Supplement to Behavioral Ecology

ISBE International Society for Behavioral Ecology Newsletter

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Editorial

Conference Workshops and Symposia

Conference season is almost upon us, and that means workshops. As these workshops often provide substantial information and new ideas to disciplines, it is important that we make sure that this information is disseminated to a larger audience.

If you are involved in, or are organizing, one of these workshops, please consider writing a synopsis for the fall issue of the newsletter (*Deadline for submission, 15 Sept 2003*). Instructions for the types of submissions pertaining to these workshops and symposia are given in the "Contributions to the ISBE Newsletter" section, found on the back page of this issue.

Let's make sure the society as a whole is kept up to date on the latest discussions and developments in your field.

Ken Otter
Newsletter Editor

Contents of this Issue

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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*.

Fisheries Society of the British Isles Annual International Symposium: Fish as models of behaviour. Norwich, UK. 30 June - 4 July 2003. Details can be obtained from:
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http://www.leicester.ac.uk/biology/fsbi

4th Göttinger Freilandtage: Cooperation in Primates & Humans: Mechanisms & Evolution
We are please to announced that the German Primate Center (DPZ) will host an international conference focusing on cooperation in primates and humans, from 09 to 12 December 2003. Invited speakers will summarize and evaluate recent empirical and theoretical work dealing with mechanisms and evolutionary consequences of cooperation, including altruism, reciprocity, kin selection, nepotism, game theory, market models, cooperative hunting, cooperative breeding, food sharing, reconciliation, coalitions, group selection and culture. Confirmed invited speakers include F. Aureli, L. Barrett, C. Boesch, B. Chapais, T. Clutton-Brock, E. Fehr, P. Hammerstein, B. König, M. Milinski, J. Mitani, R. Noe, C. van Schaik, J. Silk, R. Trivers and F. de Waal.

We cordially invite you to submit abstracts for relevant oral (15 min) and poster contributions. The conference is also open to guests without presentations. Deadline for submission of abstracts wishing to be considered for spoken papers or posters is August 1, 2003. Guests must also register in advance by October 15, 2003. Additional details available from Peter Kappeler (pkappel@gwdg.de) and the conference web site:

http://www.dpz.gwdg.de/voe_page/GFT2003/index.htm

GRANTS AND JOBS

Grants and Job postings are listed in detail on the newsletter's webpage: web.unbc.ca/isbe/newsletter/index.htm

From the Editor, *Behavioral Ecology*

Changes to *Behavioral Ecology*

In case you haven't noticed, *Behavioral Ecology* has recently made some significant changes in how it handles manuscripts and in its editorial structure. I'd like to give you an early update on what we have done and how it is going so far. On Jan. 1 2003, all submissions to the journal (except in rare cases) began being routed through an online submission service. The journal now no longer accepts paper submissions and all authors are being asked to submit via the online system. The system we are using is called Manuscript Central, provided by Scholar One, Inc. The web site for *Behavioral Ecology* can be accessed at http://beheco.manuscriptcentral.com. Detailed instructions to authors are available at that site, at the journal web site (www.beheco.oupjournals.org), or in the journal.

This change was instituted in the hopes of realizing several important benefits to the journal. First, we anticipated that submitting electronically would dramatically speed up the handling time for manuscripts. Under the previous system, manuscripts had to be mailed up to three times (author to receiving editor, receiving editor to processing editor, and processing editor to reviewer), in some cases causing delays of weeks or even months as a result. The new system should reduce that wasted time. It is too early to know if this has happened for sure, but the editors have made decisions on at least 15 MSs submitted online within the past 2.5 months, indicating a potential lowering of decision time by almost a month. As we gain experience with the system, clear the backlog of paper submissions, and equilibrate the workload among the editors, we expect handling time to drop even further.

A second benefit of the new system is that it will foster a global exchange over the content of the journal. A constraint over the previous system was that European papers tended to be evaluated by Europeans, North American papers by North Americans. However, there are experts of value to editors and authors all over the world. Now, any editor and reviewer can handle manuscripts submitted from anywhere. Reviewers will be selected depending solely on their suitability to review, with the time to get the MS to them no longer being a potential constraint. I can attest personally that this has freed me to make better decisions about potential reviewers than under the previous system.

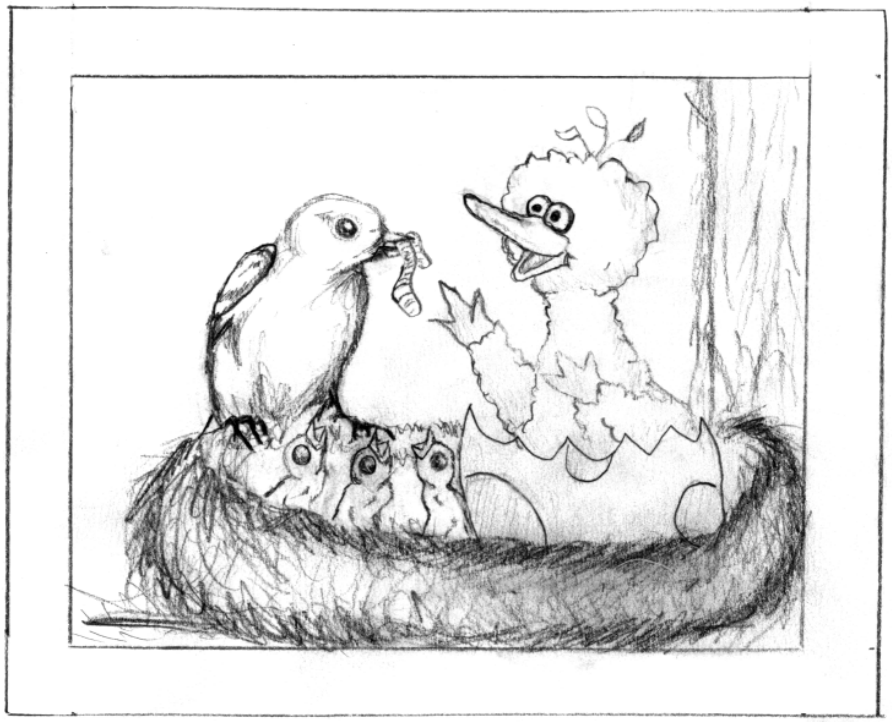
Accompanying the switch to online submission, we have instituted a change in editorial structure. We now have 7 Editors and have reached the point where we need a single person overseeing the editorial process. One editor (lucky me!) will act as Editor-in-Chief. In addition to handling manuscripts, I get to monitor the online system (which includes helping you if you have trouble getting your MS to submit correctly), assign manuscripts to Editors, and coordinate ways the Editors can further improve the journal. Through discussions in Montreal and among the Editors and Editorial Board since then, we have decided that the Editor-in-Chief will not review the decisions the assigned Editor makes on individual manuscripts. We believe quite strongly that the individual authority of the Editors to make decisions fosters a communal sense of ownership in the success of the journal. The Editor-in-Chief's primary job is to improve coordination and communication among the larger number of Editors.

At this point in time, 20 March 2003, the online system is working pretty well. We have had 83 submissions so far, a rate that if continued would produce an increase of about 10-15% in the total submissions to the journal over last year. Most authors have uploaded their MSs without much difficulty, although about 20% have had significant problems. A sizeable proportion of these are due to the authors failing to format their files correctly,

particularly Image files and files from Macintosh computer systems. I urge all prospective authors to read the instructions on the site carefully and contact me if you have questions. I note that, with some help from us, even MSs that have failed to load properly have made it out to the Editors and into the review process relatively quickly.

So, on behalf of the editors, I am happy to report we are quite pleased with the new system so far. We appreciate your support and patience as we learn more about what works and what does not over the next year. Most importantly, we urge you to send you best stuff to us. I think we can now process it more quickly, and I am confident that the already excellent journal that is *Behavioral Ecology* will become even better if you do!

David F. Westneat
Editor-in-Chief, Behavioral Ecology



Cartoon by Ryan Benzie

Book Reviews

Human Evolutionary Psychology

Louise Barrett, Robin Dunbar & John Lycett. Princeton University Press, 2002. 434 Pp.
ISBN 0-691-09621-X (hardcover), ISBN 0-691-09622-8 (paperback)

Human evolutionary psychology, a second cousin to behavioral ecology, attempts to explain the evolutionary history of human behavior from the perspective of cognitive psychology. Where behavioral ecologists recognize four different levels of explanation (Tinbergen's four questions), even though some levels may attract more attention than others (Krebs and Davies, 1997), evolutionary psychologists place their focus on the third and fourth of Tinbergen's questions, the development and evolutionary history of human behavior (Crawford, 1993; Barrett et al. 2002). In particular, evolutionary psychology holds that current human behavior arose in the "environment of evolutionary adaptedness", a mythological place to be found sometime during the Pleistocene, in which human cognitive processes were shaped in response to natural selection. In this view, the patterns of human behavior we see now are reflective of those cognitive processes that have not had sufficient time to adapt to modern environments. This approach can be contrasted with that of human behavioral ecologists, or Darwinian anthropologists, which focusses on functional questions about human behavior: everything boils down to counting babies (Crawford, 1993). The context of evolutionary psychology within the broader study of the evolution of human behavior is a key topic in the introduction, and sets the stage for the remainder of this recent textbook by Barrett, Dunbar and Lycett.

In the preface, the authors tell us that the impetus for writing this book was the lack of a broad-based text on evolutionary psychology for undergraduate courses. This fact may seem surprising to behavioral ecologists who have had a steady supply of texts since the early days of our discipline. After explaining their motivation, the authors apologize for the thickness of the book that has resulted from their effort. Although it spans more than 400 pages, including glossary and references, the book is written in an engaging style that makes it very easy to read.

The book can be broken into five sections: chapters 1 – 4 introducing the topic, the basics of evolutionary theory, kin selection, and altruism; chapters 5 – 8 covering various aspects of reproductive behavior; chapters 8 and 9 dealing with social relationships; and chapters 10 – 13 covering some of the more purely cognitive aspects of evolutionary psychology. Surprisingly, the book lacks a concluding chapter; instead, we are left with a brief summation, one-and-a-half pages long, at the end of the last chapter. A more thorough conclusion would have been in order, given the depth the authors have gone to throughout the rest of the book.

Barrett and her colleagues have taken into account the fact that many students will come to a course in evolutionary psychology with no prior background in evolutionary biology. In Chapter 2, the authors manage to condense the basics of evolutionary theory into a mere 23 pages. Here we are introduced to individual and kin selection, Hamilton's rule, parent-offspring conflict, game-theoretical models of cooperation, sexual selection, and the Handicap Principle. This synopsis is supplemented with additional details presented in text boxes scattered throughout the remaining chapters.

One topic that received too little attention and came too late in the text was phylogenetic analysis, which is presented in a text box in Chapter 8, Marriage and Inheritance. The authors correctly point out the perils of analyzing the correlates of behavior when samples are not phylogenetically independent. In addition, we are told that examining independent contrasts is an appropriate method for comparative studies. While this may appear intuitive to most behavioral ecologists, the same may not be true for behavioral psychologists. Most of the data linking modern cognitive processes to the environment of evolutionary adaptedness rely on studies of single

groups, either in the form of questionnaires presented to groups of college students or in the form of data derived from long-term studies of specific cultural groups, the Ache and Yanomamö peoples of South America, the !Kung San of southern Africa, and various tribes from the Himalayas and the highlands of New Guinea being particular favorites. The phylogenetic analyses typically used by evolutionary psychologists are at the level of relatedness among various human cultures. It would seem that any treatment of phylogenetic analysis should include the idea of comparing the group of interest, humans in this case, with various outgroups, including apes and Old World monkeys. Doing so might reveal that some of our present cognitive functions derive not from adaptation to some hypothetical environment in the Pleistocene, but rather from patterns set down much earlier in Primate evolution. This aspect of comparative analysis is not explicitly presented by the authors.

Another of my criticisms concerns the authors' presentation, throughout the book, of natural and sexual selection as a dichotomy. The idea of sexual selection came to Darwin through his observations of adaptations related to acquiring mates that seemed maladaptive in relation to survival; nevertheless, Darwin included sexual selection as a compartment within the larger idea of natural selection. Modern evolutionary biologists also view the two in this way. Fitness is the ability to recruit offspring into the next generation; whether this comes about as a result of living long and reproducing slowly or living a short life and reproducing explosively is immaterial. Traits that enhance the ability to produce recruits will be propagated throughout a population. Students reading this book may come away believing that natural and sexual selection are opposing forces, when in fact they represent different levels of a hierarchy.

Chapters 10 through 13 delve more deeply into the cognitive side of human psychology than preceding chapters. Chapter 10 introduces the idea of the brain as a collection of cognitive modules. Chapter 11 then links cognitive function to social interaction, including the idea of *theory of mind* and its normal development and relationship to normal social dynamics as well as social disorders such as autism. Chapters 12 and 13 follow with ideas about the evolution of language and culture. Both of these chapters make frequent reference back to concepts covered in previous sections, which should help students see the integration between cognitive function and the evolutionary aspects of human behavior.

Chapter 11 might have been a good place to discuss examples of deceptive behavior in animals which point to a limited theory of mind in other species. Instead we are told that humans are the only species that has theory of mind, suggesting a wider gulf between human and animal behavior than actually exists. Likewise, in chapter 13, the authors reinforce the idea of humans as the only species with culture. This idea may reflect a constant redefinition of culture in the face of evidence from other species that suggests they may have culture even if only in some rudimentary form. An idea presented in chapter 13 is that the "superlarge human brain" results from cultural selection. If culture is defined as uniquely human and humans are unique in having very large brains, the association of the two becomes teleological. Surely, this is one instance where defining culture as a continuum of behavior, and comparing across species will be essential if we are to gain a better understanding of the evolution of human behavior. Chapter 11 does present some interesting data that illustrate adaptive aspects of culture, including culture-specific behaviors that close inspection reveals are related to malaria avoidance, and the coevolution of lactose tolerance and cattle herding in different human societies. The examples are set against the authors' assertions that cultural evolution need not be adaptive for the individuals who practice a particular behavior, but rather need only be adaptive in terms of the imitative potential of the behavior.

From a teaching perspective, this book has a number of positive attributes. Numerous text boxes provide additional details on topics relevant to the main content of each chapter without disrupting the flow of the main text. Wide margins contain key terms,

and provide space for students to make notes about the text. Chapter summaries distill the key points relating to each topic. However, the authors have not provided questions which would allow students to assess their understanding of the various topics presented in each chapter, nor have they presented the students with questions seeking answers. Hopefully, the authors will consider these points in future editions of the text. Perhaps the strongest point is the large number of data figures that are presented throughout the book. These figures not only illustrate the points detailed in the text, but will also help students learn to analyze data critically.

Overall, I thought this book was well written and well presented. My criticisms probably derive from the differing world views of biologists versus psychologists. Perhaps at some point the two disciplines will arrive at a consensus on some of these issues. As a text for students who are interested in studying the evolution of human behavior, this book is a great resource and it will serve as the standard for future volumes.

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References

Krebs, J.R., Davies, N.B. 1997. The evolution of behavioural ecology. In. Behavioural Ecology: An Evolutionary Approach, 4th Edition.. (Krebs, J.R., Davies, N.B., eds.), Oxford: Blackwell Science. 3-12

Crawford, C.B. 1993. The future of sociobiology: counting babies or studying proximate mechanisms. Trends Ecol. Evol. 8:183-186.

Barrett, L., Dunbar, R., Lycett, J. 2002. Human Evolutionary Psychology. Princeton University Press.

Mother knows best: sons or daughters? A review of Sex Ratios: Concepts and Research Methods

Ian C.W.Hardy (Ed). Cambridge University Press, 2002. xii + 424 Pp.
ISBN 0-521-66578-7

Modern evolutionary theory is based on the idea that individuals are selected for their ability to efficiently translate resources into reproductive success, maximizing their genetic contribution to future generations. It makes predictions concerning optimal allocation in the more 'valuable' offspring sex (sex allocation theory). Crucial to the prediction of sex allocation is an understanding of the factors that may affect the reproductive value of sons and daughters differentially. The impetus of modern empirical sex ratio studies came from W.D. Hamilton's influential paper (Hamilton, 1967) on 'Extraordinary sex ratios' in which he gave an explanation of the female-biased sex ratios found in many arthropod species. He showed that the sex with more severe kin competition is less efficient than the opposite sex in exporting parental genes. This favors a female-biased sex ratio when the offspring of one or a few mothers mate among themselves in their natal patch before daughters disperse. Hamilton's work greatly boosted further empirical and theoretical research into invertebrate sex ratios. The result is that today we have a well developed body of sex allocation theory providing an apparently good understanding of the underlying proximate and ultimate factors that shape sex allocation in many invertebrates (Godfray and Werren, 1996). However, the selective forces of sex ratio variation in other taxa are not so well understood. This is mainly because the results of empirical sex ratio studies in vertebrates and plants are often interpreted within the framework of classic sex allocation theory, even though the life histories of these taxa clearly violate a number of the assumptions of the standard models. This formed the stage for the compilation of the book

'Sex Ratios'. Sex ratios, like most things having to do with sex, are intriguing. It is thus perhaps no wonder that Ian Hardy, the editor, conceived the idea for this book while 'lying' in bed.

This multi-authored book reviews recent theoretical and empirical developments in the study of sex allocation. It smoothly blends theories, tests, and the importance of sex ratio studies. The book consists of 20 chapters and provides an excellent overview of many aspects of sex ratio research. It falls into six parts. The first two cover sex ratio theory and statistical analysis of sex ratio data. Part 3 deals with sex-determining mechanisms, with chapters looking at invertebrates, vertebrates, and sex ratio distorters. Parts 4 and 5 focus on sex ratio research in taxa ranging from microbes, to plants and animals, giving critical appraisals of such research, and linking sex ratio studies across taxa. Part 6 finishes with the applications of sex ratio research (value and limitations) for studying adaptations.

The first part on 'Sex ratio theory' contains two chapters. Seger and Stubblefield give a clear introduction to sex ratio theory and an overview of the models of sex ratio evolution, from Darwin (1867) to the present. They focus on the various attempts in history to understand natural selection on sex ratios. In an attempt to get a better understanding of sex ratio evolution, they group models as either expected-future fitness or population-genetic models. Each kind of model has different strengths and weaknesses, and both are often essential. Pen and Weissing then make clear that empirical patterns of sex allocation in vertebrates are hard to understand because they do not fit comfortably within the framework provided by available theory. They present a series of realistic and complex models necessary to solve real sex ratio problems in vertebrates, taking into account the complications arising from vertebrate life-histories and physiology.

The book's second part describes appropriate tools for 'Statistical analysis of sex ratio data'. The statistical approaches are clearly explained and nicely illustrated with worked examples and case histories from recent sex ratio literature. Some examples were given as an exercise to analyze by the reader, but some of the examples were impossible to replicate. Boomsma and Nachman focus on the problems of analyzing sex ratios in social insects, where there is great variation in clutch size and overdispersion. Together with Wilson and Hardy in their more general chapter, these authors particularly emphasise the use of Generalized Linear models, and particularly logistic analyses, for examining sex ratio data. Krackow, Meelis and Hardy consider appropriate statistical methods for analyses of sex ratio variances and sequences of sex allocation. The statistical set is finished with a chapter by Mayhew and Pen on the comparative approach of sex ratio analyses in a phylogenetic context. This part in itself forms a very useful textbook for researchers who work on sex ratio data or plan experiments.

Part 3 deals with 'Genetics of sex ratio and sex determination'. Interesting issues are whether adaptive changes in sex ratios in vertebrates and invertebrates might be constrained by physiological and genetic sex-determining mechanisms. It has long been thought that chromosomal sex determination might constrain adaptive variation. However, recently some birds have been shown to produce extreme sex ratios, suggesting that they are less constrained by genotypic sex determination than previously thought. Furthermore, it appears that sex in some taxa is determined by an interaction between environmental and genetic factors. In the final chapter of this section, Stouthamer, Hurst and Breeuwer consider the role of sex ratio distorters on sex determination. Distorters are heritable elements that modify the sex ratio of their host to promote their own transmission. The authors give a clear overview of theories relating to the evolutionary importance of distorters, and methods for detection and characterizing distorters. Part 3 is important, because, while fascinating in their own right, understanding the mechanisms of sex ratio modification is critical if the adaptive benefits to sex ratio control are to be quantified and predictions made about optimal patterns of sex allocation.

A series of sex ratio studies are then presented and discussed on vertebrates, invertebrates in general,

social insects, parasitic hymenoptera with unusual life-histories, malaria parasites, mites, aphids (part 4), and plants and protozoa (part 5). The advent of molecular sexing techniques has meant that the study of sex allocation in birds is enjoying a welcome renaissance. Cockburn, Legge and Double show that sex ratio modification is occurring in birds and mammals. However, they also make it very clear that the current data on sex allocation are variable and the results often ambiguous. This is because the sex ratio of a system may vary in response to several factors, rather than just one. Very few species have been studied sufficiently to unravel the complexity of factors that may affect sex allocation. The authors call for adequate sample sizes, long-term studies and cleverly designed experiments to gain better insights into sex ratios.

The book concludes with a section on 'Applications of sex ratios', which concentrates on the importance of sex ratio studies. Orzack, West and Herre demonstrate convincingly that sex ratio studies are important, because sex allocation is an excellent model system for examining general questions in evolutionary biology.

This book is beautifully produced, instructive, exciting to read, and provides everything one needs to get started. Through the multi-authored nature and the comparative analyses of sex ratios across a wide range of taxa it gives us a good cohesive insight in the advances in various groups and a better understanding of when sex ratio biases should be expected (theory), when it occurs (data), and why it should be studied. The book should inspire new studies and theoretical developments on sex allocation. On the back cover of this book it is stated that this book is primarily intended for graduate and professional behavioral and evolutionary ecologists working in the field of sex ratios. While this may be true, given the broad range of topics discussed, this book should appeal to anyone working in the field of sex allocation and sex ratios, and should be present on the bookshelf of all evolutionary biologists.

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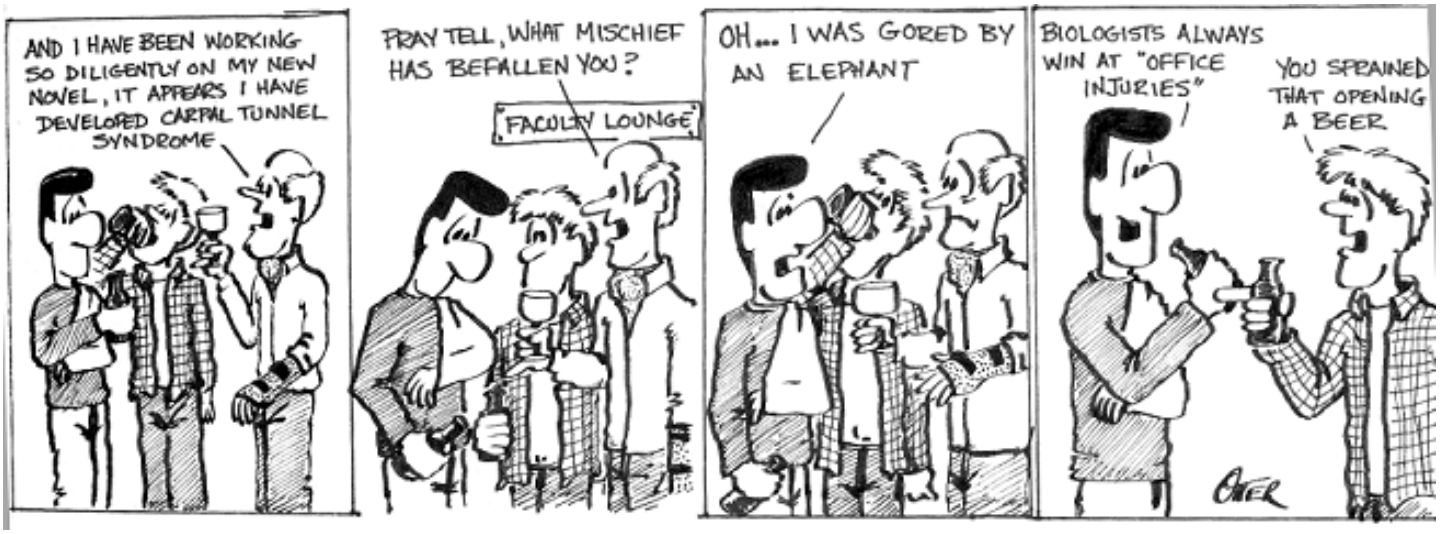
References

Hamilton, W.D. 1967. Extrordinary sex ratios. Science 156: 477-588.

Godfray, H.C.J., Werren, J.H. 1996. Recent developments in sex ratio studies. Trends Ecol. Evol. 11: 59-63.

Darwin, C. 1871. The descent of man and selection in relation to sex. London: John Murray



Commentaries

The globalization of behavioral ecology

The International Society for Behavioral Ecology has always attempted to be a truly international group. The previous nine congresses have been held in six different countries and authors from a diversity of countries are represented in the society journal. Previous articles in this newsletter have attested to the success of the latest congress in Montreal, Canada, and its ability to attract researchers with a diversity of interests (Andersson, 2002; Stewart, 2002). Here I would like to comment on possible recent changes in the nature of collaborative research programs, as suggested by the presentations of the last two ISBE congresses.

While reveling in the extensive social calendar associated with the Montreal meetings, I gained the distinct impression that the presentations involved more collaborative research between individuals from different countries than in the previous meetings. With the greater emphasis on "international collaborations" that seem to be sweeping the Australian research funding environment I was perhaps predisposed to detecting such a trend. To test this hypothesis I used a fairly simple experimental design. I surveyed the list of abstracts from the 2002 Montreal and 2000 Zurich meetings, noting for each abstract the number of authors, Universities/Institutions and countries represented. While the sample sizes vary because complete details were not always provided (despite such clear instructions by the respective conference organizers . . . .) they are sufficient to provide an answer to the original impressions.

If the author lists of the talks and posters presented at the Montreal ISBE meetings are indicative of the overall research culture, then behavioral ecologists are now collaborating with colleagues on a national and international level more than they were two years ago in Zurich. The number of Universities/Institutions has increased from a mean of 1.22 per presentation in 2000 to a mean of 1.38 in 2002 (Mann-Whitney $Z=3.70$, $p < 0.001$, $n = 549$ & 525 respectively), while the number of countries represented has increased from a mean of 1.10 to 1.20 ($Z=2.09$, $p < 0.001$, $n = 551$ & 525) with a concomitant increase in the maximum number of countries represented in any single abstract (3 vs. 4). These differences do not reflect an increase in the number of authors collaborating per se, as there were no significant differences in the mean number of authors presenting when compared between the two meetings (2.29 vs. 2.30, $Z=0.45$, $p = 0.65$, $n = 551$ & 525). Behavioral ecologists therefore still enjoy collaborating with their colleagues, but there now seems to be a greater preference for colleagues located at some distance.

There are a variety of possible reasons for the trends outlined here. The greater degree of globalization may reflect the push of granting bodies, but it may also simply reflect the greater ease of communicating and working with colleagues in other countries, or the greater "moveability" of graduates and postdocs as they search for employment on a global scale. Unfortunately none of these hypotheses can be evaluated with the data obtained here, but it would be interesting to determine if a similar trend towards greater globalization was evident in the papers published in the society journal over a similar time period.

When reviewing the 2002 Montreal meetings (Stewart, 2002) noted the excellent diversity of international foods and alcohol available to the participants. This diversity now seems to have been matched by the nationalities of the behavioral ecologists who so willingly foraged in le Quebec.

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Andersson, M. 2002. Message from the President. ISBE Newsletter 14:1-2

Stewart, I. 2002. Sweet Canada, Canada, Canada: Review of the 2002 ISBE, Montreal. ISBE Newsletter 14:5-8

Measuring allelic variability *between* individuals using microsatellites

Microsatellites are extremely convenient to use for paternity analysis, but represent some problems in trying to compare levels of genetic similarity between two individuals. This latter technique, however, would be extremely useful for determining whether genetic similarity between nesting pairs of birds influences their reproductive decisions, particularly the females' decisions whether or not to engage in extra-pair matings (e.g., Petrie and Kempenaers, 1998).

To date, comparisons between mated pairs on genetic similarity have been conducted by calculating the level of bandsharing in multilocus minisatellites between males and females (e.g., Blomqvist et al., 2002). The inference is that greater similarity (higher bandsharing) indicates more genetic similarity between individuals. However, multilocus approaches such as these suffer from many problems: the effect of linkage disequilibrium on bandsharing is often untested or inadequately tested in these species (Lewontin et al., 1991); uncertain mechanism of size length polymorphisms in multilocus regions could mean that large disparity in allele sizes may reflect few mutations (Armour et al., 1999), and thus short periods of time since two individuals were in fact genetically similar; and, finally, greater difficulty in assessing size of allelic fragments accurately.

For the same reasons that microsatellites have largely replaced minisatellites in paternity analysis, it would be advantageous to develop a method of utilizing microsatellites to compare the genetic similarity between two individuals. One of the most striking of these is that the single-repeat stepwise model of microsatellite mutation suggests that size differences in alleles reflects a more predictable time frame than does analysis of minisatellites (Coulson et al., 1998: Hancock, 1999). If two individuals started with exactly the same allelic length polymorphisms in their genetic history, then current divergence could be reflected by the individual mutational jumps. A method to quantify and compare the relative number of such mutational events which would be required to show the present level of differentiation may give a relative measure of the time two individuals' lineages have been in isolation from one another.

Otter et al. (2002) used a modified version of Coulson et al.'s (1998) d^2 index to compare allelic variability between individuals. d^2 measures the disparity between two alleles within the same individual, quantifying the difference as a relative measure of the number of single-step mutations that would have been required to create the disparity seen. To compare two individuals, Otter et al. used a technique of simply averaging all 4 pair-wise comparisons between the two alleles for

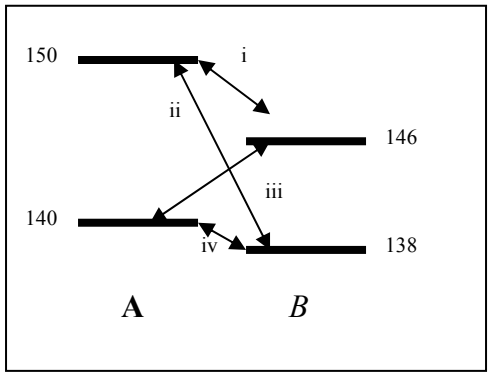


Figure 1. Representation of alleles of two individuals (A & B) being compared for d^2_b. Numbers indicate hypothetical allele sizes. Arrows with roman numerals represent pair-wise comparisons between alleles measured in number of repeat units of the microsatellite

all loci between two individuals (Figure 1).

We refer to this measure as "between pairs d^2" or d^2_b. In the case shown in Figure 1, individual A has alleles at 140 and 150bp (10 bp difference). Individual B has 138 and 146 (8 bp difference). As they are the most common microsatellites in current use in the avian literature, we will assume that the microsatellites represent dioligonucleotide repeats in the rest of the discussion. Thus, 10 bp difference would represent 5 repeat unit difference between allele sizes.

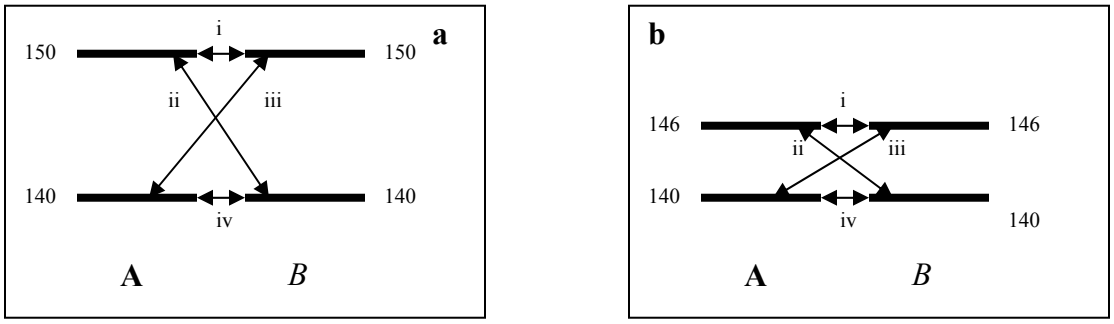
Using the technique of Otter et al. (2002) the calculation of variability for the individuals in Figure 1 would be:

$$d^2_b = \frac{i^2 + ii^2 + iii^2 + iv^2}{4 \text{ (number of comparisons)}}$$

This gives you a relative measure of disparity between the two individuals. If two individuals are genetically identical, they will have lower d^2_b than individuals who are not identical, as at least two of their pair-wise combinations will be producing zero values. Thus, it works on a *relative* level (but even here not perfectly) rather than an absolute level. However, there is one major flaw with this approach. Two individuals who are identical but have large differences in their within-individual alleles will yield a larger score than two identical individuals who are identical but have lower internal variation, even though both will *generally* be lower than two individuals who differ. See for this comparison Figure 2.

While relative comparisons using this technique will still work in general, a technique which can account for this flaw would obviously be preferential. Two individuals that are identical should yield the same low score as a comparison of two other identical individuals, regardless of the allele sizes in either dyad. Ideally both should also give a zero value indicating that there is no genetic diversity between the two individuals. In addition, when two individuals differ in allele sizes, the measure should account for this disparity in a manner that is independent of the sizes of the allelic fragments, but rather reflects the number of mutational events that would be required to explain the individual differences. This is the dilemma we recently tackled in a discussion group on microsatellites at the University of Northern BC.

Rather than focusing on the differences in absolute allele sizes, we feel that the true essence of this dilemma lies in Coulson et al.'s (1998) original intention with the d^2 index – to express a measure of allele size differences which represented the minimum number of mutational events required to explain the disparity. This is based upon the generally supported theory that microsatellite variation occurs through single additions/deletions or repeat units through slippage (Hancock 1999). Therefore, assuming a locus starts out homozygous, the idea is that the greater the



$$d^2_b = \frac{i^2 + ii^2 + iii^2 + iv^2}{4} = (0 + 25 + 25 + 0)/4 = 12.5$$

$$d^2_b = \frac{i^2 + ii^2 + iii^2 + iv^2}{4} = (0 + 9 + 9 + 0)/4 = 4.5$$

Figure 2. Two individuals with no difference in allele sizes may yield positive values using the d^2_b index alone. In addition, when comparing the dyadic comparisons in a versus b, there is no difference in diversity between either dyad, yet the larger disparity in allele sizes in a lead to a larger calculated d^2_b

disparity between the two alleles within an individual, the greater the number of mutations (and hence time) that has been required to get it there (Coulson et al. 1998). The extension of this idea with regard to comparing two individuals is that disparity in the allele size between two individuals should be measurable as the minimum number of mutations that would be required to create the present level of differentiation (see box 1). These presumably arise as either lineage from which the two individuals arose diverges from one another. As the mutations for a dioligonucleotide microsatellite will jump in quanta of two basepair, we can essentially quantify the minimum number of mutations that must have occurred in two individuals from a time when their ancestors would have been identical. Our aim was to devise a methodology that reflects this difference in the minimum number of mutations.

Based on the ideas presented in box 1, measurement of the minimum number of mutational events that account for differences in alleles between two individuals **(d^2_{bmin})** can be measured in any given microsatellite with the following equation:

$$d^2_{bmin} = ({}^1/_k (|max_A - max_B| + |min_A - min_B|))^2$$

where **k** is the number of bases/repeat in the microsatellite (i.e., for a dioligonucleuotide, k=2, for a trioligo, k=3..), and **max_A/max_B** and **min_A/min_B** refer to the absolute values of the largest and smallest alleles, respectively, in either individuals A and B being compared. Following the original rationale of Coulson et al. (1998), we have squared the equation as Goldstein et al. (1995) showed that mean D^2 between populations is a measure linear with time since divergence. This may make intuitive sense as the single stepwise mutation model does not predict that mutational size changes are directional, so mutations may occur that bring two alleles closer together, as well as farther apart. By squaring the equation, we presumably account for greater relative time required for larger disparity to occur in this back and forth step motion. The value can then be averaged across a number of microsatellites (**n** in the equation below) to gain an estimate of the average number of mutational events that separate the allele sizes of two individuals across a greater representation of the genome.

$$\text{mean } d^2_{bmin} = {}^1/_n\Sigma^n({}^1/_k (|max_A - max_B| + |min_A - min_B|))^2$$

We suggest that this measure will allow for direct comparison of genetic diversity between two individuals using microsatellites. With such an index, one can quantify the genetic similarity between breeding individuals and determine whether this influences reproductive decision making, such as the propensity of the individuals to seek extra-pair copulations or even divorce.

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References

Armour, J.A. L, Alegre, S.A., Miles, S., Williams, L.J. & Badge, R.M. 1999. Minisatellites and mutation processes in tandemly repetitive DNA. In. Microsatellites: Evolution and Applications. (Goldstein, D.B., Schlötterer, C., eds), Oxford: Oxford University Press. 24-33

Blomqvist, D., Andersson, M., Küpper, C., Cuthill, I.C., Kis, J., Lactot, R.B., Sandercock, B.K., Székely, T., Wallander, J., & Kemenaers, B. 2002. Genetic similarity between mates and extra-pair4 parentage in three species of shorebirds. Nature 419: 613-615

Coulson, T.N., Pemberton, J.M., Albon, S.D., Beaumont, M., Marshall, T.C., Slate, J., Guinness, F.E., & Clutton-Brock, T.H. 1998. Microsatellite reveals hetrosis in red deer. Proceedings of the Royal Society of London, B 256: 489-495

Goldstein, D.B., Linares, A.R., Cavalli-Sforza, L.L., Feldman, M.W. 1995. An evaluation of genetic distances for use with microsatellite loci. Genetics 139:463-471

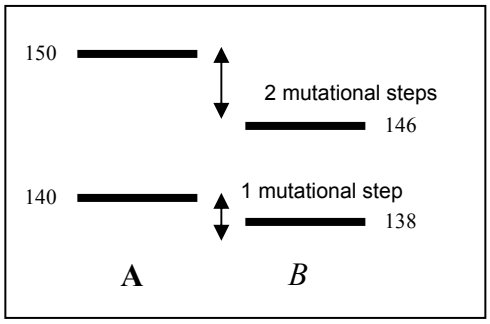
Hancock, J.M. 1999. Micorsatellites and other simple sequences: genomic context and mutational mechanisms. In. Microsatellites: Evolution and Applications. (Goldstein, D.B., Schlötterer, C., eds), Oxford: Oxford University Press. 1-9

Lewontin, RC, Hartl, DL 1991. Population genetics in forensic DNA typing. Science 245: 1745-1750

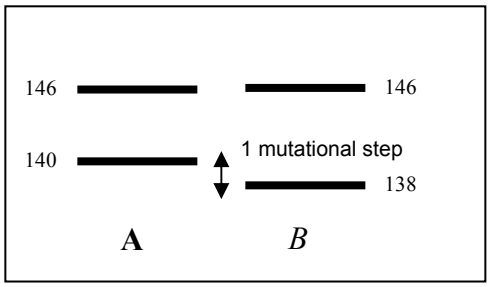
Otter, K.A., Stewart, I.R.K., McGregor, P.K., Terry, A.M.R., Dabelsteen, T. & Burke, T. 2001. Extra-pair paternity among great tits, Parus major, following manipulation of male signals. Journal of Avian Biology 32: 338-344

Petrie, M., Kempenaers, B. 1998. Extra-pair paternity in birds: explaining variation between species and populations. Trends in Ecology and Evolution

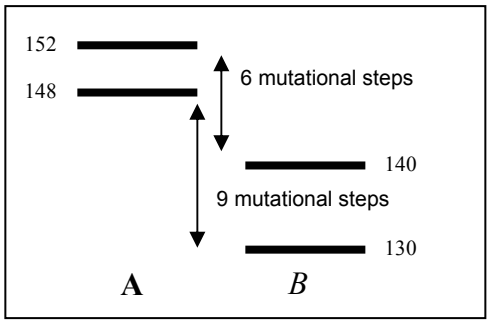
Box 3 – calculating the relative number of mutations separating allele size differences between two individuals, based on a dioligonucleotide microsatellite.



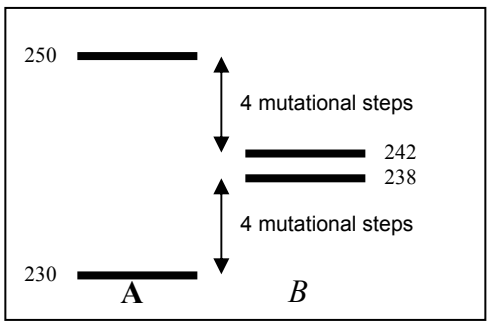
If we use our original comparison example, the two upper alleles between individuals A and B differ by 4 basepairs, representing 2 mutational steps, while the lower alleles differ by 2 basepairs (1 mutation). *Thus, the number of mutational steps is the absolute difference in allelic size between the two alleles under consideration, divided by the repeat size of the microsatellite under investigation.* If we had started with two ancestors that did not differ (i.e., both were 138/146, or both were 140/150), it would have taken a **minimum of 3 mutations** to achieve the current dissimilarity in allele sizes that we see in these two individuals today.



In the next circumstance, both individuals may be heterozygous yet there is no difference between the sizes of the two upper alleles> The only difference lies in a two basepair disparity between the lower alleles. Thus, the minimum number of mutational steps to achieve the disparity between these two individuals would be **one**.



When the allele sizes in the comparison individuals do not overlap in the same size range, the minimum number of mutational events to create the disparity can still be calculated by comparing the allele sizes of the two larger alleles and the two smaller alleles in either individual. The difference between the allele sizes in these two present individuals would require 15 mutational steps from ancestors who were identical allelically.



By using mutational steps as our focal measure, a difference in absolute sizes of the allelic fragments does not influence the outcome of comparisons. In this example, 8 mutational steps are the minimum number to account for the disparity.

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 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 fall newsletter will be Sept 15, 2003.

Ken Otter
Newsletter Editor