

Supplement to Behavioral Ecology

ISBE

International Society for Behavioral Ecology

Newsletter

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Message from the President

The Montreal ISBE 2002 meeting is now just a few weeks away (7-12 July). Luc-Alain Giraldeau and Don Kramer have done a wonderful job in organizing the conference. The program includes some exciting plenary lectures, with the first Hamilton lecture by Bob Trivers, and plenty of time for spoken and poster presentations. It should be a memorable week - do come!

There will be some changes in the editorial team of Behavioral Ecology this summer, as Innes Cuthill and Ron Ydenberg come to the end of their five-year terms. They have both done fantastic jobs and their enthusiasm and expertise have helped maintain our journal at the forefront of the field. An enormous thank you to both from all the society.

We are keen to continue our tradition of having editors with international reputations for excellent research, and I am delighted to say that Ian Owens (Imperial College, London) has agreed to take over from Innes. Ian is well known for his elegant comparative studies of bird life histories and mating systems and has a marvelous book (with Peter Bennett) just published by Oxford University Press: *Evolutionary Ecology of Birds*.

We hope to announce the replacement for Ron in the next newsletter.

See you in Montreal!

Nick Davies

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Editorial

We all understand the importance of conferences, but often do not have the opportunity to attend all the meetings relevant to our fields. Despite this, small workshops and conferences often provide opportunities for the exchange and development of new ideas in a more interactive manner than can be achieved in traditional publication. Yet, the output from these workshops is often available only to participants.

Often in the ISBE Newsletter, we highlight conferences in short reviews. This is sufficient for some workshops, especially when the results of the workshop are published in edited books or special journal issues. Reviews can then be focused and point readers to such published compendia for full details. If the workshop does not publish in this manner, however, a short review may be insufficient to handle the scope of discussions and ideas at the meeting. I would like to present a forum for disseminating lengthier accounts of such meetings.

In this issue of the newsletter, Trevor Pitcher and Geoff Hill provide such a report on the ideas presented at the 4th Meeting of the *Sexual Selection and Beyond* Conference held at the Konrad Lorenz Institute, Austria, in November

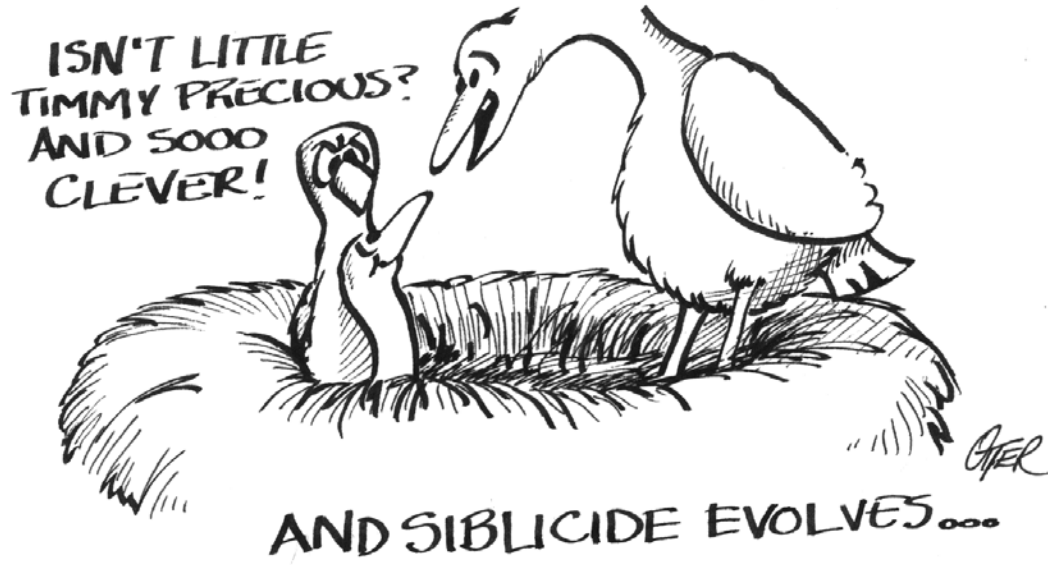
2001. I hope to encourage other participants in such workshops to present the output of their meetings in future issues.

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 not exceed 2500 words, and 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 submissions should 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. I strongly encourage graduate students and postdocs to consider contributing to writing these reports.

Deadlines for regular submission to the fall newsletter will be September 15, 2002.

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Newsletter Editor



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Society News

ISBE OFFICERS

Thank you to everyone who voted in the recent ballot.
The results are as follows:

President-elect: Jack Bradbury
Secretary: Paul Ward
Councilors: Hanna Kokko
Nina Wedell

Marion Petrie, ISBE Secretary

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 last page of the previous newsletter, or 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.

STUDENT FORUMS FOR NEWSLETTER

It is sometimes difficult for students to have a "voice" by which to express their ideas, despite these sometimes leading to major innovations in fields of research. The newsletter will begin accepting forum-style articles written by students. Deadlines for submission of these articles, which should not exceed 2500 words (excluding references), will be four weeks prior to the normal Newsletter deadline (February 15 for the spring issue, and August 15 for the Winter issue). Submissions will be reviewed by a subcommittee of the Newsletter Editor and society's executive. The top submission will be published as a fully refereed article in the Newsletter.

ISBE 2002 CONFERENCE

11th ISBE Conference 2006

At the Montreal conference in July, it is time to begin planning for the 11th ISBE conference in 2006. Those interested in arranging the conference, please send a brief preliminary note, stating the intended place and approximate dates, to Malte Andersson (malte.andersson@zool.gu.se). The suggestions will be discussed at the meeting of the executive, which selects one (or more) places and asks for a more detailed bid.

WORKSHOPS AND OTHER MEETINGS

Duetting Workshop at ISBE 2002.

Anyone going to the ISBE at Montreal and keen to discuss research on duetting? We will meet on 7 July (registration day) between 1.30PM and 5PM to talk about issues of interest - traditional and trendy hypotheses, recording and analyzing duets, playback and removal, social context of duetting and evolutionary studies on duetters. We aim to consolidate hypotheses for duetting and discuss how best to test them. If you'd like to come and contribute, contact:

Amy Rogers amy_c_rogers@hotmail.com
 Michelle Hall Michelle.Hall@anu.edu.au
 Dan Mennill mennilld@biology.queensu.ca

1st European Conference on Behavioural Biology, Münster, Germany.

31 July - 4 August 2002

<http://www.behaviour2002.de>

GRANTS AND JOBS

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

Faculty Position in Animal Behaviour at McMaster University, Canada - Applications accepted from March 15, 2002. For full details, please see advertisement on the Newsletter webpage (web.unbc.ca/isbe/newsletter/index.htm)

Book Reviews

Carnivore Conservation

J.L. Gittleman, S.M. Funk, D. Macdonald and R.K. Wayne (eds). Cambridge University Press, 2001.

ISBN 0-521-66537-

Carnivores attract attention from behavioral ecologists because of their complex social systems and high levels of parental care, and from conservation biologists because their protection is thought to afford security to other species and because they are popular with the public. Based on a meeting that convened most of the leading figures in the field of carnivore conservation, this book is impressive in reviewing virtually all of the major attempts to conserve members of this taxon. It is synthetic in that it covers levels of inquiry from the molecular through field studies to local community attitudes; it is exhaustive (24 chapters, 538 pages with another 118 pages of references), and it is timely because a great deal of conservation work is being conducted on carnivores at present.

On the positive side, there are some wide ranging up-to-date reviews of the field in this book. For example, Eric Gese writes a comprehensive and superbly referenced chapter on methods used to monitor terrestrial carnivore populations – critical reading for a wannabe fieldworker. Stephan Funk and Christine Fiorelli collate and tabulate studies of diseases in wild carnivores and discuss factors affecting their spread. In a thought-provoking chapter, Joshua Ginsberg takes us through contemporary methods used to prioritize reserve sites and indicates how these fall short for large carnivores. And in one of the only chapters that analysed rather than reviewed data, Gus Mills, Stefanie Freitag and Albert van Jaarsveld use complementarity and hotspot methods to isolate which 200 X 200 km grid squares need to be protected in Africa in order to conserve all the carnivore species on the continent. On the negative side, I found many chapters that rambled horribly; politeness prevents me from naming them. In addition, there was considerable overlap between certain chapters. For example, issues of carnivore

invasions and interspecific competition between carnivores were visited several times. Editing was clearly relaxed.

What does this book offer a dyed in the wool behavioral ecologist? Three good chapters stand out. Scott Creel provides a masterful synthesis of different forms of interspecific competition in carnivores and shows how the extent of competition depends on environmental factors. This is the best review of this topic that I have seen. Rosie Woodroffe reviews her own and previous work with Ginsberg demonstrating that large home range size across carnivore species predicts greater likelihood of extinction but that carnivore body size, female dispersal distance and human population density are relatively unimportant. This clever analysis shows how modern conservation biologists can glean important information from scattered and messy data sets. Finally, Laurence Frank and Rosie Woodroffe show how exploitation affects social structure and mating systems in carnivores and documents how exploited populations reestablish territories when harvesting stops. Behavior comes in at other places too: Todd Fuller and Paul Sievert show that carnivores expand their ranges when prey availability falls. This is occurring at a continental wide scale as a result of the huge impact of bushmeat hunting. Also, Peter Waser, Curtis Strobeck and David Paetkau explore the influence of infrequent long range dispersal on population genetic structure in carnivores.

Much song and dance has been made of how animal behavior and behavioral ecology can contribute to conservation biology. These attempts have trumpeted the number of potential connections between these disciplines, showing, for example, how ranging behavior can affect reserve design, how reproductive competition can affect population response to

harvesting, and how Allee effects can drive population extinction. If you read too much of this literature, you may start to believe that conservation efforts will stand or fall on a deep knowledge of behavior. This volume is a humble reminder that behavioral ecology has only a small role to play in conservation because the book shows how many different types of enterprise, from community based conservation schemes through to phylogenetic analyses, are making a contribution while, at the same time, implicitly showing how behavioral ecological concepts are, in some areas, beginning to infiltrate conservation theory (although not yet conservation practice).

I liked the book as a conservation aid because it brings a wide collection of authors from different disciplines under one cover – managers of conservation schemes, field workers, reproductive biologists, systematicists and geneticists – thereby introducing me to realms of literature of which I was unaware. I disliked the book because these completely different thrusts of conservation were

sometimes juxtaposed with virtually no editorial attempt to integrate them.

This is the fifth book in Cambridge University Press's Conservation Series. These books are usually based on a 2-day meeting held by the Zoological Society of London and they tend to suffer from being conference books – i.e. are poorly integrated and vary greatly in chapter quality. That said, this is one of the better ones because it has a strong theme (carnivores), has a host of very dedicated and active contributors, and is very comprehensive. If you work on carnivore behavior or carnivore ecology, or if you want to find out about the nuts and bolts of conservation biology in a circumscribed area, buy this book.

Tim Caro

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Model Systems in Behavioral Ecology: Integrating Conceptual, Theoretical, and Empirical Approaches

Lee Alan Dugatkin (Ed.). Princeton, 2001. 551 Pp

ISBN 0-691-00652-0

I thoroughly enjoyed this book. It is conscientiously aimed at students in early stages of their research careers, especially students who are actively searching for a question and a species to work on. The central goal of the book is to present case studies of how and why behavioral ecologists have selected their "model systems" of study. In doing so, the book provides students with a superb overview of the discipline, addressing questions that span the breadth of behavioral ecology and approaches that employ a range of theoretical and empirical techniques. Despite being aimed at students, the book is also going to appeal to any behavioral ecologist who is interested in these unusually personal accounts of how research programs were selected, developed and brought to fruition. Beyond "conceptual, theoretical, and empirical approaches",

the book integrates the memoirs, advice, and top-notch science of 29 of the best behavioral ecologists in the business. The contributors, to various extents, describe how major theory, experimental suitability, simple practicality and proximity, and just a life-long love of the organism influenced their choices of model systems.

The title isn't sexy. It strikes me as something that as a graduate student I would have read because it was good for me, not because it satisfied a deep curiosity. But the book is much more engaging than this. To be honest, I didn't really know what Dugatkin meant by a "model system", and the word model, combined with the equations on the cover lead me to expect a series of mathematic approaches to behavioral ecology. However, model systems here refer to taxa that are good for studying behavioral ecology and a

generous diversity of taxa are represented.

The chapters range considerably in tone, and every reader will have a different set of favorites, depending upon their theoretical and taxonomic interests, and their personality. The great thing about this book, and the feature that I think makes it most interesting for more-or-less established behavioral ecologists, is that it displays the personality of scientists doing the work. We get a sense of what has driven these people to develop the successful careers that they have. My two favorite chapters, and I think two must reads of the book, are chapter 1 by Geoff Parker and chapter 4 by Kern Reeve. Admittedly, these are two of my heroes, but the appeal is deeper. "Golden flies, sunlit meadows: a tribute to the yellow dungfly" by Parker is simply the most charming account imaginable of the career of one the giants of behavioral ecology. The honor and the credit that he gives to his favorite organism is heartwarming.

Whereas the charm of Parker's chapter is disarming, Kern Reeve's chapter is armed to the teeth. Reeve has a major philosophical point to make and this is his opportunity. Every behavioral ecologist will want to read this. Reeve argues vehemently about the nature of causality in behavioral ecology, not the old proximate/ultimate debate, though this enters into it, but rather a unified theory of animal social behavior. Reeve accuses behavioral ecologists of the sin of "causal pluralism", and he isn't afraid to point fingers. Causal pluralism in the extreme is the belief that there's a unique explanation for just about every behavioral phenomenon. While Reeve doesn't accuse the majority of us of the having this extreme view, he does accuse the average behavioral ecologist of an eagerness to argue against general theory and in favor of idiosyncratic explanations when overly simplistic predictions don't yield a quantitative fit with the data. In Reeve's opinion, this is damaging for behavioral ecology because it results in a "patchwork" of behavior stories and leads us away from a general predictive theory. My own opinion is that Reeve is probably right. I too believe that a unified, predictive theory is the goal of all science, including behavioral ecology. But it also very much comes across that he is driven by a personal ascetic. For Reeve, the theoretical elegance

of the unificationist perspective clearly provides intellectual comfort. But is he right? We'll find out as the theory develops.

There are lots of other gems among the 25 chapters and over 500 pages – too many to review thoroughly. Those of you looking for fascinating theory and empirical rigor will find great stuff for example in chapters by Sinervo, Wilkinson, and particularly the wonderfully clever experiments of Milinski. Those looking for perspective on beginning your career or perhaps switching systems will find wonderful advice (and excellent science) in chapters by Warner, Seeley, and Sherman. Those interested in reading about different approaches to behavioral ecology will find plenty of suggestions (and again excellent science) in chapters by Gerhardt, Stamps, and Holldobler and Rocas, Kamil and Bond, and Bekoff. And finally, students with a strong commitment to a special taxon, whether it is due to an ascetic connection or conservation concerns, will find the reassurance from Richard Alexander, via Richard Conner, that "there are important questions for every species"¹. This message is particularly strong in the final chapters on mammal model systems (e.g., Silk, Creel, and Conner), but it applies throughout.

Model Systems in Behavioral Ecology is a terrific book. My only note of caution is that students should probably have a solid background in the fundamentals of behavioral ecology before trying to digest all of this theory and empiricism. The book doesn't replace Krebs & Davis² and the authors generally don't have the opportunity to sufficiently introduce the subject matter before diving into their work. Yet the quality is remarkably consistent for an edited volume. All the chapters are good and all have something different to offer.

1. Gans, C. (1978) All animals are interesting! *American Zoologist*. 18, 3-9
2. Krebs, J.R. and Davies, N.B. (1997) *Behavioural ecology: an evolutionary approach*. Blackwell Science. Oxford.

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Conference Reviews and Commentaries

Why don't primatologists come to ISBE meetings?

This summer will see the ninth ISBE meeting, in Montreal. One of the most noticeable aspects of previous meetings has been the lack of primatologists. Why? Many primatologists are behavioural ecologists and study the same questions as the rest of us - why then do they avoid these superb meetings?

I recently attended the conference organised by Peter Kappeler on Sexual Selection in Primates at the German Primate Centre in Göttingen. I should say now that I was an invited speaker, for without an invitation I might not have attended such a meeting. Having done so and had a wonderfully stimulating few days, I find myself in a better position than previously to speculate about why primatologists and other behavioural ecologists so rarely meet.

It is understandable that those behavioural ecologists who study animals other than primates should not bother to attend primate conferences, but it is much less obvious why it doesn't work the other way round - why primatologists avoid ISBE meetings. Taxonomically-based meetings rarely attract biologists that work on other taxa, unless they happen to be invited. And of course, this is the strength of Peter Kappeler's biennial meetings - since their inception in 1997; he has always included a number of non-primatologists as invited speakers. The benefits of this flow both ways, and I for one found the experience an extraordinarily enlightening one.

Prior to attending this meeting I had two preconceptions; first, that primatologists felt themselves to be superior to biologists that studied any other type of animal - primates are, after all, closer to man. I also had the idea that primatologists were somewhat intimidated by the larger sample sizes and greater opportunity to conduct experiments that invertebrate biologists and ornithologists enjoy.

So, were my preconceptions confirmed? As far as

the first is concerned I saw nothing to suggest that primatologists felt themselves superior to anyone studying anything else. However, in discussing this issue with delegates, some said that within primatology a hierarchy exists, with those studying apes assuming themselves to be superior over those studying less charismatic primates, or those with fewer genes in common with themselves. But that is not a major issue, the same could be said of those who come to behavioural ecology meetings - researchers who study sea slugs probably see themselves as better than those who study slime moulds. Even among ornithologists there is a hierarchy; almost everyone assumes their bird is superior to the chickens I study! Clearly, any feelings of taxon superiority or inferiority are not the basis for primatologists avoiding the ISBE.

As far as the second issue - sample sizes - is concerned, I saw this in a very different light. The strongest impression I had from this meeting was the enormous difficulty that most primatologists have in collecting certain types of data. Many primates are extremely long-lived, take a long time to reach sexual maturity (five years for a macaque and more like fifteen for a chimp), and because they are also shy and smart, they can require long periods of time to habituate. It therefore takes primatologists much, much longer to collect even basic information on their study animals than it does for those studying most other taxa. On the other hand, long term studies means that primatologists probably know their study animals far better than most other behavioural ecologists do. The amount of effort invested in long-term primate studies also makes it easy to understand why primatologists are reluctant to conduct experiments which might disrupt social relationships - in much the same way as ornithologists studying cooperatively breeding birds have, until recently, avoided experiments. In fact, several primatologists told me that they were keen to conduct experiments,

but in addition to the problems outlined above, were often also constrained by ethical issues.

The key point of all this is that primatologist can generally study a smaller range of questions than other behavioural ecologists, and there are some questions they cannot tackle at all. Having said that, there were some great examples of experimental primate studies at this meeting. The one I liked best involved the cobalt blue scrotum of the vervet monkey: the hypothesis that scrotum colour reflected social dominance was elegantly tested and confirmed with little more than a can of spray paint!

Notwithstanding examples like this, it does seem to be true that primatologists suffer from low sample sizes, and the concomitant difficulty in testing hypotheses with the same rigour that biologists working with more numerous and tractable subjects can. Nonetheless, I think behavioural ecologists should be aware of the inherent difficulty many

primatologists experience in collecting data and adopt a more sympathetic and open-minded approach. The most telling comment I heard at this meeting, was that some primatologists who had attended ISBE meetings had been made to feel inferior by being placed in what they considered to be poor sessions!

Regardless of the taxa we study, we all have a great deal to learn from each other. Primates are utterly fascinating, and they should form a central part of our ISBE meetings: I hope in future that both sides will welcome each other with more open minds.

Tim Birkhead

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The Sexual Selection and Beyond Conference, 4th meeting

Konrad Lorenz Institute, Vienna, Austria, 8-10 November 2001.

Sexual selection has entered an interesting phase, having passed through a shift in paradigms in the 1970s and 1980s when concepts like female mate choice, both cryptic and overt, and honest signaling were new, exciting, and controversial¹. Much focus of late lies in working out the mechanisms by which honest signaling can occur and hence the value of the signal to the receiver². Not surprisingly, mechanisms for honest signaling and strategies for paternity assurance were the primary topics of discussion at a recent symposium "Sexual Selection and Beyond" sponsored by the Konrad Lorenz Institute in Vienna. The meeting brought together twenty researchers from Europe and North America and the group was selected to represent a wide range of topics in sexual selection and a full spectrum of professional experiences from well-established authorities to graduate students. Official symposium topics included Immunological Ecology, Sperm Competition, Carotenoids and Melanin, and Aggregations and Sociality.

While all of the talks were united by their focus on

sexual selection, it seemed that most talks followed one of two themes: (1) honest signaling and the mechanisms that allow for honest signaling in pre-copulatory mate choice, and (2) male and female strategies associated with post-copulatory mate choice. The pre-copulatory mate choice talks focused on song and plumage coloration in birds and how hormones, condition, and disease can affect the production and maintenance of these traits. The post-copulatory mate choice talks focused on mechanisms by which females could potentially bias paternity (towards one male over another), how sperm competition and/or sexual conflict affects the evolution of morphology and behavior, and how cryptic female choice and sperm competition are inter-related. Many talks focused on female control of processes³ and also challenged some of the most fundamental sperm competition assumptions and hypotheses⁴. Overall, it was exciting to see the integration of neuroendocrinology, immunology, reproductive physiology, population genetics, and molecular biology in the new approaches to

answering old questions.

Carotenoid and melanin-based plumage coloration has long been a favorite topic for studies of sexual selection. In recent years, increasing research has focused on the idea that such ornamental traits serve as indicators of immunocompetence with testosterone (T) acting as the mediator between investment in ornament production and investment in immune defenses⁵. One problem has been that molt occurs after breeding when testosterone levels for most birds are minimal⁶. Kate Buchannan (U. Bristol, UK) presented new data that may resolve this paradox. With her colleagues, she implanted birds with large doses of testosterone during breeding, but with much reduced testosterone during molt. She found that even small doses of post-breeding T had significant effect on the melanin throat patches of males while T levels during breeding affected the immune system. In further studies of the throat patch of house sparrows, Radovan Vaclav (Konrad Lorenz Institute, Vienna) emphasized the condition-dependent nature not just of the ornament but also of behaviors associated with ornament display. He showed that large-patched males do better in holding resources but smaller-patched males feed offspring more. The net effect is that females paired to medium-ornamented males do best. Geoff Hill (Auburn U., AL, USA) presented data that indicated that songbirds with carotenoid-based plumage coloration do not directly trade-off use of carotenoids for ornamentation and use of carotenoids for immune enhancement (see Ref. 7 for review). Parasites, nutrition, and access to carotenoid pigments affect plumage coloration, but carotenoid supplementation does not enhance immune function. Simon Griffith (Oxford University, U.K.) presented a summary of studies on melanin and carotenoid coloration showing that both traits can signal important aspects of male quality.

Environmental stress has become a focal topic of evolutionary biologists studying sexual selection because an individual's stress level should be of interest to prospective mates and because stress can disrupt a wide array of biological processes including the production of ornamental traits⁸. Whether environmental stress can affect bird song has been a contentious issue for years⁹. Laszlo

Garamszegi (Pierre and Marie Curie University, France) injected Sheep Red Blood Cells into breeding Collared Flycatchers (*Ficedula albicollis*) to simulate a parasitic infection and showed that such an environmental stress reduced song rate. On the other hand, Clive Catchpole (U. Bristol, UK) summarized work on song repertoire size, mate choice, and brain development in Marsh Warblers (*Acrocephalus palustris*). His lab group has shown that development of the brain center responsible for repertoire size is relatively insensitive to stress during early development and that repertoire size is heritable. The effects of stress on molt was another topic of discussion. Karen Spencer (U. Bristol, UK), showed that stress during early development impairs the immune system and affects the speed at which Starlings (*Sturnus vulgaris*) molt feathers as young adults in the fall. Molt speed has been shown in other species to be a sexually selected trait, so these results provide new insight into how the natal environment can affect ornamental traits. Juan Moreno (Museo Nacl. Ciencias Nat., Spain) showed further links between molt and condition by presenting data that molt depresses the immune system and may constrain the start of breeding in Collared Flycatchers. This presents an interesting explanation for one of the most ubiquitous avian life history traits – the lack of overlap between breeding and molt.

Sperm competition has been an area of intense study for several decades in sexual selection and yet we are still only beginning to fully understand and appreciate the ultimate and mechanistic processes involved. Tim Birkhead (U. Sheffield, U.K.) provided an excellent historical overview of some of the key findings and figures in the field including Darwin, Bateman, Trivers, Parker, and Eberhard and finished with some exciting new empirical data and ideas for future exploration. Birkhead presented novel findings and insights suggesting that sperm competitive ability is likely maternally inherited, sperm quality rather than just number has a large influence on the outcome of sperm competition, and cryptic female sperm choice is very difficult to demonstrate empirically. Charles Cornwallis (U. Sheffield, U.K.) then presented findings that support the notion that male sexual interest is rejuvenated by the presence of a novel female (the “Coolidge

effect”) in fowl (*Gallus gallus*). Cornwallis took this idea a step further by matching the renewed sexual interest with actual sperm numbers and found that rejuvenated sexual interest is matched with increased sperm numbers in subsequent ejaculates. Wolfgang Forstmeier (University of Wuerzburg, Germany) attempted to explain why male birds continue to sing at such high rates once they are already paired. It has been hypothesized that male birds advertise their quality and attempt to attract extrapair mates by singing at higher rates¹⁰. However, Forstmeier found that females do not prefer potential extrapair mates based on singing rates but rather based on song quality (amplitude and frequency modulation). Rupert Marshall (U. Bristol, U.K.) presented novel findings with respect to song characteristics (repertoire size) and genetic diversity in the Marsh warbler. He outlined a technique for using degree of microsatellite band sharing as a measure of genetic similarity between individuals. He then showed some intriguing preliminary data with positive associations between ornamental display and genetic diversity and with higher overall diversity within offspring than expected by chance. There are many potential applications for this new measure of heterozygosity. Finally, Tom Pizarri (Swedish University of Agricultural Sciences, Sweden) presented an interesting model which examined the evolution of male sexual traits that are harmful to females. He suggested that these harmful male traits evolve in response to sexual conflict and yet could evolve without being costly to females, which runs counter to current thinking.

Although many talks pushed “beyond” sperm competition, several other talks suggested we should instead look “back” and be cautious about attributing too many comparative or behavioral patterns to sperm competition theory when alternative explanations may exist. Sperm ejection with respect to sperm competition has recently garnered much attention¹¹. However, Fabrice Helfenstein (University of Pierre and Marie Curie, France) and co-workers presented novel findings in Kittiwakes (*Rissa tridactyla*), suggesting sperm ejection may have little to do with sperm competition. Helfenstein reported that it is common for female Kittiwakes to eject their mates’ sperm after copulation. Sperm ejection occurred according to some intriguing

temporal patterns and in relation to mate quality, even though there is little or no sperm competition in this species (i.e. no extrapair young in this species).

Trevor Pitcher (University of Toronto, Canada), then presented comparative findings using testes data (a measure of sperm competition intensity) from over 1000 species of birds from all major zoographic regions of the world, and showed that sperm competition may not be as potent a force in the evolution of sexual dimorphism as once thought. He suggested instead that traditional explanations based on social mating systems remain the best predictors of dimorphism in birds¹². Pitcher also stressed that sperm competition studies suffer from a “temperate zone bias”¹³, and that sperm competition varies with geographic area, with more tropical regions having species with much smaller testes (i.e. less intense sperm competition) relative to their temperate zone counterparts.

In the final section, Aggregations and Sociality, Fredrik Widemo (Uppsala University, Sweden) presented findings from years of field work on the Ruff (*Philomachus pugnax*). Recent studies suggest that males are expected to take relatedness into account when deciding where and with whom to lek and genetic structuring across leks is therefore expected¹⁴. Widemo presented behavioral and genetic data suggesting that kin selection is actually much less important than once thought in the evolution of lekking. Katherine Thuman (Uppsala University, Sweden) then followed with her findings regarding adaptive sex allocation in Ruffs. Sex allocation theory predicts that females should bias the production of offspring towards the sex that maximizes their own fitness and factors likely to affect adaptive sex ratio include female condition and male attractiveness¹⁵. Thuman found some evidence of non-random sex allocation by female ruffs at both the individual and population level in relation to female condition.

Future challenges

The future of sexual selection, like the future of all biological sciences, appears to lie in the broadening of perspectives and the integration of subdisciplines. Where ten or fifteen years ago most behavioral ecologists had little interest in what physiologists, immunologists, or even molecular geneticists had to

say, the new generation of biologists studying sexual selection are often being cross-trained in evolution, behavior, and one or more “lab disciplines”. Not surprisingly individuals and labs that are integrating multiple disciplines into their studies are producing some of the most exciting work and most of the breakthroughs in understanding how sexual selection works¹⁶. New areas that will require multi-disciplinary training and that will undoubtedly push forward the field of sexual selection include exploring mechanisms of sperm competition and cryptic female choice, mechanisms that enable the biasing of sex ratio, and the interplay between immune function and reproductive success. For those biologists who were comfortable with a narrower approach to the study of sexual selection, it might prove to be intimidating and disconcerting to have to use and understand unfamiliar techniques from such a range of biological fields. But nobody said that pushing the boundaries of science would be easy.

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