



International Society for Behavioral Ecology

Newsletter

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Editorial

I am extremely happy to start this (my penultimate) editorial by announcing that Mariella Herberstein of Macquarie University has joined the Newsletter as the Associate Editor. This is the first Newsletter that Mariella has worked on, and she will assume the Editorship next summer as I step down and a new Associate Editor is appointed.

In working with Mariella over the past few months, I know that the Newsletter will be in great hands. It has been exciting for me to work with someone with so much enthusiasm, as well someone who can bring a new perspective for the Newsletter. The expansion of Editorial staff has allowed us to take on a greater amount of content (this issue is the largest we have ever produced, and there are already 10 book reviews, plus two more of the Congress' symposia reviews, lined up for the Spring 2007 issue!). Mariella also has a number of exciting new ideas for the future of the Newsletter, and is planning to send out a short survey this winter to determine the direction ISBE members would like to see the Newsletter take. Please support her by continuing to contribute as Mariella breathes new life into the Newsletter.

As is typical of the issue following our biennial meetings, this issue contains a review of the meeting in Tours (pp. 20-23), as well as Minutes of the ISBE Society Meeting (pp. 24-25) and the report of Editor-in-Chief of *Behavioral Ecology* (pp.25-27). Marlene Zuk, our new President, makes her inaugural address with a critical assessment of gender biases in our discipline (pp. 16-18). This is an article that all of the membership should read and begin the work of determining how to overcome such biases in the future.

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This issue also has five book reviews, including the first review of a non-English book – *Muchos más que plumas* (Juan Carlos Senar). The review is written in English with a Spanish summary by Juan Francisco Ornelas (pp.28-30). Three reports on symposia that were held at the congress in Tours are printed here, with plans for the remaining two symposia to be reported in the Spring 2007 issue.

I thank all the contributors for extremely insightful reviews, and for the support that all contributors have given me over my years as the Editor.

Contributions for the Spring Newsletter are due **1 March, 2007**, and can now be sent to either myself or Mariella.

Ken Otter
Newsletter Editor

CONTRIBUTING TO THE ISBE NEWSLETTER

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

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

Workshop/Conference Reviews: Workshop and/or Conference reviews should be prepared in one of the following two formats. **Brief synopses** (max 1500 words) may be submitted by either participants or conference organizers at the regular newsletter deadlines. These can include synopses of workshops that will be published in more detailed accounts (book or special journals), and should include information as to where the information will be published. **Longer reports** (max 3000 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 Editors 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 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 on topics relevant to the society will be considered for publication. Authors of such articles should contact the Editors at least **one month** prior to regular submission deadlines to outline the content of the article. The Editors may request submission of the article earlier than regular deadline should outside reviewing be deemed necessary.

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

Deadlines for submission to the Spring newsletter will be 1 March 2007.

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President's Message

Quiz: what proportion of plenary speakers at ISBE meetings between 1996 and 2006 have been female? (*answer at end of message*) If you incorrectly guessed higher, perhaps it will help place the result in perspective to know that the Society for the Study of Evolution has only awarded the Dobzhansky Prize, given to promising young investigators, to a woman once in its 25-year history. The *American Naturalist* has never had a female editor, and *Evolution* has had only one. (*Behavioral Ecology* only recently went over to a system with an Editor-in-Chief, but none of the three people serving in this capacity have been female). This pattern is not unusual: in both Europe and North America, the vast majority of scientists at the professorial level or equivalent are male; in the University of California's 9-campus system, just under 80% of faculty in the life sciences, including all levels, are men.

A common initial reaction to this information is that we simply need to wait for the latest cohort of scientists, which is less male-biased, to come through the system and correct the imbalance. While it is true that a substantial proportion of science Ph.D.s are now given to women, particularly in biology (current estimates are around 46% in the United States and 35 – 65% in Europe), this has been true for some time, and these proportions simply do not translate into equity after the scientists' careers proceed (Schubert and Sinha 2004). Many women have been trained in biology for several decades, but their professional progress has stalled. Academic science contains several bottlenecks that filter out women, both after they receive a Ph.D. but before obtaining a permanent position, and after becoming a faculty member but before achieving extremely high status. This is exemplified by, for example, becoming a named professor, being elected to the National Academy of Sciences or the Royal Society of London – or being invited to be a plenary speaker at a major international conference.

After hearing this information, many people then conclude that the problem is either that women don't want such positions or opportunities, perhaps because they have difficulty achieving what we sometimes call a "work/life balance" or – more controversially, as former Harvard president Larry Summers discovered – that women are less able or less qualified than men.

At the surface, these are both plausible explanations, and even if we find the latter distasteful, as scientists

we should be prepared to consider all of the options.

We should not shrink from the possibility that innate proclivities differ between the sexes, making women less likely to achieve scientific prominence.

But relatively few people stop to consider an alternative hypothesis: that it is our evaluation that is flawed, not what we are evaluating. A closer look at the evidence supports a different and more disturbing reason for the paucity of women at high ranks. People exhibit bias, often unconscious, in their evaluations of men and women (Valian 1999, 2005; Barnes 2006). Ample data show that both sexes tend to over-value the contributions of men and under-value those of women. By the time women are eligible for consideration as winners of awards or keynote speakers, they have already experienced such covert discrimination. The situation is then compounded by the use of previous indicators of success to decide on future rewards, setting up a feedback loop in which women are not selected because they were not selected previously.

In a landmark study of such bias, Wennerås and Wold (1997) documented unequal evaluation of male and female applicants for biomedical postdoctoral fellowships; women needed roughly twice the publications to be awarded the same number of "impact points" as men. More recently, complaints about the all-male awardees of the first annual NIH Director's Pioneer Award led to a revamping of the program (Novak 2005). In 2005, the program's second year, 6 of the 13 awards went to women.

Abundant evidence from controlled studies supports the notion that we all use information about the sexes differently when making decisions; when asked to evaluate male and female contributions to a task, both men and women attributed more of the work to male members, particularly when little explicit information was given about each member's contribution (Heilman and Haynes 2005). When 147 heads of psychology departments were sent fictitious resumes of potential faculty members and asked to suggest the rank (assistant, associate, or full professor) that each would be assigned in their department, ranks were higher when the same resume had a male name than when it had a female name (Fidell 1975). Letters of recommendation for successful women applicants to medical research positions were significantly shorter than those for men, and focused on the applicant's

teaching ability and motivation, rather than research skills or creativity (Trix and Psenka 2003).

We also differentially attend to information depending on its consistency with our preferred outcome. Subjects asked to gauge which of 2 students were most intelligent used less information to decide that a dislikable individual was not intelligent (Ditto and Lopez 1992). People are astoundingly good at *post hoc* rationalization of their decisions. In hypothetical college admissions decisions, subjects justified favoring Black over White candidates by claiming that grades were more important than number of Advanced Placement courses when Black applicants had higher grades; when Black applicants had lower grades, subjects claimed that the number of AP courses was more important (Norton et al. 2006).

Furthermore, we all believe that we are less biased than the average person, though we believe that others are distressingly likely to be subject to outside influences (Gilbert 2006). Similar findings pervade the literature on jury composition and courtroom proceedings.

How does this apply to choices of male plenary speakers or prestigious award winners? Several forces interact in such decisions. First, people rely on “cognitive availability” – the formal term for a name or other item initially coming to mind when one starts making a judgment (Steffens et al. 2004). Thus, the first person to come to mind for an award may be someone who previously was in a symposium, or who recently won a different award. If members of a particular group, whether women, foreigners, or people from lesser-known institutions, have not been garnering attention already, they are handicapped in the often informal nominating procedures that lead to additional attention. The resulting accumulation of disadvantage can lead to enormous disparities between groups (Valian 1999), and lead to the perception that “there aren’t any eligible women” for nomination.

Kim Sullivan and her colleagues have found that when people are presented with a list of possible candidates that includes both men and women, they nominate both sexes, but when they are asked to generate names *de novo*, they tend to nominate only men (personal communication). Future winners may also be “matched” to previous winners, so that one develops an image of a keynote speaker, or a National Academy of Sciences member, as being white and male, even though such attributes are obviously irrelevant, and thus becomes more likely to feel that another white male fits the image of the awardee more closely.

The ability to rationalize one’s decisions is also important in perpetuating bias, because it is easy to look at the winners of prizes or keynote speakers and note that they are all highly qualified to be in their positions. This may well be the case, but it ignores the existence of a group of potentially equally well-qualified candidates who were overlooked. Informal procedures, in which a group suggests candidates until satisfied, are particularly prone to such problems; women are vulnerable to being dismissed on the basis of criteria that would not be used for men. Ditto and Lopez (1992) refer to such behavior as “motivated reasoning”, and it can subtly color the outcome of a process even when participants believe themselves to be treating everyone without regard to gender, ethnicity, or other extraneous information.

Good intentions, therefore, are not enough. A belief in equity does not necessarily lead to equitable outcomes. We need conscious efforts to correct bias; the more that independently and objectively derived criteria are used to pick candidates, and the more that people are given a list of potential winners, rather than simply asked to generate names, the better. I am not suggesting that we promote women simply because they are women. Awareness of bias, and the correction of it, is not exhibiting favoritism or preference to certain groups. It is supplying justice. Finally, I hope that the answer to my question posed at the start of this article will be significantly different – and more equitable – in the President’s message from the 2016 ISBE Newsletter.

Marlene Zuk, ISBE President

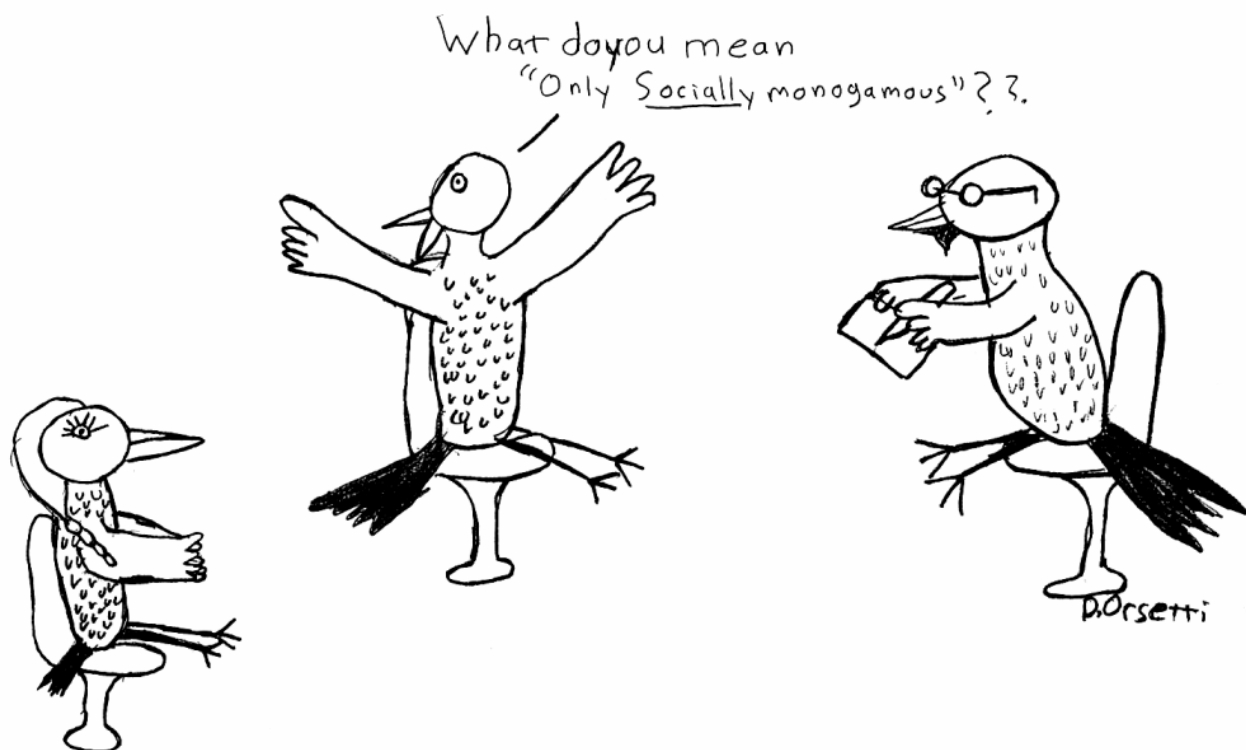
ANSWER: 22%

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Cartoon by Damon Orsetti

Society News

Most Society News – workshops, conferences and job postings – is now publicized on our website (web.unbc.ca/isbe/newsletter). This allows ads and announcements to be posted shortly after receipt so that deadlines falling between newsletter distributions can be advertised. If you would like to advertise workshops, conferences or job postings of interest to the society, contact Ken Otter (otterk@unbc.ca) or Mariella Herberstein

MEMBERSHIP AND SUBSCRIPTION OPTIONS

Subscription to Behavioral Ecology is no longer required to be a member of the International Society for Behavioral Ecology. Everyone now has the option to join the society without taking a subscription to the journal. Such memberships will receive the Newsletter and announcements for the biennial conference. For those who wish to continue their subscription to Behavioral Ecology as well as be a member of the society, this option is also available. Information on this process is found on the society's (web.unbc.ca/isbe/ISBEmembership.htm) and Oxford University Press' *Behavioral Ecology* webpages (beheco.oupjournals.org).

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).

ISBE 2008

The twelfth congress of the International Society for Behavioral Ecology will be held at Cornell University in Ithaca, New York, 9th-14th August 2008. Look for updates on the official website:

<http://isbe2008cornell.org/>

For more information contact
info@isbe2008cornell.org



INTERNATIONAL SOCIETY FOR BEHAVIORAL ECOLOGY
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JOB AND STUDENTSHIP POSTINGS

Between the previous issue of the Newsletter (18(1)) and this issue, there have been **five faculty, three post-doc, and several PhD postings** on the Newsletter's website. However, since application deadlines often fall between physical copies of the Newsletter being distributed, members should make sure they check out the website pages frequently:

<http://web.unbc.ca/isbe/newsletter>

- **select "Ads and Positions" to see all currently available jobs.**

If you wish to post an advertisement for faculty, postdoc, graduate student, or field assistant positions in your lab or department, please send these to Ken Otter or Mariella Herberstein (see emails above).

WORKSHOPS AND MEETINGS

Conferences of other societies or workshops that may be of interest to the Society's members can be advertised on the Newsletter website. Titles and dates of conferences will be listed here, more detailed information will be posted on the webpage. Please send information on any conferences and/or workshops that you are involved with that may be of interest to ISBE Members to Ken Otter or Mariella Herberstein (see emails above).

Animal Behavior Society – 21-26 July, 2007.
Burlington, Vermont, USA.

<http://www.animalbehavior.org/ABS/Program/>

Association for the Study of Animal Behaviour: ASAB hosts several meetings and workshops each year. Details can be found at:
<http://asab.nottingham.ac.uk/meetings/index.php>

ISBE 2006 Conference Review

Entering the air-conditioned Vinci Centre in Tours was a welcome relief for those of us recently arrived from a southern hemisphere winter, hit hard by the mid-30 temperatures raging in France. The conference centre, built entirely from Leonardo da Vinci's 16th century diagrams of a futuristic, Star Trek-style mothership, was conveniently located and spacious. All visitors were impressed by the modern, comfortable lecture theatres and the glamorous, determined staff in matching white satin sailor suits.

Session times across the five theatres were regulated by recorded frog and cricket calls, with a few minutes of 'rainforest ambience' between talk slots. This technique has proved effective at past ISBE meetings and we look forward to further innovations in signaling at future meetings; we propose scents and vibratory cues.

During breaks in the program, some of the most popular venues for conference attendees included the shady park next to the conference centre, Tours' many excellent bakeries and the old town square with its exposed beam architecture, relaxed summer atmosphere, and extraordinary 'les giraffes' 2.5 liter beer vessels.

The dormitory accommodation favored by most participants was some distance away in the pleasant, leafy grounds of la Cité Universitaire de Tours. The large windows in every room provided access to the cool night breezes; invaluable given the heat and the absence of towels for post-shower drying. The morning

buses to whisk delegates into town were extremely welcome. The crush of delegates squeezing onto the public transport home at night (aka *the sweat bus*) was probably largely unwelcome for the local Tours commuters, but we hope the discomfort was attenuated by the many engaging discussions on sperm competition and mating strategies they would have endured en route.

As usual, there were several informal contributions to the perennial discourse about the perceived overrepresentation of birds/insects/any other disliked animals. Perhaps this ongoing tension explains why many talk and poster titles provide only a common or species name without reference to any higher phylogenetic affiliation. Only when the first picture of a crested spiny shankshot appears on a screen does it become apparent whether it is bird, beast, bug or bacteria.

General trends @ ISBE

A very brief analysis of the spoken and poster presentation confirms, once again, that birds remain the taxon of choice for behavioral ecologists (Figure 1). Almost 50% of spoken papers and 40% of posters reported on some aspect of bird behavioral ecology. Mammals (including humans) and insects are battling for second place. Surprisingly, reptiles and amphibian contributions were scarce. There were no obvious (or statistically significant) biases in the distribution of taxa

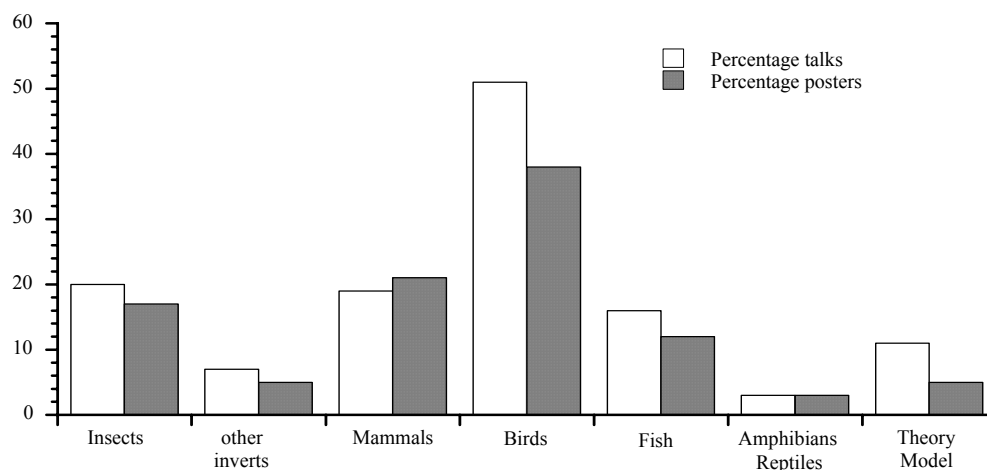


Figure 1. Distribution (%) of taxa in oral and poster contributions at ISBE 2006

between oral and poster presentation (Figure 1).

A more detailed analysis of the range of topics (only oral presentations) both from the 2006 and the 2004 conferences (Table 1) clearly shows that *Sexual Selection* is king! In both conferences, this research area scored the highest number of contributions, followed closely by *Life History*. It appears that *Multiple Mating* and *Sperm Competition* recorded an increase in contributions this year, while *Genes and Behavior* and *Sex Allocation* a decrease. Overall, contributions spread across more topics in 2006 compared to 2004.

Anecdotal evidence suggests this year's Peacock Index

may be at a record low. In the past, peacock photos were reassuringly common examples of adaptations to sexual selection, handicap hypotheses, signaling, etc. The winner of this year's Peacock Index Award for most peacock pictures is actually studying peafowl (Adeline Loyau, Université Pierre et Marie Curie), so this may be an appropriate year to end this congress assessment technique.

Plenaries & Hamilton Lecture

The six plenary speakers, also referred to as the League of Gentlemen, treated us to several diverse topics

Table 1. Distribution (%) of topics among oral presentations at the 2004 and 2006 ISBE conferences.

Topic	2006 (%)	2004 (%)
Sexual selection	8.1	11.8
Life history	6.9	8.2
Predator-prey	6.6	4.5
Habitat use/dispersal	5.7	5.5
Acoustic signals	5.7	3
Mating strategies	5.4	5.8
Social behavior	4.5	4.2
Signal evolution	4.5	3.9
Multiple mating	4.5	1.2
Cooperation & conflict	4.2	6.1
Maternal effects	4.2	3
Communication	3.3	2.7
Sperm competition	3	0
Conservation	2.7	3
Foraging	2.7	3
Mimicry/Aposematism	2.7	2.7
Hormones/physiology & behavior	2.7	1.5
Sexual conflict	2.4	2.7
Sex allocation	1.8	3.9
Group living/territoriality	1.8	0
Parental care	1.5	4.5
Reproductive strategy/investment	1.5	3
Brood parasites	1.5	2.7
Fighting & assessment	1.5	1.2
Recognition systems	1.5	1.2
Breeding systems	1.5	0
Kin recognition	1.5	0
Learning	1.5	0
Altruism	1.5	0
Human biology/behavior	1.5	0
Behavior & genes	1.2	4.2
Parasites & Immune function	0.9	4.5
Behavior of populations	0	1.5

pertinent to Behavioral Ecology. Both Peter Hammerstein and Karl Sigmund demonstrated that economical modeling is not dead and there is still plenty of scope for theoreticians in behavioral ecology to tackle issues aligned with economics or sociology. Alex Kacelnic's plenary on optimality and rationality pushed concepts even further by examining biological, philosophical, psychological and economical concepts of rationality/optimality only to leave us with the distinct feeling that grackles have a much better understanding of these concepts than we ever will. Luc-Alain Giraldeau entertainingly demonstrated that evolutionary game theory can be observed in the laboratory if animals arrive at the same solutions as EES through behavioral flexibility rather than selection. Tim Caro's call for behavioral ecologists to save planet earth could not have come a minute too early. In fact some pessimists amongst us are asking whether anything can save this planet at this stage. Caro argues that as behavioral ecologists we need to promote outreach of the applied aspects of our work. Finally, John Endler dazzled us with bowerbird plumage and ornament color showing that ornaments do not elaborate plumage but rather are selected for maximal contrast. The Hamilton Lecture by Geoff Parker was nothing short of an ode to the humble yellow dungfly. His fascinating review traced the major developments in behavioral ecology over the last few decades drawing examples from Parker's own work on this enigmatic animal.

Highlights from the sessions

Highlights from the sessions on communication include talks by James Dale of the Max Planck Institute for Ornithology ("*Social control of bill coloration in zebra finches*") and Denise Pope of Trinity University ("*Cryptic signaling synchrony in the fiddler crab *Uca tangeri**"). Both speakers had used some elegant experimental methods to test whether behaviors observed in lab and field populations did in fact have signaling functions. The talk by Nichola Raihani (University of Cambridge, "*Adaptive deception in pied babblers*") spurred some interesting debate over the definition of deceptive signals.

In other sessions, pollinator learning and foraging were reviewed and updated by significant contributions from Nehal Saleh ("*Are they really repellent? The enigmatic role of the foraging bumblebee's scent mark*") and Elli Leadbeater ("*Finding flowers by proxy: Socially facilitated learning in an insect*"), both of Queen Mary University of London.

During the Wednesday morning sperm competition session, some great images were shown by Paul Ward (Zoologisches Museum der Universität Zürich, "*Field experiments on cryptic female choice, and anatomical details of the choice system*") and Simone Immler (University of Sheffield, "*By hook or by crook? Morphology, competition and cooperation in rodent sperm*"). Photos from these talks beautifully illustrated how females might control the release and use of sperm from their sperm storage organs after copulation, and how sperm can travel in rafts connected together by velcro-like hooks.

The conference featured a number of talks on learning, with a specific session devoted to this topic. The highlights of this session were Neetje Boogert's talk about the spread of innovations in starlings. She even managed to show off her Dutchness with a cheese sandwich analogy. Another highlight of this session was Isabelle Coolen's talk about social learning in crickets. Outside of the learning session, another learning themed highlight was Ben Chapman's presentation on information transmission in guppies. It appears that whilst learning is still a minor theme in behavioral ecology it is on the way up.

Surprisingly, almost 50 % of the oral presentations on *Predator-Prey Interactions* and *Antipredator Behavior* focused on the behavior of non-vertebrates. Like ISBE meetings in the past years, we learned that prey as well as predators optimize foraging behavior. For instance, Arnold Fertin and Jérôme Casas from the Université de Tours ("*Optimality of antlion trap construction*") showed that the most impressive catching technique of antlion larvae involves constructing a perfectly conical trap. Other remarkable invertebrate studies presented in Tours focused on the phylogeny underlying form and function of silk decoration in spider webs ("*Molecular phylogeny and web decoration polymorphism in the orb-web spider genus *Argiope* (Araneae: Araneidae)*") by Matt Bruce from Utrecht University and co-workers) and the behavioral mechanisms underlying spatial patterns in a stream community ("*Effects of habitat and scale on spatial associations between interactive predators and prey in a small stream community*") by John Hammond and co-workers from the University of California). Vertebrate study animals included bats, fishes, rodents, marmots, birds and meerkats. For example, Stefan Halle and co-workers from the University of Jena combined observational data with field experiments and convincingly demonstrated that rodent activity is synchronized at the population level and is not risk averse ("*Flexible, but not risk-sensitive: the paradox of arvicoline rodent activity*"). A

major theme this year seemed to be the predator response to the warning coloration of insects, and undoubtedly some presentations, such as the one by John Skelhorn and Candy Rowe from the University of Newcastle, who used the sexy term “receiver psychology” in their talk “*Predator psychology and the evolution of insects’ defense secretions*”, will set the scene for forthcoming studies in this area.

Poster Sessions

Those brave enough to plunge themselves into the milieu of >500 posters during the poster sessions were rewarded with an outstanding visual feast. Position was everything to poster-holders and as usual, those dealt a space in the corner behaved like satellite males at a lek. However, those possessing endurance were rewarded with beer on the fourth night of the poster-marathon, graciously provided by the publishers. The quality of poster presentations was outstanding and rivaled that of the oral sessions. The prize-winners for posters this year were (1) Hanne Lovlie (poster 88: *Male sexual harassment shapes daily re-mating patterns in feral hens*), (2) Marja Jarvenpaa (poster 460: *Algal turbidity and sand goby reproductive behavior*) and (3) Lutz Fromhage (poster 64: *Paternity protection strategies in a terminally investing spider*). Although the judges had a difficult decision, these posters displayed excellent science with a high level of visual appeal and clarity.

Social Stuff

After a hard day of conferencing there is nothing that a Behavioral Ecologist likes more than a cold beer, and it doesn’t get much better than the 2.5 liter “Le Giraffe”: a meter high tube of beer with a tap at the bottom, the perfect accompaniment to increasingly incomprehensible conversation. We as committed correspondents felt it was our duty to partake in the drinking of a number of these vessels and we can report that they do the job. The centre of “Le Giraffe” drinking (although some of the more La-di-da delegates were observed drinking wine) was in the old town a short walk from the conference venue, so getting there wasn’t a problem. Getting home, however, was another story for those of us staying in the student residences. Of course, the lure of “one more drink” remained strong, delaying the inevitable journey on the *sweat bus* to nowhere.

Soccer (football) Tournament

On Wednesday afternoon in temperatures reminiscent of summer on Venus, the players and supporters of the 12 ISBE 2006 soccer teams (after the World Cup we have to call it football in Australia) were bussed out to the venue on the River Cher. Unfortunately, the grounds person was on holidays on grass planting day and thus the pitches resembled the surface of Mars. Needless to say, the blood flowed freely from numerous gashes and grazes. Despite the conditions, the games were played in a good but competitive spirit (although the team of your correspondent was neither good, nor competitive) with the team from Norway taking the final (again) with France second (always the bridesmaid, never the bride?) and Canada third. The organizers must be commended for providing ample water in bottles, water pistols and those things used to spray fertilizer on grass. The ‘Tough guy and most committed player’ award goes to Lutz Fromhage for standing in goal for two penalty shootouts in a row (although he does lose points for doing it in his jeans and losing the second shootout). The ‘commitment to science (AKA biggest nerd)’ award goes to Fleur Champion de Crespigny for practicing her talk despite the world class action going on around her and the attention of passing motorists.

AGM

On a disappointing note, the Society’s AGM, open to all members of the society, was almost exclusively attended only by the current executive and journal editors.

Mariella Herberstein, Astrid Heiling, Greg Holwell, Anne Gaskett and Matt Bruce (now at Utrecht).

Behavioral Ecology Group

Macquarie University, Australia

International Society for Behavioral Ecology, Minutes of the Business Meeting, Tours, 25th July 2006.

Agenda

1. News from the Executive Meeting (Marlene Zuk)
2. Journal report (Andrew Bourke and Cathy Kennedy)
3. Treasurer's report (Marlene Zuk)
4. Newsletter (Ken Otter & Mariella Herberstein)
5. Closing remarks (Marlene Zuk)

The President, Marlene Zuk, conducted the meeting. About 20 members were present, including Society officers.

1. Marlene Zuk summarized news from the Executive Meeting, held on 23th July.

- a. The Society was in sound financial condition, and the Executive had decided to use annual income to help students and other needy members to attend ISBE meetings. The Society would also retain a reserve, to help with down payments on meeting venues and as insurance to meet unforeseen costs.
- b. The ISBE meeting in 2008 will be held at Cornell University from 9th to 14th August, with possible symposia on the 15th. Further information is available at: <http://isbe2008cornell.org/>. The location of the 2010 meeting was still being discussed, while the 2012 meeting would be in Cape Town, South Africa.
- c. Marlene welcomed new Society officers and thanked those who had just completed or were continuing their terms. Nina Wedell (Councilor), Hanna Kokko (Councilor), Malte Andersson (Past-President) and Paul Ward (Secretary) finished their terms. Jack Bradbury becomes Past-President and Patricia (Pat) Monaghan is the new President-Elect. Rob Magrath takes over as Secretary, and Rebecca Kilner and Michael Jennions begin terms as Councilors. Walt Koenig (Treasurer), Mats Olsson (Councilor) and Naomi Langmore (Councilor) continue in their positions.
- d. She reminded those present to let students know that individuals could become members of the ISBE without subscribing to the journal. This may boost membership.

2. The journal report was given by Andrew Bourke (Outgoing Editor-in-Chief) and Cathy Kennedy (Oxford University Press). *For specific details, please see Editor-in-Chief's Report pages 25-27*

Andrew reported that *Behavioral Ecology* is doing well. The modest decline from 2004 to 2005 in individual subscriptions and a slight decline in institutional subscriptions was compensated for by a strong increase in access via consortia and OUP's Developing Countries Initiative. Overall, income from the journal is rising.

Journal submissions continued to rise, while the number of manuscripts published remained at about 140 per year. The acceptance rate has been about 30%, although this might have to drop slightly, and the time to first decision was about 60 days.

The impact factor of the journal has risen to 2.9, the highest it has been, and above comparable journals such as *Animal Behaviour*.

Recent developments include online subscription since Sep 2004, online advance publication since Nov 2004, and a redesigned cover including an author's color image since Jan 2005. OUP has also digitized back-issues of the journal, given authors free pdf access 12 months after online publication, and has had optional Open Access since Apr 2006.

Andrew thanked all those who have contributed to the Journal's success, including: the reviewers; Cathy Kennedy, Caitlyn Haase, Jenny Fulford and colleagues at OUP; the outgoing Editor (Marlene Zuk) and Board members (Theo Bakker, Jonathan Newman and Mary Reid); and incoming Editors (Naomi Pierce, Mark Hauber, Rob Brooks, Will Cresswell), Editor-in-Chief (Mark Elgar) and Board members (Mark Blows, Rebecca Kilner, Lotta Kvarnemo, Jutta Schneider, Bill Sutherland).

Heribert Hofer thanked Andrew for his efforts as Editor-in-Chief, sentiments endorsed by all.

Cathy Kennedy said that OUP considered *Behavioral Ecology* a model journal, and it had been a pleasure working with Andrew Bourke. The journal is doing well in times of great change in publishing due to electronic publishing and Open Access.

3. Marlene Zuk summarized the financial situation

outlined in Walt Koenig's Treasurer's Report. The society was doing well financially, with an income of about \$60,000 US per annum. Profits would be used to establish a reserve and help the needy attend ISBE meetings. The report was approved by a show of hands.

4. Ken Otter and Mariella Herberstein gave the Newsletter Editor's report. Mariella is the incoming Associate Newsletter Editor (a new position), and will take over from Ken as Editor after a period of at least one year's transition. A new Associate Editor would then be appointed. The new editorial structure may allow the newsletter to have a broader scope.

Since the last conference, there have been 4 regular issues of the Newsletter and one special election issue, with a total of 80 pages. There were 18 book reviews, 2 commentaries, information on the 2004 conference and a report of a non-ISBE workshop.

Ken encouraged submissions of book reviews, commentaries, announcements and synopses of workshops for future issues. Upcoming events would also be announced on the Newsletter's web site – web.unbc.ca/isbe/newsletter. The Fall issue would include book reviews, including the first review of a non-English book, and reports from the 2006

conference.

Mariella suggested and sought ideas about the future of the Newsletter. She intended to survey members on ideas, and suggested that we might consider articles on research groups, a series giving practical advice for those early in their careers, and (as a counterbalance perhaps?) more humor.

Jack Bradbury thanked Ken for his ongoing efforts with the Newsletter, and Mariella for volunteering take over. Ken thanked the Society and its members for their support and Mariella for agreeing to share the burden.

5. Marlene Zuk asked for any other business. There were no concerns about the issues on the agenda, but the poor attendance at the business meeting prompted informal discussion about how this could be remedied, and so how more members could take an active role in the society. Ideas included better advertising, a more appropriate name (eg "society meeting" rather than "business meeting"), door prizes, etc. Please send Marlene any ideas!

Rob Magrath, ISBE Secretary

Editor-in-Chiefs' Reports, *Behavioral Ecology*

Outgoing Editor-in-Chief's Report

I recently heard someone airing the view that scientific journals will soon be redundant. Before long, they said, researchers will just post their manuscripts on their own websites, or on institutional websites, where they'll be accessible to all. We would then live in a world of readily available scientific information with no journals, no submissions, no reviewers, no editors, no publishers and, most importantly from this person's standpoint, no publisher's profits. (Of course the profits of Internet Service Providers would rise, but that doesn't matter as much.) Well, I don't know what the future holds, and our predictions will only return to haunt us. But I can't help thinking that, if researchers travel down this path, people would get together after a few years and, faced with the growing mountain of undifferentiated information looming over them, would say, 'Here's an idea. Let's group our papers into subject areas to make

them easier to find, and get them vetted so that readers have some assurance of quality. To keep it fair, the vetting can be done by members of our own research community, so everyone gets a shot at being both author and reviewer. Hmmm, someone will need to oversee and organise all this. So we'll need editors, and people to publish the product. We could call the whole enterprise a *journal*.'

This tale is by way of making the point that, as we all know, scientific publishing is in a phase of rapid change. New developments combine the possibility of many novel benefits to readers and authors with powerful pressures to travel down untrodden paths whose end-points remain uncertain. Nonetheless, my strong feeling is that the basic apparatus of journals, submissions, reviewers and so on will not cease to serve an essential purpose. Against this background, I am

pleased to report that, since the period covered by the last EIC's Report in Autumn 2004, our society's journal, *Behavioral Ecology*, has continued to thrive. Let me start with some statistics, then move on to how the journal has been meeting the demands of the changing publishing environment.

The statistics reveal a journal in excellent health. In 2004, the number of submitted manuscripts was 382, up 5% on the previous year. In 2005, the number of submitted manuscripts was 415, an increase on the previous year of nearly 9%. The first half of 2006 saw a further rise, with 243 manuscripts submitted up to 30 June. To keep costs down, the size of the journal has been kept steady, with 142 papers published in 2004 and 143 published in 2005. The acceptance rate has likewise remained steady, being 30% in 2004 and 27-32% in 2005 (some 2005 papers are still awaiting final decision, which precludes the calculation of an exact acceptance rate for 2005 at present). However, if submissions continue to rise and the journal's size is to remain stable, the editors will inevitably have to reject a greater percentage of manuscripts. Despite handling considerably more manuscripts, the editors have managed to bring down the time between receipt of a manuscript and the first decision. On average, this interval was 67 days in 2004 and 61 days in 2005. Finally, *BE*'s impact factor has undergone a welcome increase. In 2004, the impact factor was 2.189 (having dipped from 2.473 in 2003), but in 2005 it was 2.943. This is the highest achieved by *BE* and puts the journal some way ahead of the two other journals with the most similar content, *Animal Behaviour* and *Behavioral Ecology and Sociobiology*.

The situation as regards subscriptions is also generally good. In common with many journals, *BE* is experiencing a trend whereby subscriptions from individuals and from individual institutions are falling whereas subscriptions from consortia of institutions are rising. The fall in individual subscriptions almost certainly stems from researchers and students increasingly gaining electronic access to the journal via their home institutions. However, *BE*'s publisher, Oxford University Press, appears optimistic. It reports that the reductions in subscriptions from individuals and individual institutions are moderate relative to those experienced by other journals and appear likely to be offset by the rise in consortial subscriptions. In addition, access to *BE* has greatly increased as a result of OUP's Developing Countries Initiative, whereby people in developing countries are given free or subsidised access to a package of OUP journals. Furthermore, because of the way the prices of

subscriptions differ across individuals, institutions and consortia, the income from *BE* (which is split between OUP and ISBE) has been rising.

A key feature of the changing publishing environment is the leap in quality of online functionality. OUP has been proactive in introducing to the journal a number of improvements that this development has made possible.

Of course, the journal has had online submission and processing of manuscripts since the start of 2003. Foremost among the innovations is that, from November 2004, all accepted papers have received online advance publication roughly 6 weeks after acceptance. Since the online paper counts as the first official publication of the work and is citable via its DOI, this development has effectively eliminated the problem in the print-only era of lengthy delays occurring between acceptance and publication. In January 2005, we introduced a redesigned cover featuring authors' digital colour images. The result has been a succession of stunning colour covers that have greatly enhanced the visual appeal of the journal. Earlier this year OUP completed the digitisation of the back numbers of all its journals. In the case of *BE*, this digital archive (issues from 1990 to 1997) is now available free to all ISBE members. In addition, in April this year *BE* joined OUP's Optional Open Access scheme, whereby authors of accepted manuscripts are offered the choice of publication via either the traditional subscriber-pays model or an author-pays model. If take-up of Open Access publication is high, income to ISBE from the journal may be affected, so ISBE and OUP will be closely monitoring the scheme. Early indications are that take-up is not going to be high (there was a single taker between April and July 2006), but this may of course change. Finally, at the 2006 meetings of the Editors, Publisher and ISBE Executive, it was agreed that content of *BE* would be made free after 12 months from publication. It is hoped that these last two innovations will meet the demand by some funders for investigators to make their published research freely accessible upon or soon after publication.

Many people have worked extremely hard to deliver these improvements and to maintain the journal's high standards of production and scientific quality. In 2004, a total of 584 individuals reviewed manuscripts for *BE*; in 2005, this figure was 613. I offer grateful thanks to them all. I would also like to record thanks to Caitlyn Haase and her colleagues in the OUP Production Office in Cary, North Carolina, as well as our main OUP link, Cathy Kennedy, who is Senior Journals Editor at OUP in Oxford. In addition, I thank my Editorial Assistant,

Jenny Fulford, who is remaining with the journal as I step down as EIC. The journal's Editorial Board continues to act as an invaluable source of advice and support. I thank outgoing Board members Theo Bakker, Jonathan Newman and Mary Reid, and welcome with gratitude new Board members Mark Blows, Rebecca Kilner, Lotta Kvarnemo, Jutta Schneider and Bill Sutherland. Much of the work of the foregoing individuals is invisible to authors. By contrast, the work of the editors, necessary as it is, probably at times seems all too apparent. Faced with annual rises in submission levels, the editors have worked especially hard over the past two years, and deserve the thanks of us all. I offer particular thanks to

outgoing editor Marlene Zuk, and to the two editors who have joined us since the last EIC Report, Naomi Pierce and Mark Hauber. Thanks too to incoming editors Rob Brooks and Will Cresswell. Finally, I extend a grateful welcome to my successor as EIC, Mark Elgar. The journal is in the hands of an excellent team and seems well positioned to remain at the forefront of publishing in our field, whatever forms this takes in future.

**Andrew Bourke, Outgoing Editor-in-Chief,
*Behavioral Ecology***

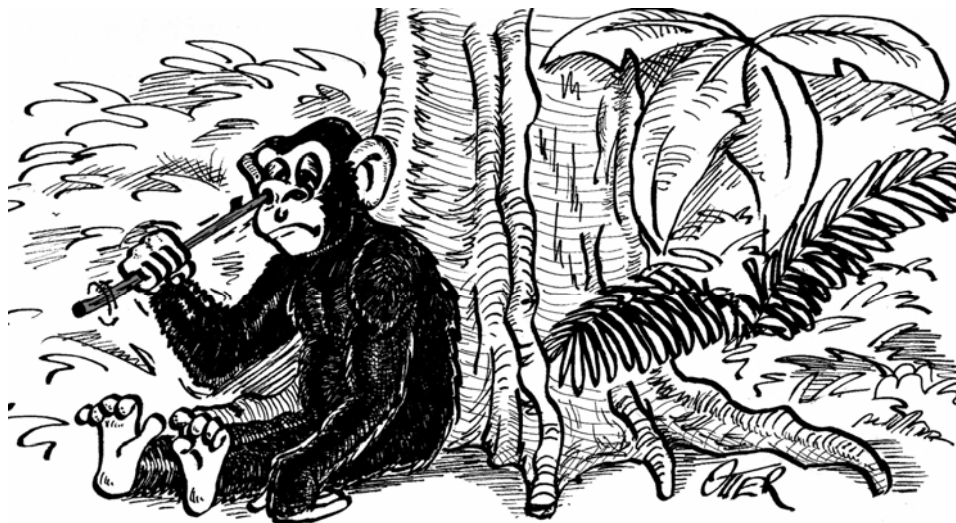
Incoming Editor-in-Chief's Report

As Andrew Bourke reveals in his report, the journal has an enviable reputation and this is in no small part due to his outstanding contribution as Editor-in-Chief.

The success of any journal depends primarily on the quality of the papers we publish, and authors send their best papers to journals that make defensible decisions within a reasonable period of time. Andrew has been responsible for a number of important initiatives associated with the speed of the editorial process and, importantly, ensuring that the editors of *Behavioral Ecology* have similar perspectives on what makes a paper acceptable for publication. The submission rate of papers to *Behavioral Ecology* continues to increase; while this extremely satisfying metric reflects the reputation of the journal, it also creates non-trivial pressures on the time commitments and decision-making processes of our editors. We

shall expand the number of editors to ten, but any further increase may compromise our capacity to ensure a high level of consistency in our decisions. This issue becomes even more acute since there are no plans to expand the size of the journal, with obvious implications for the acceptance rates. A second challenge is to ensure that *Behavioral Ecology* leads the way in publishing both new perspectives in the field of behavioral ecology, and new applications of these perspectives to other fields of biology. The editorial team is currently exploring ways of addressing these challenges. In the meantime, I'd like to take the opportunity of thanking Andrew for his role as Editor-in-Chief; he leaves the journal in excellent shape and the society has benefited substantially from his very considerable time and thoughtful insights.

**Mark A Elgar
Editor-in-Chief, *Behavioral Ecology***



EXAMPLES OF TOOL-USE RARELY SEEN ON BBC WILDLIFE

Book Reviews

*Editor's note – the following review is the first non-English book to be reviewed in the Newsletter. Juan Francisco Ornelas reviews *Muchas más que plumas*, Juan Carlos Senar's new book in Spanish on avian plumage coloration. In addition to reviewing the content of the book, Ornelas considers the potential for publishing in other languages to spread the interest in Behavioral Ecology to other areas of the world. The review, in English, is followed by a Spanish summary.*

Mucho más que plumas.

Juan Carlos Senar, *Monografies del Museu de Ciències Naturals No. 2*, Institut de Cultura, Adjuntament de Barcelona, 2004, 190 pp.

ISSN 1695-8950 (paperback)

Conspicuous colors, enlarged tail feathers, and other visual signals have played a prominent role in the theory of sexual selection since Darwin (1871). Some of the most convincing studies of sexual selection have shown, by combination of field observations and experiments, that such traits improve mating success (reviewed by Andersson 1994). Birds are the most thoroughly studied group as regards visual signals, yet comparative evidence and patterns of usage of the signals incorporating phylogenetic information are scarce. In this book, Senar (2004) synthesizes research on a daunting array of topics relating the function of color in feathers beyond their utility in protection. The result is a concise and comprehensive review of the research published in English to the Spanish audience (although it is not intended to be an extensive review). The author also does a good job illustrating classical experiments (although the quality of color plates in the text is often low) and describing key methodological issues with respect to almost every conceivable functional aspect of bird feathers. Of particular value are the author's efforts in identifying weakness and strengths of experimental designs, knowledge gaps and research areas, and offering previously untested hypotheses that all together could stimulate future research.

The book comprises nine chapters and three of them comprise the core of the book. Each chapter is highly structured with specific objectives, very creative and informative subheadings, review of the literature relating to that objective, and a summary. In most cases, each chapter ends up with a photo of some of the most influential intellectuals (Burt, Götmark, Hill, Møller, Rhower, Slagsvold, Zuk) and a legend describing their most significant contributions. Chapter 1 introduces feather structure, molting, and color - mainly melanin-based coloration and carotenoid-derived coloration - as driven by three basic functions: protection against abrasion, protection against predators, and intraspecific communication. Senar then discusses these functions in

order to set the stage for the rest of the book. Chapter 2 is the heart of the book and the best-crafted chapter. Senar uses research on the transmission of signals by both the colors themselves and the color pattern to create an excellent introduction to scientific methodology and experimentation. The author explains the methods and results of well designed and elegantly executed experiments so that the reader can learn both the significant research in this field and, more importantly, to design experiments (e.g., variables, the use of controls, replication). Undoubtedly, this chapter is a must research tool for students (and researchers) planning on experimental research in behavioral ecology. Chapter 3 describes briefly the way color and color signals are typically measured, as well as feather molt. Chapter 4 addresses some of the correlations between the so-called dominance signals and age and sex. Chapter 5 is also an important chapter as it discusses many hypotheses that address sexual selection (i.e., sexually-selected traits). Again, the reader is thrilled with elegant experiments and argumentation to tease apart some of the hypotheses (and provide alternative hypotheses). Chapter 6 deals with delayed plumage maturity, including a discussion of the adaptive and non-adaptive explanations. Chapter 7 discusses plumage coloration in terms of camouflage, and an interesting discussion regarding plumage coloration patterns of predators. Chapter 8 discusses the potential of plumage coloration (i.e., color quality) as a bio-indicator of habitat quality. The final chapter concisely sets new directions in the field, recognizing that the evolution of plumage coloration traditionally studied as independent trajectories (i.e., one color trait), is perhaps best viewed as the product of evolutionary change in multiple potentially independent traits with multiple constraints.

With an engaging narrative, Senar has done a superb job in covering almost all aspects of color signaling in birds in 190 pages! If I had one disappointment, it would be

the use of phylogenies and the comparative method to understand the functions of color signals and feather ornamentation in a historical context (i.e., color signals are not necessarily evolutionary gains). This omission is perhaps justified by the relative lack of information in this field. Given the rich diversity of color signaling among tropical birds, there is a need for methodological research into the comparative biology and ecology of plumage coloration. There have been several noteworthy efforts to do this for some bird lineages (e.g., Badyaev et al. 2002). However, the scope of most studies about color are limited to a relatively small subset of birds, such as sparrows, finches, Old World flycatchers, swallows, chickadees, siskins, and goldfinches. This narrow focus has resulted in a somehow unbalanced view of the biology of plumage coloration. Hopefully this book will make an impact on aiding behavioral ecology research in Central and South America where some of the most bizarre and extravagant examples of bird coloration occur, specifically the complexity of iridescent plumage coloration of hummingbirds and quetzals and trogons, and colorful birds such as manakins, euphonias and tanagers. Having books in Spanish adequately distributed would also potentially increase the ease in promoting behavioral ecology research in the Neotropics.

In spite of having a mere of 190 pages of text that took me a full week to get through this book (accompanied with good coffee from the surrounding area of my hometown), the book is written in an engaged fashion. Coffee helped me to detect several typographical errors that proofreaders missed from the first to the last chapters. Nevertheless, these errors, language use (e.g., “ordenador”, “coste”) and common names (e.g., “luganos”, it took me a while to detect the list of common names) do not detract from the value of the book. The main objective of the book is to reach a broad audience, from the general public to graduate students, newcomers and researchers interested in a dynamic research topic. I believe Senar has done an excellent job in this regard!

Summary of Review in Spanish

Colores conspicuos, plumas alargadas de la cola, y otras señales visuales han jugado un papel prominente en la teoría de selección sexual desde Darwin (1871). Algunos de los estudios más convincentes de selección sexual han demostrado, combinando observaciones de campo y experimentos, que tales rasgos incrementan el éxito reproductivo (revisado por Andersson 1994). Aunque las aves son el grupo más estudiado en lo que se

refiere a señales visuales, poco se ha hecho por incomparar evidencia comparativa e información filogenética para entender los patrones de uso de las señales. En este libro, Senar (2004) sintetiza la investigación existente sobre una serie de tópicos relacionados a la función del color de las plumas más allá del de la protección. El resultado es una revisión concisa y entendible de la investigación publicada en inglés para una audiencia hispano parlante (aunque no intente ser una revisión extensa). El autor también hace un buen trabajo ilustrando experimentos clásicos y describiendo detalles metodológicamente claves con respecto a casi cualquier aspecto funcional concebible de las plumas de las aves. De particular valor resalta el esfuerzo del autor por identificar debilidades y fortalezas de diseños experimentales y vacíos de conocimiento en áreas de investigación, ofreciendo hipótesis no probadas que en su conjunto podrían estimular futuras investigaciones.

El libro está compuesto por nueve capítulos y tres de ellos constituyen la esencia del libro. El Capítulo 2 es el corazón del libro y el capítulo mejor logrado. Senar usa la investigación sobre la transmisión de señales por el color y patrones de coloración para crear una excelente introducción al método científico y a la experimentación. El autor no solo explica los métodos y resultados de experimentos elegantemente diseñados y bien ejecutados para que el lector pueda no solo aprender sobre la investigación relevante en el campo sino para que observe como se diseñan buenos experimentos. Sin duda, este capítulo es una guía de investigación para estudiantes e investigadores que planean realizar investigación en ecología de la conducta. En el capítulo 4 explora las correlaciones entre las señales de dominancia con la edad y sexo de las aves. El capítulo 5 también es importante ya que discute muchas hipótesis sobre señales que son seleccionadas sexualmente. De nuevo el lector es provocado con experimentos elegantes y argumentación para discernir entre algunas de las hipótesis (además de ofrecer hipótesis alternativas). En el último capítulo, Senar plantea de manera concisa nuevas direcciones en el campo reconociendo que la evolución del plumaje, tradicionalmente estudiado como trayectorias independientes y univariadas, podría ser mejor visto como el producto de cambios evolutivos múltiples (multivariado) con múltiples limitaciones.

Con una buena narrativa, Senar ha hecho un buen trabajo cubriendo casi todos los aspectos sobre señales de color en aves en solo 190 páginas. Amén de algunos errores tipográficos, debo señalar dos problemas en este

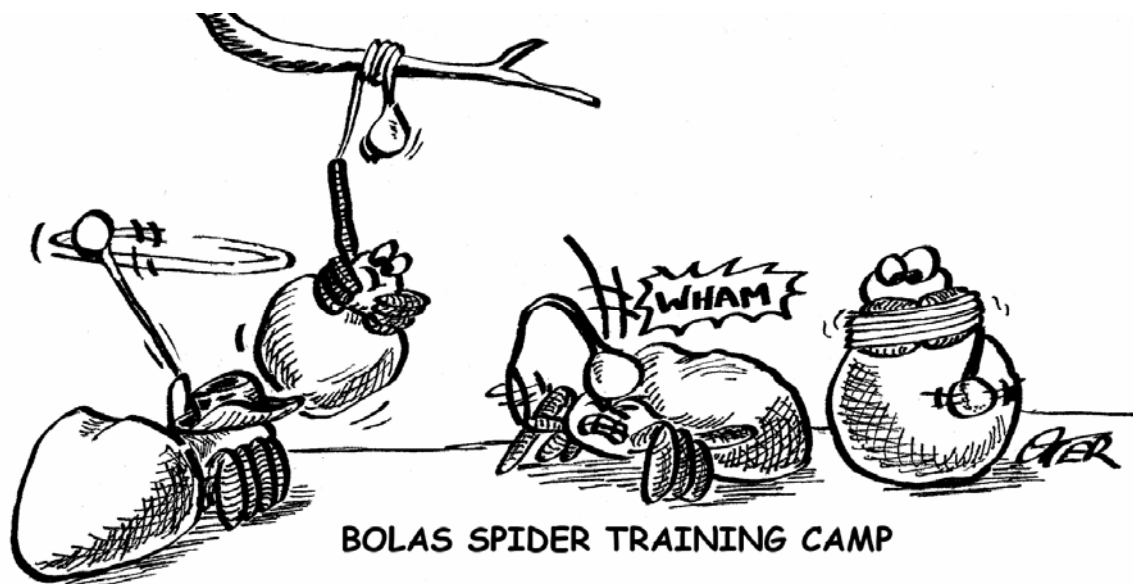
campo (no necesariamente del libro): (1) un sesgo en la visión de que las señales visuales de color y patrones de coloración en el plumaje de las aves son ganancias evolutivas, y (2) que la mayoría de los estudios se han hecho en un número limitado de especies (en su mayoría gorrones y golondrinas), produciendo una visión desbalanceada acerca de la biología de la coloración del plumaje. Con una buena distribución y escrito en español, este libro de revisión podría ayudar a que la ecología de la conducta se desarrolle en los Neotrópicos donde comúnmente ocurren aves de gran colorido con plumajes y señales visualmente extravagantes. Su estudio seguramente cambiará nuestra visión y entendimiento de la evolución y función del color en aves.

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Integrating Primatology into Behavioral Ecology

Seasonality in Primates: Studies of Living and Extinct Human and Non-human Primates.

Diane K. Brockman and Carel P. van Schaik. (ed), Cambridge University Press, 2005, 590 Pp.

ISBN 0-521-82069-3 (hardcover)

A fundamental challenge to the life sciences is explaining the differential effects on phenotypes of endogenous (e.g., genetic), exogenous (e.g., climate) and epigenetic (e.g., maternal effects) factors. Phenotypes may vary in time and space because of stochasticity alone, and *phenotypic drift*, rather than local adaptation, may explain certain features of animal behavior (e.g., “diet switching”). The topic of environmental heterogeneity, including temporal heterogeneity (e.g., “seasonality”), is important to behavioral ecology because different regimes may influence the selective values of specific genotypes and phenotypes, and because temporal factors strongly influence patterns of dispersal and the resulting gene flow within and between groups.

The study of seasonal effects on primate populations has a long history (e.g., Carpenter 1934). For example, temporal heterogeneity of Costa Rican tropical dry forest environment may have selected different responses by mantled howlers to qualitatively different conditions: a dry season and a wet season, both lasting for approximately six months each year. Temporal heterogeneity in this system favors investment in survival among adults and reproductive “bet hedging” rather than investment in offspring survival (Jones 1997). There is no *a priori* reason to suggest that other primate species, including humans, will deviate from general treatments regarding the causes and consequences of temporal heterogeneity and its tradeoffs. Recent theoretical work, however, shows that differential life history tactics and strategies are a function of the environmental information available to organisms (Kussel and Leibler 2005). In the present review, I intend to suggest that additional research on the topic of temporal heterogeneity is needed and that certain of Brockman and van Schaik’s conclusions [e.g., “Overall...the impacts of seasonality on social behavior vary enough to prevent clear generalizations.” (p. 10)] are premature.

In the Preface (p. xiii) to *Seasonality in Primates*, the editors describe their major objectives as examining “how seasonal variation in food supply affects what primates eat, where they search for [food], how active they are, and when during the day they are active, as

well as how these responses affect their body sizes, their social lives, the timing of their reproduction, and the composition of their ecological communities”. Brockman and van Schaik suggest “several general patterns about these seasonal responses” and apply these generalizations to human evolution. The idea that many human traits have been favored by a history of heterogeneous events, including seasonality, has long been recognized in the anthropological, psychological, and biological literature (e.g., Crook 1972). Indeed, adaptations to environmental heterogeneity are understood to be signature mammalian traits not in any manner limited to, or remarkable only in, primates (e.g., Feldhamer et al. 2004).

Seasonality in Primates includes 19 chapters divided into six parts titled: Introduction; Seasonal habitats; Seasonality and behavioral ecology; Seasonality, reproduction and social organization; Seasonality and community ecology; and, Seasonality and human evolution. In this review I discuss five chapters which appear to me to be of potential interest to behavioral ecologists rather than those chapters that may be of more exclusive interest to primatologists. Three of these five chapters, in addition to Chapter 16 mentioned below, are co-authored by Carel van Schaik, highlighting this anthropologist’s prominence in primatology. van Schaik has had the greatest influence in primatology through his writings on infanticide, the behavioral ecology of primate mating systems, including the differential ecological roles of primate males and females, and culture in orang-utans, and some of his work may have broad import for other social mammals (e.g., Sterck et al. 1997; van Schaik et al. 2004).

In Chapter 2, van Schaik and Kristina Pfannes evaluate tropical climates and phenology with a meta-analysis of results from 106 primate studies. The authors’ detailed quantitative examination of features of tropical plant distribution and abundance in relation to climate reveals fine-grained differences in continental patterns of fruit production, fluctuations in responsiveness of leaf flush, flowering, and fruiting to seasonal variations in rainfall, and correlations between latitude and

patterns of leaf flush and flowering. As interesting as this chapter is, it basically serves to reinforce classic work conducted by Ted Fleming and his colleagues (Fleming et al. 1987, Fleming 2005), ecologists who are not cited by van Schaik and Pfannes. Corlett and Primack (2006, p. 107) have recently pointed out that “cross-continental comparisons have had a long and fruitful history in primate studies” but that the “narrow taxonomic focus of these comparisons has...been a limitation”. This *caveat* applies to Chapter 2 as well as other contributions in *Seasonality in Primates*.

Studying baboons (*Papio*) in East Africa, Susan Alberts, Jeanne Altmann, and their collaborators oversee what has long been primatology’s most productive and scientifically valuable fieldsite devoted to the study of Cercopithecinae. In Chapter 6, these researchers discuss their investigations of “seasonality and long-term change in a savanna environment”. Alberts and her co-authors begin their treatment with the sort of fact causing an immediate “Ah, ha!” moment because it is a point of information all primatologists should know but probably don’t (I didn’t). Interestingly, among all “savanna-dwelling primates”, only baboons and humans exhibit continuous rather than seasonal breeding. It is suggested that non-seasonal breeding may account for the ecological success, including wide geographical distribution, of both species, a hypothesis worthy of investigation for other groups of social mammals (e.g., Mycetinae, *Alouatta*; Murinae, e.g., *Rattus*). Regardless of one’s preferred animal model, all behavioral ecologists will gain by reading Chapter 6 which, in my opinion, is the richest contribution to *Seasonality in Primates*, both for the evidence documenting the flexibility of baboon socioecological responses, for the insightful comparisons between baboon and human responses to seasonality, and for the potential of many of the authors’ observations to have general import. For example, Alberts and her colleagues emphasize the importance of behavioral switching in response to environmental heterogeneity, a topic that only recently has begun to be explored for mammals at the phenotypic and genotypic levels (Choi et al. 2005).

Chapter 10 is a creative narrative chapter on life history theory in which Brockman and van Schaik provide a preliminary test of the question, “Why be seasonal, and if so, how?” Modifying earlier ideas, these authors propose a new model, the *income-capital continuum model*, intended for application to organisms (e.g., primates) “whose reproductive cycle often far exceeds the annual season of increased food abundance” (p.

295). Brockman and van Schaik indicate that their model is strongly predictive, differentiating among groups of primates with alternative reproductive strategies and, by implication, responses to temporal heterogeneity. This contribution may have significant heuristic value for other taxa and may have predictive value when treated mathematically. It is noted that certain of the ideas in Chapter 10 are strongly reminiscent of “fitness set” theory and the concept of *grain* in ecology (Emlen 1973, pp. 58-95).

Van Schaik is probably best known for compiling large datasets across primate taxa and employing multivariate and graphical techniques in search of significant patterns. With these approaches, he and his colleagues address “seasonality and primate communities” in Chapter 15 concluding, significantly, that the density and abundance of primate consumers do not appear to depend upon keystone species. As these authors suggest, their findings may highlight the importance of resource switching and/or metabolic adjustments to seasonal fluctuations in food resources. Chapter 15 documents that “individual species respond differently to temporal variation of food quality and abundance” (p. 459). In future studies, within-population patterns of resource exploitation (e.g., of *phenogroups*: Jones 2005) and the relationships between seasonality, dispersal, and species richness also need to be assessed. Hypothetico-deductive research programs addressing the relationship between local interactions, community ecology, and temporal heterogeneity will require that studies of primates be integrated with cross-taxa, cross-continental comparisons (Fleming 2005, Corlett and Primack 2006) in a search for general principles based upon theoretical and empirical treatments.

In Chapter 19, Brockman attempts a synthesis of the volume’s themes and findings by asking, “What do studies of seasonality in primates tell us about human evolution?” Although her discussion is highly speculative, one of its strengths is its emphasis upon differential tradeoff responses exhibited by primates to temporal environmental heterogeneity. In a helpful table (p. 545), Brockman summarizes 17 results from contributions to *Seasonality in Primates* which, in her view, provide “predictions” (*sic*) about human evolution. As Brockman points out, all of the results emphasize the importance of behavioral flexibility (see Jones 2005) in primate, including human, evolution. Chapter 16 on “seasonality, social organization, and sexual dimorphism in primates” by J. Michael Plavcan, van Schaik, and W. Scott McGraw as well as Chapters 6 and 15 reviewed above provide the strongest

empirical support in the present volume for Brockman's ideas, many of which have received treatment in other publications (e.g., Fleagle, 1999).

In my opinion, several topics fail to receive sufficient attention in *Seasonality in Primates*. First, variation (e.g., temporal heterogeneity) will not impact differential reproductive success among individuals unless it impacts the "decisions" of individuals, a perspective rarely mentioned in the book. Second, little emphasis is placed upon seasonality as a form of *stress* and resultant implications for local adaptation and evolution. I also don't recall any references in the book to "inclusive fitness" although differences in seasonality between populations of the same species can yield significant differences in group productivity (see Cant and Johnstone 2000) and, presumably, reproductive success (Jones 1996). Third, the relationship between temporal heterogeneity, polymorphism (genotypically induced and/or regulated alternative responses), and polyphenism (environmentally switched alternative responses) are not discussed in the present volume. Finally, few if any references are made to the potentially important effects of within-individual, situation- and condition-dependent variations in response to temporal heterogeneity. Despite these personal reservations, Brockman and van Schaik's volume is a welcome addition to the primate literature which will contribute to our knowledge of vertebrate behavioral ecology and evolution in changing regimes. *Seasonality in Primates* will be a useful reference work for specialists and students and would be a stimulating text for upper-level undergraduate or graduate seminars or as supplementary reading in specialized or general courses in behavioral ecology, sociobiology, and animal behavior.

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Evolutionary Pathways in Nature

John C. Avis. Cambridge University Press. 2006. Pp 286

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Advances made in molecular genetics, particularly in DNA sequencing, that arose during the 1980s and 1990s (Avis 1994, 2004) revolutionized phylogenetics.

The ability to derive evolutionary lineages based on molecular similarity - independent of phenotypic characteristics - suddenly opened the field for testing whether morphological traits reflect shared ancestry or evolutionary convergence. So began a proliferation of research on which phenotypic characteristics of extant species were mapped onto their molecularly-derived phylogenies (Phenotypic Character Mapping, or PCM).

With the ability of gene sequence analysis to estimate the relative time since extant lineages shared a common ancestor, one was now able to test whether particular traits were the ancestral (symplesimorphies) or derived (synapomorphies) characters. Whole new fields of study and new analysis techniques arose, such as Felsenstein's (1985) and Harvey and Pagel's (1991) comparative methods via the use of independent evolutionary contrasts.

It is this explosion of research that sets the tone of Avis' new book *Evolutionary Pathways in Nature*. The book is essentially a collection of short essays reviewing research on phenotypic character mapping that have shed light on evolution in a number of topic areas. These are grouped thematically into chapters bearing titles that describe the related themes between the essays.

After an introduction to the discipline and the history of the topic in Chapter 1, Avis directs readers straight to one of the most useful sections in the book – the Appendix. The Appendix first makes a convincing case for the need of independently-derived phylogenies if one is interested in investigating evolution through character mapping. Avis then outlines the typical procedures used for phylogenetic character mapping; the author assumes some familiarity of the details of molecular methodology in deriving phylogenies on the part of the reader (referring those that do not to more advanced reading on the topic), and instead skips straight to the critical questions and problems associated with character mapping. Starting with assigning the known character states of all extant species on the terminus of the phylogeny, one is faced with how to determine the ancestral character states at interior nodes. Avis outlines and compares the two most prevalent procedures – Maximum Parsimony,

where the minimum number of evolutionary events to derive the current character states of extant species is assumed, and Maximum Likelihood, which takes into account the relative branch length and potential evolutionary time for traits to evolve within each lineage in order to determine the most likely ancestral condition. The appendix then ends with a discussion of the Independent Contrasts technique (Felsenstein 1985, Harvey and Pagel 1991). These statistical techniques are particularly useful when testing predictions that current character states are associated with particular environmental conditions. Related species may possess particular character states in similar ecological circumstances due to shared ancestry, rather than convergent evolution. To counter these biases, character states at all internal nodes are calculated by either maximum parsimony or likelihood techniques, and instances within the phylogeny where characters states diverge between adjacent nodes identified. By contrasting such instances of character divergence and determining whether these correspond to consistent differences in other environmental or life-history circumstances (like shifts in diet or habitat preference), one can look for evolutionary correlates while correcting for phylogenetic relationships.

Chapter 2 through 5 (titled, in sequence: “Anatomical Structures”; “Body Coloration”; “Sexual Features and Reproductive Lifestyles”; and “More Behaviors and Ecologies”) outline a plethora of examples in which DNA/Molecular phylogenies have aided in resolving debate over the ancestral character states of various extant species. In chapter 2, Avis highlights several cases where phylogenetic lineages based on molecular evidence suggest that certain evolutionary “laws” – such as Dollo's law that traits, once lost, do not re-evolve – may not be as iron-clad as once supposed. Phylogenetic character mapping is used to investigate topics ranging from aposematicism in poison dart frogs through parthenogenesis in lizards, invertebrates and fish. In many of the individual essays, multiple instances of evolutionary convergent events are shown to occur. However, attempts to correlate this convergence with the environmental circumstances that produce them are less common than highlighting the unexpected relationships between lineages revealed by molecular phylogenies, or the ability of these phylogenies to resolve questions about ancestral character states. There are several notable instances

where such attempts (often using independent contrasts techniques) have been made, such as the correlation between sex-role reversal and monogamous/polygamous mating systems in the pipefish and seahorses. However, I often found that once convergent evolution had been demonstrated via phylogenetics, I was left wondering what had been the evolutionary force that had shaped such phenotypic similarity between divergent lineages.

The essays in chapters 6 (“Cellular, Physiological and Genetic Traits”) and 7 (“Geographical Distributions”) were distinct in their focus from the remainder of the book. Chapter 6 provided numerous examples of molecular evolution not necessarily seen in overt phenotypic characters. Of particular interest were examples of chemical/physiological convergence among diverse taxa in such characters as foregut fermentation, snake venom, antifreeze proteins and electric currents in fish. Avis also discusses lateral gene transfer – a phenomenon in which certain DNA segments appear to be transferred - via introgressive hybridization, transposable elements or host-parasite transfer - among otherwise reproductively-isolated, and often disparately-related groups. Chapter 6 ends in a fascinating account of the forensic use of genetic phylogenies in rapidly evolving retroviruses. Chapter 7 maps phylogenies and character traits on physical geography to investigate inter-relationships and historical dispersion patterns of organisms. In this chapter, Avis outlines how molecular genetics has helped in resolving the physical origins of species from “Madagascar’s chameleons” to the “evolutionary cradle of humanity”.

Evolutionary Pathways in Nature is written in an easily tractable and engaging style that will keep the interest of novices, and also has sufficient detail to retain the attention of readers more familiar with the topic. The book is intended more as a discussion of evolutionary theory as opposed to details on molecular genetic techniques – if you are inclined towards that topic, you would do well to pick up Avis’ (2004) *Molecular markers, natural history and evolution*. The essay-style format allows for a “pick-up-and-put down” type of read, as each independent essay is only a few pages long. However, this also makes the book feel like a collection of somewhat isolated pieces at times. There is little introduction within each chapter to create a thread linking the essays, and there is no conclusion to each chapter. Catch-all chapter titles, like “More behaviors and ecologies” of chapter 5, emphasize more tangential linkages between essays. The essays in the middle chapters, while individually intriguing, at times

tend to merge into a litany of studies that simply advocate the utility of phenotypic character mapping in resolving evolutionary debates. Yet overall, Avis does an impressive job of highlighting the importance of the molecular genetics revolution in breathing new life into evolutionary research via phenotypic character mapping.

As a new graduate student, I recall the stir created when Sibley and Ahlquist (1990) published their DNA-DNA hybridization studies – the controversies were not among the many phylogenies that closely matched those derived previously, but specifically in those cases where genetic techniques pointed to different affiliations between groups than did morphology-based phylogenies. In most cases, this interest is justified; the miss-assignment of morphologically similar species that in fact have independent evolutionary histories potentially conceals instances of convergent evolution. Yet, a key question of the genetic revolution is not raised until one of the essays in Chapter 5 entitled “feeding and echolocation in whales” outlining the debate over which branch of Cetaceans (Mysticetes or Odontocetes) the sperm whale is placed. Based upon which Order the sperm whale is affiliated, there are different interpretations of what constituted the ancestral state of the original whales – baleen versus teeth, two blowholes versus one, and whether echolocation as the ancestral trait that is lost in the Mysticetes. Many of the debates of this issue were turned on their head when original molecular evidence suggested sperm whales were grouped with the Mysticetes, rather than the assumed Odontocetes. New evidence may, however, put sperm whales *back* in Odontocetes, in which case this debate will revert to earlier interpretations of the appearance and foraging tactics of early whales. In a key statement (p 128), Avis concedes that “PCM-based conclusions can be revelation, but they can also be highly sensitive to any errors in phylogenetic reconstructions themselves”. While phylogeny character mapping has been revolutionized with genetic techniques, we still need to consider that not all molecular phylogenies are in congruence. As pointed out in chapter 6, there are potential confounds, such as lateral genetic transfer between otherwise reproductively isolated lineages, that can simultaneously confound phylogeny construction, but also provide insight into fascinating evolutionary questions.

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Antipredator Defenses in Birds and Mammals

Tim Caro. Chicago University Press, 2005. 591 Pp.

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In *Antipredator Defenses in Birds and Mammals*, Tim Caro synthesizes an enormous body of research on prey defenses. The author has done an excellent job of creating a single cohesive work from subject matter that has often been widely scattered. I believe this well written and researched book is a major contribution to behavioral ecology, and not just because of what is contained in the book, but for what is conspicuously absent.

At first glance, some readers may be off put because the book is confined to birds and mammals and certain topics such as habitat use and community structure have been excluded. To the author's credit, he not only acknowledges and defends his decisions in the preface, but points the reader to the relevant references for excluded subject matter. I think the author's decision to narrow the scope of the text in these minor ways has resulted in a more focused and readable book. Even though the text is focused on birds and mammals, when needed, the author references important work on fish and insects.

Caro structures the book according to a hypothetical chronological predatory sequence following Endler (1991). This organization is different from the overlapping material previously covered in Krause and Ruxton's excellent book *Living in Groups*. Although I am a big fan of *Living in Groups* and have used it for teaching an advanced undergraduate class, I think the chronological structure of Tim Caro's text makes the subjects more comprehensible and easier to follow. I would not hesitate to use this book to teach future classes, and I believe that this book will become a required text for many graduate students.

The first chapter discusses predator recognition and defines some important terms used in the study of predator defenses. The author's precise use of certain terminology, and his justifications for particular usage

are appropriate and hopefully some of his ideas will be adopted in the future. This chapter is followed by one on morphological defenses to avoid detection. Although much of the subject matter for this chapter has been derived from work on insects, the author does a good job addressing the subject matter's relevance to birds and mammals. The third chapter concerns behavioral mechanisms to avoid detection, and this section mostly focuses on nest site selection and predator sensitive foraging. The first three chapters say very little about the ability of predators to detect prey, and when the subject is addressed, it is often assumed that predators are finding prey visually. Rather than being an oversight, I believe the paucity of data in the book is a reflection of the lack of knowledge about mechanisms of predator-prey detection.

Chapters 4 and 5 focus on group size and vigilance, and factors affecting vigilance. In general, these chapters are a good review and synthesis of the vigilance literature. I applaud the author for explicitly making the point that vigilance has a different function when done before versus after the predator has detected the prey. This is an important distinction that has unfortunately been confused by some authors. I immediately noticed some missing references in these two sections, or references that could have been mentioned in various other contexts. Although it may be possible to nit-pick this book to death, I believe that most of the omissions in regard to references were minor or trivial. Even though I think some minor changes could have been made to the book, I was generally impressed by the thorough and detailed nature of the text; very few stones were left unturned in writing this book. When the reference section is a whopping 88 pages long, there are bound to be some minor omissions!

Chapters 6 and 7 address conspecific warning signals

and signals of unprofitability. The author does an outstanding job of explaining the potential anti-predatory functions of these behaviors, and explores the evolutionary and proximate mechanisms which could lead to these behaviors. In my opinion, the eighth chapter on antipredator impacts of grouping should have been placed before chapters 6 and 7 as to transition more smoothly with the vigilance chapters. This disconnect was most evident to me in the subsection on within-group spatial position. The author references some studies showing differential mortality and predator attack rates on edge and front edge individuals, but failed to reprise the vigilance and spatial position data mentioned in chapter 5 which provides strong support for existing theory.

Chapter nine focuses on morphological defenses. The latter section of chapter nine convincingly addresses the issues and controversies over the relation between body size in primates and predation. Chapter 10 addresses nest defense, and was the only chapter in the book which I found a bit dull. I'm sure many ornithologists would strongly disagree with my opinion. Chapter 11 is a good overview of mobbing and group defense. I like how the author defined mobbing, and found that this section introduced several possible avenues of future research. Chapter 12 reviewed flight and behaviors of last resort. At some points, this last section read like a giant list of possible antipredatory behaviors. Given the huge diversity of possible predator-prey combinations, this is not surprising.

The final chapter combines various aspects of some previous chapters. The relationships between morphology and behavior, differences in antipredator response among and within prey species, and predator-prey coevolution were all discussed in detail. The book ends with a list of ten questions that the author believes should be the focus of future research. I like the fact that the author has included this section, although many of the questions that struck me as being the most interesting and in need of attention after reading the book were not included in the list. This wonderfully written and researched summary of antipredator behavior was a massive effort, and I applaud the author for tackling such a major endeavor. I think this book will be an inspiration for scientists working on these issues, and will help drive the field in new directions.

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Patterns of Behavior: Konrad Lorenz, Niko Tinbergen, and the founding of Ethology

Richard W. Burkhardt Jr. University of Chicago Press, 2005, 648 Pp.

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Ethology's Ecologies

We all know that history matters, but sometimes it is helpful to be reminded why. Richard W. Burkhardt Jr., Professor Emeritus of History at the University of Illinois, provides such a reminder towards the conclusion of his absorbing, meticulously researched account of the origins of ethology. As suggested by Burkhardt (pp. 472-3), research into the works and lives of our scientific predecessors, whatever our fields of study, can:

- lend our own work authority and context, as we come to understand, appreciate, and reference earlier instantiations of concepts of interest;
- provide “inspiration in the efforts of kindred spirits”, as we learn for example how our predecessors overcame operational and conceptual challenges;
- highlight concepts that have subsequently fallen by the wayside, now free for discovery and reinterpretation (concept mining); and, most importantly,
- enrich our ability to reflect critically on the meaning of our own scientific activities, particularly as it relates to our individual times, places, and circles of colleagues.

The attentive reader of Burkhardt's volume will find much to contemplate and value along these lines, with regard to our own discipline of behavioral ecology.

The organizing principle of *Patterns of Behavior* is that the ebb and flow of scientific inquiry and achievement depends not just on the world of ideas — for example the core concepts of an emerging discipline — but also, and perhaps more so, on the world of people and personalities that produces, disseminates, and defends those ideas. This principle is now familiar, in part because of the influence of the philosopher of science David Hull (e.g., Hull 1988), although this was not the case when Burkhardt began his research. Burkhardt proves to be an engaging and authoritative guide to “Ethology's Ecologies”, as he phrases it. Above and beyond a vast published literature, Burkhardt draws upon a significant body of unpublished work, including

excerpts from his own interviews with Lorenz and Tinbergen, and a wealth of correspondence among Lorenz, Tinbergen, and an all-star cast of 20th century behavioral scientists including Wallace Craig, Oskar Heinroth, Margaret Morse Nice, Julian Huxley, William Thorpe, Erwin Stresemann, David Lack, and, especially, Ernst Mayr, who had also advised Burkhardt's doctoral studies. *Patterns of Behavior* thus offers readers a front-row seat to the development of ethology, as it unfolded against a fascinating political backdrop of global tensions, world war, subsequent reconstruction, and the interplay of British, American, and Continental European scientific personalities and traditions.

Patterns of Behavior focuses, naturally, on Konrad Lorenz and Niko Tinbergen, the two central architects of ethology. The careers of these men were complementary and intertwined to a degree that some readers may not have realized. What set Lorenz and Tinbergen apart, we learn, was not only their intellectual talents but also their persistence and skill in galvanizing institutional support for their research programs, and their ability to win over colleagues, both junior and senior. Burkhardt suggests that ethology could have presumably found a “viable niche” (pg. 158) earlier on, via Charles Otis Whitman, Craig, or Huxley, all of whom had crafted pioneering research programs, and had mulled the potential fit of behavioral studies within (and among) the more traditional realms of biology, psychology, and philosophy. Yet all three were, in the end, derailed. The (pigeon-centric) research programs of Whitman and Craig in the United States were severely stunted by financial woes. To wit, Craig at one time lamented to a colleague that he “must keep hens; while I watch their behavior we can eat their eggs, and later we can put the specimens themselves in the pot. I must keep large pigeons as well as doves; we can eat the squabs” (pg. 47). The scramble for resources, as well as a lack of self-confidence and feelings of intellectual isolation on the part of Craig (p. 175), left little time for synthesis and institution-building, and the early American ethological perspective was soon overshadowed by the emerging field of comparative psychology. Huxley in Britain might also have jump-started the study of animal behavior, on the heels of his influential 1914

paper about mating rituals in great-crested grebes. A skilled spokesman for his work, Huxley was a “master of organization, synthesis, and presentation” (p. 124). Yet the ambitious Huxley believed he could make stronger impacts in other arenas, particularly evolutionary biology, and in the end his most important publication (1942) made little attempt to integrate animal behavior into the broader topics of ecology and evolution.

Burkhardt paints a detailed picture of how Lorenz and Tinbergen emerged as major players and then imagined, first independently and then jointly, possibilities for animal behavior as a formal discipline. Both men enjoyed, early in their careers, the support of sympathetic families and colleagues. Lorenz, a son of privilege, grew up on a family estate with woods, ponds, and facilities in which he could tend and watch animals. In medical school at the University of Vienna, Lorenz found an encouraging mentor in the comparative anatomist Ferdinand Hochstetter, under whose guidance he pursued the idea that patterns of behavior can be useful in reconstructing phylogenetic relationships among species. Tinbergen grew up within a rising Dutch naturalist tradition, manifest in popular books, school nature clubs, and, of particular relevance for Tinbergen, the newly founded Dutch Youth Association for Nature Study. Tinbergen soon discovered that he preferred to be outside than to be in school, and was transformed when he visited a German field station and learned that field research could be pursued as a vocation. Within a few short years, both scientists had become leading researchers in their respective countries. Lorenz’ first publications, on the behavior of hand-reared jackdaws, drew the favor of the leading German ornithologists Stresemann and Heinroth. Under Heinroth, who Lorenz came to regard as his most influential mentor, Lorenz began to articulate a distinction between innate and learned behavioral patterns, as illustrated in his influential 1932 *Triebhandlungen* and 1935 *Der Kumpan* manuscripts. Tinbergen, meanwhile, enjoyed the mentorship of a number of talented naturalists including Jan Verwey, Fritz Portielje, and C.J. van der Klaauw, and shortly thereafter began to pursue his famous doctoral studies on homing behavior in digger wasps. Tinbergen came to be known for his emphasis on observations of animals in natural habitats, and for using simple, precise experimental approaches to test questions about behavioral mechanism and function.

Consistent with Burkhardt’s thesis, we learn that both Lorenz and Tinbergen possessed key personality traits and talents — “youthful energy, programmatic

brashness, and conceptual promise” (p. 103) — that enabled them to build upon their early successes. Lorenz had, above all, the “gift of gab”, as we used to say in New York — he could fill a room and charm an audience. His skills and enthusiasm as a lecturer and raconteur helped pave the way for favorable reception of his written work, especially for his 1935 *Der Kumpan* manuscript which came to earn rave reviews from the likes of Huxley, Nice and Craig. Tinbergen was markedly, and famously, more low-key than Lorenz — he played, in effect, Ego to Lorenz’ Id — but he was no less effective in spreading his message. Perhaps most notably, Tinbergen developed, at the University of Leiden, a training program called the “block practical” which, in contrast to more traditional training approaches, provided students with hands-on guidance in the myriad challenges of field study. Tinbergen thus directed a rising, expanding cohort of continental field biologists towards an ethological perspective. Lorenz and Tinbergen finally met, at the Leiden “Instinct” symposium in 1936, Lorenz later noting that he had been surprised to find that Tinbergen was so young (only 29) given all that he had already achieved. The connection forged between Lorenz and Tinbergen at this symposium, and the following year at Lorenz’ private research station in Altenberg, proved central to the founding of ethology. At Altenberg, in addition to conducting joint studies on instinctive behavior (egg-rolling in greylag geese, innate responses to aerial predators), the two men observed how their approaches — Lorenz the farmer, Tinbergen the hunter, as they thought of it — were complementary, and how in synergy could define a research program for a new discipline of ethology. Central to ethology, both agreed, would be the objective and experimental study of behavior in natural settings, an approach that was largely absent from both American and European research programs. Both men later claimed their time at Altenberg as the happiest in their lives. Tinbergen visited America in 1938, where he received, due in large measure to Nice’s advocacy of Lorenz’ work, a warm reception from psychologists, biologists, and naturalists, keen to learn more about the ethological program and what it had to offer.

A Hollywood script writer would be hard-pressed to conceive a more intriguing turn of events when, with the onset of World War II, Lorenz rose in stature within the National Socialist regime, whereas Tinbergen, who had resigned from the University of Leiden in protest of the German occupation, was held as a prisoner of war. As Burkhardt notes, significant attention has been paid in recent years to the nature of

Lorenz' ties to National Socialism (e.g., Klopfer 1994, Schleidt 2001). Burkhardt devotes a full chapter to exploring these ties and making sense of Lorenz's behavior in the complex terrain of Third Reich biology. We learn that Lorenz was pleased when the Nazis came to power in Austria in 1938, above all because he believed it would enhance his career possibilities. When he joined the Nazi Party a few months later, Lorenz imagined this would help him secure a regular scientific position (which, incredibly enough, he still did not have at this time). He promoted his animal behavior studies with the claim that in studying the breakdown of instinctive behavior patterns in domesticated animals, one could recognize comparable dangers of genetic deterioration in civilized, human societies. Without becoming a strident ideologue (Burkhardt notes, for example, that Lorenz never published derogatory statements about Jews), Lorenz signaled to those in power his willingness to be an actor on the stage of Third Reich biology. Eventually he did receive a professorship, at the University of Königsberg, although he served in that capacity only briefly before being called up for military service. It thus seems, as we follow Burkhardt's account, that Lorenz's wartime efforts to warn about genetic decay in civilized society were most closely catalyzed by his own concerns for career advancement. Years later, when pressed on the subject, he would allow that he had been "naïve" about the intentions of the Nazis. However, as Burkhardt puts it, Lorenz was never willing to contemplate the idea that "in promoting ideas of racial hygiene and using a language of 'elimination,' he had possibly made an indirect or inadvertent contribution to a program that resulted in genocide." (p. 278). Post-war "exposure" of Lorenz' Nazi-era writings came to foster mistrust of Lorenzian ethology, particularly in America. Burkhardt notes, to illustrate that the comparative psychologist T.C. Schneirla was active on the political left and was "not disposed to regard Lorenz's career in the Third Reich as easily forgettable" (p. 368). Schneirla would convince his student Daniel Lehrman to write the now-classic critique of Lorenzian ethology (Lehrman 1953).

Less widely-discussed, but perhaps more important for the future of ethology, were the impacts of World War II on Tinbergen. In addition to having suffered intense psychological damage as a prisoner of war, which may have primed later bouts of depression, we learn that Tinbergen came to be dissatisfied with post-war Dutch society, which he regarded as inappropriately conservative for the time and era. Tinbergen also came to feel overburdened by new administrative and

teaching duties at Leiden. These dissatisfactions catalyzed his impending move, in 1949, to Oxford, a change of environment that would significantly broaden his research program and that of the nascent field of ethology.

According to Burkhardt, the original core "Lorenzian" ethological program was perhaps best articulated at the 1949 symposium of the Society of Experimental Biology, "Physiological Mechanisms in Animal Behaviour". In Burkhardt's retelling, this symposium stands not just as a landmark event for ethology but also as testament to the post-war resilience and leadership of Tinbergen, who by then had made amends with Lorenz. At the symposium, an animated rift unfolded between Hans Lissman and, in absentia, Erich von Holst, over the relative importance of central and peripheral mechanisms of control (Strangely enough, Lissman translated and presented von Holst's paper, mocking it in delivery). The symposium also featured Karl Lashley's classic paper "In Search of the Engram" (Lashley 1950). Most importantly for the future development of ethology, the symposium formally introduced two classical models of behavioral control; Lorenz' "psycho-hydraulic" model of instinctive action, and Tinbergen's hierarchical model of the organization of drives. These two models have more in common than this reviewer had realized, particularly in their joint aims to explain the integration of internal states and external stimuli (as suggested in part by von Holst), and in their mutual reliance on Craig's 1918 paper on appetites and aversions. It is particularly instructive to read Lorenz' musings, in a letter to Thorpe (p. 323-4), about how the two models might be jointly applied to explain complex behavior.

Burkhardt then walks us through ethology's subsequent "adaptive radiation" (p. 327), which was guided in particular by Tinbergen's 1951 book, *The Study of Instinct* (Tinbergen 1951) and his 1963 paper published in *Zeitschrift für Tierpsychologie* (Tinbergen 1963). In these works Tinbergen outlined the goals of Lorenzian ethology, but also formally expanded ethology's reach into the realms of ecology, adaptation, and evolution, consistent with the intellectual environment Tinbergen was experiencing at Oxford, under Alister Hardy and with colleagues such as Charles Elton, E.B. Ford, and David Lack. Interestingly enough, we learn from Burkhardt, Tinbergen was originally hesitant to include chapters on behavioral function in *The Study of Instinct*, because of concerns that they would draw attention away from questions about "the causes underlying instinctive behavior" (p. 372). Tinbergen's decision to include these chapters ultimately helped

jump-start the growth of behavioral ecology, imagined earlier by Heinroth (Podos 1994) and later kicked into high gear by the likes of Williams, Hamilton, and Trivers. This indeed might be ethology's greatest legacy. The negative side of the Tinbergen expansion, however, was that it became increasingly difficult to identify a coherent ethological core, as reflected in Tinbergen's characterization, in a letter to Burkhardt, of ethology as a "curious ragbag" (p. 5). The diffusion of ethological research in the 1960s and 70s, along with mounting critiques of ethological perspectives on behavioral development, led some observers, perhaps most famously Edward O. Wilson (1975), to question the continued viability of the discipline. Whether or not ethology continues to thrive as a distinct discipline, or alternatively has been subsumed into related and offshoot disciplines, is an open question that has occupied behavioral scientists for some time (e.g., Bateson & Klopfer 1989). Burkhardt implicitly provides his opinion on the matter by concluding his history of ethology with the late 1970s.

In the end, irrespective of one's views on whether ethology persists as a formal discipline, Burkhardt's account is well worth our while. Of particular relevance to readers of this newsletter, I believe, is the opportunity to resurrect concepts that have since fallen by the wayside (paragraph #1, bulleted point #3). This is by no means an easy task, as our knee-jerk tendency when reading historical accounts such as Burkhardt's is to dismiss past iterations of concepts and models as being out-of-date, losers since replaced by winners, perhaps not worth our limited time and energy. As we learn more about the people behind the science, however, it becomes increasingly difficult to dismiss their ideas outright – and, if we're not careful, some new (old) ideas begin to take root in our own minds, like weeds in a well-tended garden.

Towards this end, Burkhardt's account suggests, at least to me, that we behavioral ecologists must be missing research opportunities in our tendency to overlook the concepts of instincts and drives that were so central in early articulations of ethology (e.g., Craig 1918, Tinbergen 1951). It is convenient to assume that critiques levied at these concepts (e.g. Lehrman 1953) have since rendered them invalid. It is also convenient to ignore concepts such as these that do not fit neatly within our standing conceptual and operational frameworks (but remain, I would argue, preserved within the bar of Wilson's (1975) dumbbell model). However, just because we have forgotten how to study (or perhaps even talk about) drives and instincts, does

not mean they are not worth renewed attention. We have to remember that a main goal of the early ethologists was to observe animals as objectively as possible, even if these scientists were not, as Lorenz had exaggerated, "happily free from even a working hypothesis" (p. 312). For how much longer must we dismiss the ideas and collective intuition of our ethological predecessors?

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ISBE 2006 Symposium Reports

Do behavioral syndromes represent a paradigm shift?

Organized by D. Réale, A. Sih, A. Bell & N. Dingemanse

Behavioral ecologists have typically relied on the optimality approach, and studied behavior in single contexts. This approach generally assumes that animals facing a change in the environment will adopt the behavior that gives them the highest fitness benefit/cost ratio. This approach also focuses on the average response of a population to environmental changes and, in doing so, has neglected variation in individual behavior. Recent work on behavioral syndromes (i.e. suites of correlated behavioral traits, across contexts and over time), which focuses on individual variation in behavior rather than on average responses, has called the traditional approach to studying behavioral adaptation into question. The goals of this symposium were to discuss novel insights into the study of the functional significance of behavior that can be provided by the concept of behavioral syndromes. Our aims were to propose some tools available to researchers that can be used to integrate behavioral syndromes into their research, and to suggest that simple changes in how we conduct experiments (i.e. using the same individuals in different treatments) can change the interpretation of our results.

The consensus at the symposium was that behavioral syndromes are currently generating a lot of interest and curiosity in the community. More than 60 papers presented during the conference mentioned behavioral syndromes. Sixty people signed up to participate to the symposium and showed up on Saturday morning, despite a long night before at the banquet. Many others expressed an interest in attending the symposium, but could not do so because of the limited number of places available. Most attendees were graduate students that were curious about how to integrate behavioral syndromes into their projects, and wanted to know more about this and related concepts.

Andy Sih started by providing an overview of how the behavioral syndromes approach differs from the classical behavioral ecology approach. Sih provided new thoughts on evolutionary questions that could be developed within the framework of behavioral syndromes and on how to integrate behavioral syndromes into classic issues in behavioral ecology (e.g. sexual selection, mate choice). He especially encouraged more work on the importance of social skill and social sensitivity for cooperativeness and social behavior.

Following this introduction, Sasha Dall and Max Wolf presented two theoretical papers on why consistent behavioral types should exist in a population. Presenting a game theory model on the evolution of trust, Dall showed that increases in 'sociality' (e.g. the number and value of social interactions) can favor the maintenance of individual variation in trust and trustworthiness. Wolf showed how the trade-off between current and future reproductive success can maintain variation in risk aversion among individuals in a population, and how this variation can be expressed in different contexts.

The 3 following presentations by Denis Réale, Daniel Sol and Niels Dingemanse dealt with various methodological approaches for the study of behavioral syndromes. Réale demonstrated the benefits of a mixed effects model approach to the study of behavioral syndromes and the test of adaptive hypotheses, and how this approach can facilitate the estimation of individual behavioral profiles from replicated measurements of behavior on the same individual. Sol integrated the study of personality into a comparative analysis framework. He considered the current lack of comparative studies on personality (with the exception of pioneer works by R.S. Greenberg and K. Mettke-Hoffmann) and showed how comparative studies would improve our understanding of the ecological role of personality traits. Dingemanse developed a framework that allows comparison among populations to determine how selection and genetic drift shape variation in personality traits and behavioral syndromes, both within and between populations.

Using a detailed description of an empirical study on perch, Carin Magnhagen demonstrated how to incorporate behavioral syndromes in a social context. Magnhagen showed that the presence or absence of conspecifics can have strong influences on the expression of different behavioral types of an individual. Alison Bell closed the series of presentations by summarizing the current knowledge on behavioral syndromes and the pros and cons of different approaches for its study. One important message was that the whole idea of a syndrome requires a correlation between behaviors, so individuals need to be measured more than once in order to measure correlations. Given our current knowledge on the prevalence of behavioral syndromes,

Bell indicated that researchers should be vigilant for a potential 'file-drawer effect' and encouraged the audience to publish results showing low correlations between behavior traits. She mentioned that we were in the early stages of knowing which behaviors are domain specific or domain general, and that the lack of correlation between behaviors is therefore of great interest.

The ensuing discussion was lively, and benefited from the active participation of many audience members. Two points in particular were discussed at length:

1) A major concern was the lack of a theoretical framework. Several attendees remarked on the absence of null models (i.e. the existence of ecological circumstances and evolutionary constraints that would lead to the absence of correlated suites of behavioral traits), which limits our ability to investigate the importance of behavioral syndromes. As a related issue, members of the audience also questioned the need for incorporating behavioral syndromes into their studies, given that the classical behavioral ecology approach has been successful at explaining the way animals behave for the past 35 years. In response to these issues, it was pointed out that most of the ideas underlying behavioral syndromes come from evolutionary biology and that there is a theoretical background (i.e. correlational selection, modularity, canalization, pleiotropy or linkage disequilibrium) that can be used to explain why we should, or should not, find suites of correlated traits. One point emerging from the discussion was a variation in approaches preferred by the participants; some people favoring the hypothetico-deductive approach classically used in behavioral ecology and the others defending an inductivist approach. It appears that we are on the

starting point of developing a theory on behavioral syndromes that will probably need both approaches.

2) The second major point raised was that the current popularity of research on behavioral syndromes may increase the risk of 'fishing expeditions' and discovery of spurious behavioral correlations. Some participants argued that encouraging the reporting of negative results brings out important issues of statistical power. The discussion reached a general consensus that publishing negative results should be accompanied by strict attention to sample size and statistical issues. Several presentations had proposed ways of analyzing behavioral syndromes that should limit these problems. It should be noted, however, that showing the presence or the absence of correlations between behavioral traits is only the first step for a study on behavioral syndromes. More importantly, this type of study should examine the role of such correlation in the behavioral ecology of our model species, and the reason for its presence or absence. It was suggested that an important part of the confusion surrounding behavioral syndromes is that there are several ways (i.e. mechanistic, developmental, historical and functional) to explain their occurrence, and that we are just beginning to explore these different perspectives. In the end, behavioral syndromes may be a good opportunity for behavioral ecologists to integrate Tinbergen's four questions into their research program. Although several issues have to yet be clarified, we are confident that behavioral syndromes have great potential, and will provide opportunities that will enrich the field rather than impoverish it.

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Integrating cooperative breeding into theoretical concepts of cooperation

Organized by R. Bergmüller, R. Bshary, R. Johnstone and A. Russell

A half-day workshop involving 55 participants was held on July 29, 2006, in conjunction with the 11th ISBE congress, with the goal of discussing whether theories developed in cooperative breeding research could be integrated into cooperation theory. Cooperative breeding should be a prime model for the study of cooperative behavior in animals. Hence, it is puzzling that the rich body of empirical evidence in this field has remained largely separated from cooperation theory. We believe that there may be two reasons for this. Historically, since Hamilton first proposed his inclusive fitness theory, kinship has provided an obvious explanation for helping behavior in cooperative breeders, with subsequent findings that most helpers are related to the offspring they help raising. Perhaps due to this compelling solution for the previously enigmatic phenomenon of cooperative breeding, empiricists did not pay much attention to questions concerning the stability of cooperative breeding resulting from direct benefits. However, more recently it has become clear that kin selection is not sufficient to explain all cooperative breeding. For instance, indirect fitness benefits due to helping are rarely enough to compensate for not breeding independently. Competition between relatives can outweigh kin benefits and there are a number of species where unrelated individuals breed cooperatively. Furthermore, relatedness within cooperative breeders does not rule out direct mechanisms of cooperation because kin groups may sometimes result from the benefits of philopatry rather than the benefits of helping relatives *per se*.

Due to these reasons, a number of concepts involving direct benefits in cooperative breeders (e.g. pay-to-stay, group augmentation or prestige) have received increasing interest, but remained without an obvious connection to cooperation theory. This is not surprising considering that many existing theoretical concepts do not appear to allow a simple accommodation with the sometimes complex forms of cooperation in cooperative breeding animals. This gap between theory and empirical evidence may be the second reason for the prevailing separation between cooperation theory and the study of cooperative breeding.

In the round table discussion, we suggested that time is ripe to attempt an integration of both fields in order to achieve a more unified approach to cooperation and cooperative breeding. We invited researchers working in the fields of cooperation and cooperative breeding to

discuss the usefulness and feasibility of such an approach. As a starting point for the discussion, we suggested an approach for integration. Out of the confusing number of existing ideas and concepts in cooperation theory, we selected those that appear to be relevant for cooperative breeding (by-product mutualism, pseudo-reciprocity and reciprocity) and introduced them briefly. For the purpose of integration, we attempted to identify some crucial parameters for the maintenance of cooperation that allow to distinguish among these concepts (i.e. investments or no investments involved, contingency of investments, direct or indirect interactions, only positive (beneficial) or also negative behaviors (punishment) involved). In a next step, we assigned the different concepts of cooperative breeding to the appropriate concepts of cooperation with the help of a decision tree based on the parameters. Below, we briefly summarize some of the main points that emerged during the following discussion.

In cooperative breeders individuals help to raise offspring that are not their own. This traditionally narrow sense definition usually focuses on the central questions why helpers stay, help and reproduce below their potential. However, only a part of the known cooperatively breeding species is covered when using this approach, as the variability of existing phenomena may not allow compressing the diversity of cooperative breeding into one single model. As a first step towards a closer integration, the traditional approach may provide a useful starting point. However, future analysis must attempt to include also the broad range of existing systems that do not fit in this perhaps simplified classification of cooperative breeding.

Somewhat surprisingly, none of the participants argued that kin selection may be sufficient to understand cooperative breeding, possibly indicating a paradigm shift in this field. We focused on direct benefits from cooperation or helping in cooperative breeders, but it is clear that for a comprehensive treatment, direct and indirect benefits need to be considered. Disentangling the combined effects of kin based and non-kin based cooperation and their interactions remains a future challenge.

As our decision tree is a tool for integration rather than an all inclusive framework of cooperation theory, it incorporates only some important and basic concepts of cooperation that appear to be relevant for

cooperative breeders. Consequently, the decision tree only includes the parameters useful in distinguishing between the different concepts. When applying these parameters, however, it becomes evident that some important aspects relevant to understanding cooperative breeding are insufficiently treated in existing cooperation theory:

First, cooperation theory often implicitly assumes symmetric payoffs and interactions. However, in nature, such a situation is more likely to be an exception rather than the norm. Particularly in species with dominance hierarchies, as in cooperative breeders, asymmetric interactions should crucially influence individual investments and the resulting outcomes of cooperative interactions. To understand cooperative breeding, cooperation concepts that incorporate these asymmetries are needed.

Secondly, almost by definition, cooperative breeding is an N-player situation where usually at least two breeders and one helper contribute to raise offspring. However, as interactions between more than two players are notoriously difficult to model, it is often assumed that most situations can be reduced to interactions between two players, i.e. a helper and a breeder. However, it seems likely that in future we will need solutions to theoretically treat N-player interactions to also cover social dilemmas. This would allow treating questions like how and whether individuals in cooperative breeders contribute to a common good (e.g. raising offspring, territory defense etc.). Also, the disagreement between predictions derived from reproductive skew theory and the available data seem to make it necessary to consider at least both breeders and a helper instead of only two players. Additionally, future models should also include the possibility of alternative strategies between the sexes because of existing differences in helping and dispersal behavior. The inherent difficulties in modeling N-player situations indicate that we still await substantial advances in this field.

We conclude that besides having had a very enjoyable meeting and an especially lively and interactive discussion, it was an important first step to bring together researchers working in the currently unconnected fields of cooperative breeding and cooperation theory. The integrative approach may be useful in creating a more unified framework of cooperation that allows analyzing the various observed phenomena in a more consistent way and detecting gaps that need to be filled in both fields. However, the discussion also highlighted a number of issues that need clarification, empirical support and theoretical advance before a comprehensive uniting approach can be achieved.

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Ralph Bergmüller and Redouan Bshary
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The evolutionary ecology of genetic quality

Organized by T. E. Pitcher & H. L. Mays

At the most basic level, evolution can be thought of in terms of gene frequency changes over generations. Fundamental to understanding evolution therefore is the notion that, in terms of evolutionary fitness, some individuals in the population are genetically of higher quality than others. While this notion of genetic quality is central to any understanding of biological evolution there is considerable work remaining to both better define genetic quality in terms of theory and to better measure variation in genetic quality. For instance, good genes models of sexual selection rely on the idea that fitness is heritable, which contrasts sharply with the non-additive form of genetic quality associated with compatible genes models of sexual selection, which is not heritable. Understanding genetic quality is relevant in studies of multiple mating, cryptic female choice, exaggerated male sexual ornaments and numerous other phenomena near and dear to behavioral ecologists. Several recent reviews have focused on additive, good-genes genetic quality (Hunt et al., 2004a; Tomkins et al., 2004) and many have focused on non-additive forms of genetic quality, namely genetic compatibility (Mays and Hill, 2004; Neff and Pitcher, 2005) or complementarity (Pialek and Albrecht, 2005). In efforts to highlight the latest developments we organized a symposium on the evolutionary ecology of genetic quality as part of the 11th Congress of the International Society for Behavioral Ecology in Tours, France on 29 July 2006. Eight speakers, including post-docs, junior faculty, and more established researchers, presented results from their research programs. The talks were well attended with approximately 60 attendees representing research groups from around the world.

Crickets, chickens, flies and fishes

Numerous groups have studied genetic quality from the perspective of a number of different model systems. Three model systems loom large in the recent empirical literature addressing the question of female mate choice for genetic quality: crickets (family: Gryllidae), salmonids (family: Salmonidae) and the red jungle fowl (*Gallus gallus*). In crickets there are many behaviors that could potentially act as signals of genetic quality, and social dominance is a likely candidate. Amanda Bretman (University of Exeter, Cornwall, UK) presented research showing that female

field crickets (*Gryllus bimaculatus*) invest more in egg number when mated to dominant males, which are presumably superior sources of genetic quality. However, these findings also raised the possibility that males may be passing compounds to females during mating, such as prostoglandins that may influence egg number. If so then there is the potential for sexual conflict in this system where males increase their reproductive success by manipulating females away from an optimal lifetime fecundity. Claus Wedekind (University of Lausanne, Lausanne, Switzerland) reviewed the genetic architecture of survivorship in whitefish (*Coregonus sp.*). For whitefish good genes benefits are evident in terms of embryo mortality with a significant negative relationship between offspring mortality and the size of male sexual ornaments (i.e. breeding tubercles, (Wedekind et al., 2001)). Additive good genes effects on embryo mortality are strong in whitefish but these effects also vary considerably across different stages of embryo development. Tom Pizzari (University of Oxford, Oxford, UK) discussed research on sexual selection in the red jungle fowl in relation to inbreeding avoidance and choice for dissimilar MHC (major histocompatibility complex) genotypes. Jungle fowl provide unique opportunities because experimental designs that incorporate free choice, staged mating and artificial insemination can be performed to allow for distinctions between pre-copulatory mate choice, sperm allocation and female sperm utilization or post-copulatory choice. Pizzari and his colleagues found that in staged mating experiments female jungle fowl retain more sperm from unrelated males compared to matings with related males. A similar result was obtained for MHC similar versus dissimilar males but the effect did hold in the artificial insemination experiments suggesting differences in paternity biasing between pre and post-copulatory stages.

Another important yet unresolved question in the field of sexual selection is: Why do females multiply mate when all they obtain from males are genes (i.e. sperm)? Two presentations highlighted the potential costs and benefits of polyandry. Paul Ward (University of Zurich, Zurich, Switzerland) presented research on a classic system in behavioral ecology, the yellow dung fly (*Scathophaga stercoraria*). Females store sperm from several matings in spermathecae and females with four rather than three spermathecae are better able to

control the paternity of their offspring. However the development of four spermathecae carries with it a non-trivial cost. Ward stressed the importance of measuring the costs associated with discerning among males of differing genetic quality and experimental manipulation in the study of cryptic female choice. Tom Price (University of Exeter, Cornwall, UK) discussed female mate choice in another classic dipteran model system, *Drosophila*. *Drosophila pseudoobscura* females mated to males with a meiotic driving sex chromosome suffer substantial fitness costs as they produce only daughters. Driving males are undetectable from non-driving males creating a potential problem for females in populations where they may encounter males with the meiotic drive allele. However, because meiotic driving males are poor sperm competitors when pitted against non-driving males multiple mating females appear to reduce the likelihood of having their eggs sired by driving males through polyandry.

The human side

Empirical work in identifying the role of genetic quality in mate choice has not been limited to non-human animals. Indeed much of the existing work on MHC based mate choice for genetic compatibility grew from human mate choice studies. S. Craig Roberts (University of Liverpool, Liverpool, UK) summarized research on genetic quality in human mate choice. Roberts reported that facial attractiveness is a good indicator of heterozygosity at MHC loci. The same result was obtained if only isolated patches of facial skin were presented in choice trials. However, signals of a potential mate's genetic compatibility may be at odds with good genes based signals. Whereas all females should agree on the optimal good genes sire, females will differ in their optimal genetically compatible sire. Understanding the interaction between good genes based sexual selection and mate choice based on genetic compatibility remains an open area of research. Roberts also identified some critical methodological points in the empirical study of genetic compatibility, heterozygosity and mate choice pointing out that for both humans and peafowl (*Pavo cristatus*) measures of genetic similarity are correlated with heterozygosity (Roberts et al., 2006). This finding should be carefully considered in studies attempting to disentangle female choice for good genes and compatible genes.

A diversity of approaches

Tackling the topic of genetic quality requires a diversity of approaches. While most of the symposium was devoted to experimental work there remains some need for theoretical clarification and meta-analyses of genetic quality studies. Jacek Radwan (Jagiellonian University, Krakow, Poland) explored the lek paradox by examining the support for the various mechanisms responsible for maintaining heritable variation in sexually selected traits. Various mechanisms have been proposed, including mutation-selection balance, frequency dependent selection, overdominance, variable selection and meiotic drive, however considerable research is needed to elucidate the relative importance of these mechanisms in maintaining genetic variation in nature. In exploring the potential mechanisms underlying the maintenance of genetic variance in sexually selected traits Radwan pointed out various avenues of future research. For example, one way in which genetic variation could be maintained for sexually selected traits is if overdominance occurs at those loci underlying expression of ornaments. In this case heterozygosity should correlate with ornament size.

Along with other participants in the symposium, Luc Bussière (University of Zurich, Zurich, Switzerland) emphasized both the importance of a quantitative genetics approach as well as life history theory in understanding genetic quality. Bussière discussed this approach in reference to the idea of good genes as life history traits in the black field cricket (*Teleogryllus commodus*). Increased male call rates result in increased attractiveness. In the experiments described, food was increased to alter condition and therefore affect call rate. Increased diet meant more calling behavior, and thus higher attractiveness, but shorter lifespan. Bussière emphasized the need for caution in using longevity as a proxy measure of good genes as this relationship is dynamic depending considerably on the environment and thus male condition (Hunt et al., 2004b).

Conclusions and future challenges

Research into the relationship between genetic quality and sexual selection appears to be vibrant and growing. Several recent reviews and this symposium have summarized previous work in the field and have pointed to new avenues of research. Future breakthroughs in the study of genetic quality appears to lie in the increased use of quantitative genetic

approaches to: assess the magnitude of additive and non-additive genetic effects on survival and reproductive success (e.g. Birkhead et al. 2005), identify the genes that underlie genetic quality and mate choice (see Fitzpatrick et al. 2005 for a review of the candidate gene approach), partition genetic quality variation to specific alleles and combinations of alleles (see Pitcher and Neff 2006 for a novel genetic algorithm), and examine gene by environment interactions (e.g. Welch 2003).

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