studies carried out on the host. However, for the majority of parasites described, it is unknown to what extent they actually harm their host and simply counting the number of parasite species provides an inaccurate measure of their effect on host fitness. Another problem is that many of the parameters of the social organization of insects that have been predicted to influence parasite load are not independent. For example, colony size is correlated with the number of queens per colony. Moreover, variation in queen number is correlated with the mode of dispersal of sexuals, and these factors have all been proposed to influence parasite load. Clearly, interspecific comparisons currently do not provide a strong test to evaluate

the relative role of the factors that have been proposed to influence parasite load in social insects.

Schmid-Hempel is well aware of these problems. For example, in the Preface he states that: "frustratingly few of the ideas already found in the literature and those formulated here can actually be tested rigorously" (p. ix). We believe that the best avenue to make progress in the understanding of coevolution between parasites and social insects is to conduct experiments in some model organisms. Indeed, Schmid-Hempel and his colleagues have started to pave the way in this direction with their work on bumblebees. For example, some of their recent experimental studies suggest that increased genetic diversity within colonies reduces the susceptibility to parasites. This approach is needed in other taxa of social insects. Obviously, the honeybee is a good candidate because of the commercial interest in this species and its well-known biology. It is, however, still unclear whether domestication has altered the epidemiology of parasites in this species. Another good candidate is the fire ant (*Solenopsis invicta*) which has also received considerable interest due to its economic importance in the introduced range. The fire ant is comparatively well studied with 21 parasite species already been identified. Interestingly, the load of parasites varies over its distribution range with a higher load in the native populations in South America than in the introduced range in the United States. This ant is also interesting because it has two forms of social organization, with colonies having either one or numerous queens.

In conclusion, this book is highly recommendable, not only to students of social insects but to everyone with an interest in coevolution and parasites. It provides a comprehensive review of the available data on parasites in social insects. Schmid-Hempel has to be praised for the

Herculean work necessary to compile this enormous data set. The book also highlights the fact that studies on the role of parasites on the evolution of social organization of insects are still in their infancy. Hopefully, this book will stimulate new experimental studies on the role of parasites in social organisms.

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