
INTERNATIONAL SOCIETY FOR BEHAVIORAL ECOLOGY

ISBE NEWSLETTER

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From the president

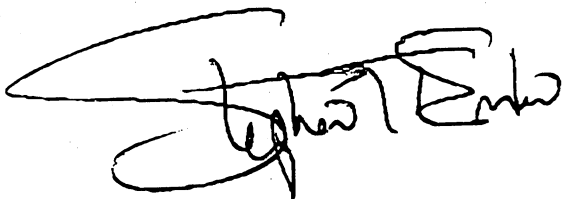
In this, my first contribution to the Newsletter as President of ISBE, I wish to comment briefly on each of the three primary purposes of our society. The International Society for Behavioral Ecology functions 1) to sponsor periodic scientific meetings for behavioral ecologists, 2) to promote scientific research in behavioral ecology (primarily through the publication of our journal), and 3) to increase awareness of behavioral ecology.

1) We recently concluded our *7th Biennial Congress* at Asilomar, CA. The meeting brought together 587 colleagues from 34 countries - 283 of whom were from outside of North America. Many of those present commented on the growing "maturity" of our field, citing both the diversity of topics under investigation and the high quality of the individual presentations. For those of you unable to attend, brief reports on the meeting can be found elsewhere in this Newsletter. Organizing such a conference is a major act of service to the Society. Special thanks are offered to Janis Dickinson and Walter Koenig who served as chief planners, hosts, and crisis-solvers both before and during the congress.

2) *Our journal, Behavioral Ecology*, continues to grow in excellence. New subscriptions increased by 8% last year, making *Behavioral Ecology* the fastest growing of the more than sixty professional journals produced by Oxford University Press. Of course the quality of a journal depends on the dedication and decisions of its editors. The Society owes a large debt of gratitude to Larry Wolf, Paul Schmid-Hempel, and Marc Mangel for their years of leadership and service in this capacity. Larry and Paul recently completed their terms and we welcome Ron Ydenberg and Gunilla Rosenqvist as their replacements. We also welcome Innes Cuthill, who has assumed responsibility as a fourth editor (giving us two editors on each side of the Atlantic). Marc will be "retiring" in July of 1999 and the Executive is beginning a search for his replacement.

3) Finally, what are we doing to *increase awareness* of our discipline? I commented on this important issue in the Presidential Address that I delivered at Asilomar, some of which is excerpted in the Forum Section of this Newsletter. As you will read there, I hope that each of you will accept an increased responsibility to become more involved in communicating the excitement and the importance of what you do to others - to both professional colleagues and lay persons alike. There will be reviews of the Asilomar Congress in upcoming issues of both *TREE* and *Science* (in addition to this Newsletter). These will help alert colleagues in other fields to some of the advances occurring within our discipline. Together with officers from the Animal Behavior Society and the Society for Integrative and Comparative Biology, I will be travelling to Washington, DC to discuss the importance of behavioral research with officials at the National Science Foundation (NSF), an important funding source for our field. The success of our attempts to promote the study of behavioral ecology will benefit greatly by the active participation of all of us. I hope you will get involved.

This is an exciting time for behavioral ecology. I look forward to serving the Society in the two years ahead.



Stephen T. Emlen

Editorial

The content of the Newsletter depends largely on you, dear members of our Society, and I am very pleased to see that you took up the challenge to participate (witness the size of this Newsletter). In the Forum section of this issue the success of our last meeting is clearly reflected. No less than four contributions provide opinions on the importance of our field and/or on the evolution of its research topics. In the future, I hope to publish letters in response to these essays or new views or opinions about our field.

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

The next issue of the Newsletter will come out with the May/June issue of *Behavioral Ecology*, so copy that reaches me **before 15 April 1999** can be included.

Please send your contributions to my new address: **from 15 January 1999** onwards I will be at the

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Society News

Election of ISBE Officers

Congratulations to Marion Petrie who was elected our new Secretary. Her report on the General Business Meeting can be found below.

Nominations for new Officers

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

President-Elect
Treasurer
Councillors (two positions)

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

Please send suggestions for the short-list to me by 15 February 1999. There's no need to contact your potential nominees at this stage. We will confirm that short-listed candidates are willing to stand for election.

Nick Davies

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Pitelka Award

It is my pleasure to announce the winners of the 1998 Pitelka Award for excellence in behavioral ecology research. This award, which is given to researchers within five years of their doctorate, is decided by a sub-committee of the ISBE council, and is based on publications in Behavioral Ecology in the past two years. This year there are two winners: Jan Komdeur of the University of Groningen, and Bart Kempnaers of the Konrad Lorenz Institute, Vienna. Congratulations to both!

Tim Birkhead
Past President

Journal Editor

Mark Mangel will be stepping down as one of the North American editors in the summer of 1999. Interested persons or persons with suggestions for replacement, please contact either our president or any current editor.

Conference News

The VIII International Behavioral Ecology Congress will be held in Zurich, Switzerland, probably from 8 to 12 August 2000. A formal announcement will be mailed to members at a later date.

For further information or suggestions, contact Paul Ward (pward@zoolmus.unizh.ch).

Minutes of the General Business Meeting ISBE

Asilomar Conference Centre, Monterey,
California July 1998

Steve Emlen (SE, the incoming President) opened the meeting and introduced the new Secretary Marion Petrie and new members of the Executive Committee, Jane Brockman and Andre Dhondt. He thanked the outgoing officers; president, Tim Birkhead, Secretary, Patty Parker and Councillors Mark Elgar and Rauno Alatalo.

SE then introduced Janis Dickinson (JD) and asked her to present the local organising committee report. He thanked Janis for organising an excellent meeting. Janis received warm applause.

JD thanked everyone on behalf of herself and co-organisers. Janis reported that there were 594 registrants at the meeting representing 33 countries. 63% of registrants came from outside the US. There were 480 presentations and 370 spoken papers. This allowed everyone who wished to give a spoken paper but resulted in a large number of concurrent sessions.

Journal matters

SE reported that Paul Schmid-Hempel had retired as Editor and that it took two new European editors, Innes Cuthill and Gunilla Rosenqvist, to replace him. There are now two North American editors, Marc Mangel and Ron Ydenberg (RY) and two European editors. SE thanked Paul for his services and welcomed the two new editors.

RY reported that the Journal was doing well and that the submission rate was still high. Previous backlog problems had been solved and

now papers appear in 5 or 6 months after acceptance. On average the refereeing process takes 3-4 months.

Don Kramer added that it was very important for members to support the journal by encouraging library subscriptions and sending their best papers there.

The Oxford University Press representatives (Steve Johnson and Cathy Kennedy) reported that the journal will be on-line within a year, and that now there were 324 Library subscriptions.

Someone from the floor asked whether being on-line meant the journal will be free. The OUP representatives explained that an on-line library subscription results in a site licence available (for a fee) to an I.P. address with a valid password.

There were now 1200 subscribing members and membership went up by 200 in the last year largely because membership was a requirement to attend the Monterey meeting.

Someone from the floor asked whether it was an Executive decision to require ISBE membership to attend meeting. SE said it was.

SE then reported that members of the Editorial Board of the journal serve for a 6-year period with a third of the board rotating off every 2 years. Steve Emlen reported that Jonathan Newman, Mary Reed, Anne Houde and Theodore Bakker had all agreed to be new members of the editorial board. Serge Daan, Paul Harvey, Rob Warner and Manfred Milinski would be rotating off the editorial board.

SE also reported that the Executive Committee had agreed to adopt the same ethical guidelines about the use of animals in research as formulated by the Association for the study of

Animal Behaviour and the Animal Behaviour Society. Research published in the society's journal will, in future, have to conform to these guidelines (which are published in the January issue of the journal *Animal Behaviour* each year).

It was reported that Marc Mangel will be stepping down as Editor from next July and that the executive were open to suggestions of people who would be interested in serving as a North American Editor.

Financial matters

SE jokingly reported that the ISBE was the "most broke" society he had ever been involved in. The society had a running balance of about \$16,000. This was not a large nest egg and the executive had decided that it would not be doing anything to spend this money in the future. However, it was hoped that we would have paid off our initial debt to OUP (for establishing the journal) within 5 years and that after this time the society could think about spending money.

Pitelka Prize

SE reported that this prize is available to people who are within 5 years of gaining their PhD and who have published in *Behavioural Ecology*.

Future meetings

Paul Schmid-Hempel (PSH) presented a report in the absence of Paul Ward, the main organiser, of the next meeting which will be held in Zurich. The most likely dates for this meeting will be 8th -12th August 2000.

Registration fees will be slightly lower than at Asilomar but accommodation costs will be slightly higher. The overall cost of the meeting will

be about the same as attending Monterey. There will be different registration rates for members and non-members. PSH also reported that it was the organiser's intention for there to be fewer talks in order to reduce the size and length of sessions and to allow more time for discussion.

SE said that a couple of potential organisers had been approached with a view to organising the meeting in 2002, and that it was hoped that this meeting could be held in a place other than Europe or North America. SE also stated that if anyone would like to hold a future meeting then the Executive would like to hear from you.

New business

SE asked if anyone wanted to raise any further matters. There was no response from the floor so SE called the meeting to a close by saying "Go disco!".

Marion Petrie
Secretary

Donated Subscription Programme

Please help colleagues in need. Every donation will help increase scientific contacts across the world. In a time when nationalism is again raising its ugly head, this is more important than ever. For details, see the newest issues of our journal *Behavioral Ecology*.

Spousal Membership

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

Grants and Jobs

VOLUNTEERS

Approximately 30 volunteer positions are open in 1999 at the American Museum of Natural History's Southwestern Research Station in Portal, Arizona. The volunteer program is run annually and offers students in biological sciences outstanding opportunities to observe and become involved with scientists doing field research. Food and lodging are provided to volunteers in exchange for twenty-four hours per week of routine chores, with the remaining time available for research activities. The program is open to both undergraduate and graduate students; the latter may pursue their own research projects. Faculty knowing of promising students should alert them to this opportunity for professional experience toward, development of, and evaluation of their career goals. Volunteers are needed between March 14 and November 1. Appointments are for part of this period, with a minimum appointment of six weeks. Applicants for spring positions (March-May) should submit applications by February 15, summer volunteers (June-August) by April 1, and fall volunteers

(September-November) may apply any time. For applications, write: Dr. Wade C. Sherbrooke, Director, Southwestern Research Station, American Museum of Natural History, Portal, AZ 85632 USA; telephone 520-558-2396; e-mail: swrs@amnh.org

SOUTHWESTERN RESEARCH STATION STUDENT SUPPORT FUND

The American Museum of Natural History awards several grants each year of approximately \$400-\$800 to graduate students or postdoctoral students pursuing research at its Southwestern Research Station in the Chiricahua Mountains, Portal, Arizona. Information and application forms for this program and other Museum grant programs can be obtained by writing: Office of Grants and Fellowships, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192. Application due date: Feb. 15, 1999. Address questions concerning the Station to: Dr. Wade C. Sherbrooke, Director, Southwestern Research Station, Portal, AZ 85632 USA; telephone 520-558-2396; e-mail: swrs@amnh.org

SEASONAL OFFICE ASSISTANT

Assist in operations of biological research station office and nature shop: taking reservations, answering phones, greeting guests, supervising volunteers, etc. Begin March 14, 1999, through September 1999. Five-day week; salary \$235/wk, plus room (shared) and board. Applicant must be punctual, organized, enjoy people, and be interested in living in a remote setting (Chiricahua Mountains) and working with biological researchers. Biological training an asset. Call and send résumé to: Dr. Wade C. Sherbrooke.

Forum

Relevance and Responsibility in Behavioral Ecology

(from the Presidential Address to the Seventh International Congress of Behavioral Ecology, Asilomar, CA., August 1, 1998)

There is a tradition in the International Society for Behavioral Ecology (ISBE) for the incoming president to give an address at the time that he/she assumes office. I have decided to use this forum as a bully pulpit to make a simple argument: that we, as behavioral ecologists, have a responsibility both to our own science and to basic science in general, to communicate the excitement of our research, the importance of our research, and the relevance of our research, to as broad an audience as possible.

There is a tendency for many working scientists to isolate themselves from the public, to hide behind the doors of academia and to use the walls of their universities as ivory towers to protect themselves from the probing questions and demands of the outside world. I don't argue that this isn't an efficient way to get science done. But such isolation has a cost in that it contributes to an increasing gulf in understanding between those of us who do science and the rest of society who not only use the results of science in their daily lives, but who also determine the position of science in society.

We are gathered here together at the last ISBE meeting before the new millennium. Twenty-five years ago, the Nobel Prize was

awarded to three pioneering behavioral ecologists, Konrad Lorenz, Niko Tinbergen, and Karl von Frisch. Since that early beginning, our field has grown and matured tremendously. Today, the state of our discipline is stronger than ever. These meetings reflect that strength. Many of you have commented positively on both the diversity of the topics of the paper and poster sessions and on the high quality of the individual contributions.

But this is also a time when governments around the globe are re-assessing their science policies and re-evaluating whether science should continue to be supported through public funds. If the answer is affirmative, what types of science are to be funded, and at what monetary levels? We find, more than ever, that the value of basic science is being challenged and that scientific priorities are becoming defined in terms of short-term economic gains.

My argument today is that it is essential for practicing scientists to become more actively involved in the public dialog about science. If we isolate ourselves in our laboratories, in our classrooms, or at our field sites, then scientific policy decisions will be made by persons who are illiterate about science; they will be made in the absence of adequate and appropriate input and expertise.

As one indication of just how wide the gulf has become between the policy-makers and the actual practitioners of science in the United States, it was recently reported that only 20 of the 435 members of the House of Representatives have a science or engineering background; of the 100 members of the U.S. Senate, there are only two

individuals with such scientific training; and there are none in the President's Cabinet (Augustine, N. 1998 *Science* 279: 1640-1641). The same issue of *Science* magazine that provided this information recounted a story of an administrator from the U. S. National Aeronautics and Space Administration being questioned on the need for continued funding for meteorological satellites since we already have a national weather channel on television that provides such information! (Augustine, 1998, *ibid.*)

If we are going to reverse this pattern of ignorance about what science is and how science is done - and if we truly believe that basic science provides the critical ideas upon which much of applied science and technology are based, then we, ourselves, must become more actively involved in the process of communicating that message. We need not abandon our primary mission of doing science, but we must also seek out opportunities to communicate what we do and why we do it whenever possible.

As behavioral ecologists, we are in particularly good positions to enter the public dialog on science. There are two reasons why this is true. First, the questions we ask and the organisms we study are of inherent interest to the public. The popularity of the "Discovery" channel and other nature-oriented programming on television attests to the public's interest in our subject matter. In North America alone, 63 million people claim an interest in watching wildlife (1996 National Survey of Fishing, Hunting, and Wildlife-associated Recreation, U. S. Fish and Wildlife Service publication). People have a craving to learn more about *what* animals do, and *why* they do it - in essence, they are interested in the decision rules that govern animal behavior.

And who is better qualified to explain such topics, and to generate enthusiasm and excitement while doing so, than the persons actually performing such research - namely, ourselves?

The second reason why we behavioral ecologists are particularly well-suited to bridge the information gulf that exists between scientists and the public is that the answers that we discover to our research questions are frequently of considerable importance for understanding what I refer to as the human condition. To the degree that decision rules that unconsciously influence our own behavior have been shaped by natural selection operating during our ancestral past, then many of the predictive models that we develop for understanding non-human species will be relevant and applicable to certain questions regarding our own species. In essence, the study of behavioral ecology provides us with an evolutionary "window" through which we can better view and understand ourselves.

My message today, then, is one of *involvement*: to encourage us not only to vigorously pursue our science, but also to share our excitement with non-scientists, to explain our discoveries to the public, and to pursue the practical implications of our discoveries with policy-makers.

I personally have been involved in three areas of basic research that turned out to have practical applications. These involved studies of (1) the orientational cues used by migrating birds, which led to the development of meteorological algorithms for predicting the volume of migrants aloft and thereby for minimizing the occurrence of, and damage resulting from, bird-aircraft collisions (Richardson 1974); (2) the importance of resource

distributions in shaping the social organization of animal societies, which contributed to the development of required "social soundness analyses" of the impacts of proposed development schemes on the social organization of the recipient peoples by organizations such as the Agency for International Development (Emlen 1976, 1980); and (3) the effects of genetic kinship and social dominance upon cooperation and conflict in animals that live in family-based societies, which is suggesting new, biologically-based solutions for reducing human family violence and dysfunction (Emlen 1997).

In none of these studies did I start out with the intention of finding solutions to applied problems. But the line between basic and applied science is often blurred, and results often have unexpected implications. To paraphrase the well-known movie character, Forrest Gump: "Relevance happens".

I suggest that the relevance of our work is often greater than we are willing to recognize. The reason, as discussed previously, is that we study *why* animals behave the way we do (in an adaptive sense), and *how* their evolved decision rules cause them to do so (in a mechanistic sense). This, in turn, allows us to predict how animals will behave under a variety of conditions. If our findings are sufficiently robust to be generalizable across different taxa, then it is inevitable that many will be found to be applicable to humans as well. Being relevant is not a bad thing. It means that we can contribute to the public dialog on science at many different levels.

Theoretical and empirical advances in behavioral ecology have in the past, and will continue in the future, to advance our

understanding of the human condition. We should recognize and embrace the relevance of what we do, and make its importance known to others. If we each accept an increased responsibility to communicate our findings beyond our immediate audience of peers, to the public, we can narrow the information gulf that currently separates scientist from non-scientist. We owe it to our discipline, as well as to basic science in general, to do no less.

Stephen T. Emlen

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ISBE98: Handicaps at the Meeting

Judging by the audience-to-seat ratio, Tom Getty's talk "Why the handicap principle is superfluous" had to be the best attended talk of the Monterey meeting. Nothing pulls them in like a crafty title, and the promise of a happy ending featuring the victorious butt-whipping of a reviled villainous notion. Definition is communication's thankless

chore. Getty played down his title, to apparent audience disappointment, by cautiously defining "superfluous". The handicap business have always suffered severely from imprecise definition (alternate view - has long thrived on it). Getty's definition of "handicap" required that, at equilibrium, signallers who use signals of increasing magnitude suffer increasingly large costs. A bigger handicap weight should be of greater impediment to a fast horse than a smaller one was to a slow horse.

Getty split with Grafen by allowing males of higher quality to gain more when females estimate their quality to be marginally higher. Under this assumption signallers of higher quality do not have to pay more for their signals than low-quality signallers at equilibrium. Handicaps are then not necessary for stable signalling. The audience reaction was most enthusiastic.

The same cannot be said of the reaction to Seth Bullock's preceding talk. This is interesting, because Bullock reached much the same conclusions as Getty, from similar assumptions, the major differences being that 1) Bullock is pro-handicap 2) with a more liberal definition of "handicap". Bullock calculated the parameter space within which communication was evolutionary stable, and used a simulation to show that honesty was less likely to evolve near its boundaries, where honest signals would be quieter. His definition of "handicap" (signals stabilised by their inherent costs) was quite mainstream. Getty called this redefining handicap so that it works, and so it may be.

The difference is between a signal which is 1) costly to amplify and too costly to exaggerate and 2) one which is that plus for which individuals

with larger ones must have paid more. Subtle. I suspect most tofu-and-potatoes field biologists would have no qualms about applying the term "handicap" to the former alone. An alternative to renaming such things "inherent cost of production stabilised signals" is to clearly define several sub-types of handicaps.

At the same meeting Pete Hurd presented a simple taxonomy of signals based upon the source of stabilising costs. He identified three types of handicaps (strong, weak and interaction), along with a clear definition of conventional, and other, signals. Hurd tied signal form to model form, and blamed the unhealthy fixation on handicapping signals upon the near universal use of action-response games (which are constrained to produce handicaps of one sort or another).

The definition of "handicap", and the status of signalling models in general rest upon a neat separation of costs and benefits. This conflict with natural history realities, particularly if the signal also serves a direct function, as was pointed out at Asilomar by Arnon Lotem, Richard Wagner and Sigal Balshine-Earn, "The overlooked signalling component in non-signalling behavior". A behaviour of direct use may be subtly, yet significantly, bent to a signalling purpose. Attention to quantitative variation in kin care, begging, predator avoidance, and other behaviours may demonstrate a partial communication function, Lotem believes.

Peter L. Hurd
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ISBE98: 7 Was a Lucky Number

The International Society for Behavioral Ecology is thriving. Its 7th Congress, which took place recently (27 July-1 August) at the spectacular Asilomar Conference Center near Monterey California, was attended by 600+ people and featured 474 talks and posters. A look at the taxa and topics presented yields a snapshot of behavioral ecology today. The evolution of the field can be seen by comparing proceedings of this Congress with those of previous years. Mart Gross (1994, *TREE* 9: 358-360) conducted such analyses for the first five ISBE Congresses (1986-94). I extended Gross's longitudinal comparison, using his definitions of subject areas for continuity.

At Asilomar, subject areas ranked as follows: (1) reproductive strategies (32% of all talks and posters), (2) social behavior (22%), (3) mechanisms (16%), (4) population biology (11%), (5) survival strategies (9%) (6) life history (6%), and (7) applied topics (4%). The relative importance of (1) and (2) are not surprising. Reproductive strategies (including research on mating systems, sexual selection, and parental care) have perennially ranked first, accounting for 30-35% of presentations at every ISBE Congress. At Asilomar, many presentations contrasted species' social and genetic mating systems, using molecular techniques to infer relatedness and gain deeper insights into mechanisms of female mate choice. The number two topic was social behavior (including kinship, cooperation, aggression, dominance, and communication), with a similar proportion of presentations as in 1994 (19%). This year the area was represented especially by models of conflict and cooperation and reproductive

partitioning (skew) in groups, and quantitative tests of such models.

Undoubtedly the biggest change since four years ago was a jump in research on behavioral mechanisms, from sixth place (5% of presentations) in 1994 to third (16%) in 1998. Mechanisms includes learning and memory, hormones, genetics, chemical and other signals, and methods for assessment. At Asilomar, the shift in this direction was manifested by presentations on mechanisms of signalling, recognition, parasitism, and sperm competition, cognitive ecology, adaptive energetic allocation and, especially, the interplay between hormones and the immune system. Increasing interest in mechanisms of behavior also is evident in the latest (4th) edition of *Behavioural Ecology* (J. R. Krebs and N. B. Davies, eds., Blackwell, 1997).

The other four topical areas - survival strategies, population biology, life history, and applied subjects - ranked similarly relative to each other at Asilomar as they had in 1994 and previously, but there were relatively fewer presentations in each area. Declines were especially noticeable in the proportion of talks and posters on survival strategies (including foraging, predator-prey relationships, exploitation and parasitism, and territoriality), which dropped from 23% in 1986 (2nd) to 16% in 1994 (3rd) and to 9% in 1998 (5th), and life histories (including sex allocation, reproductive effort tradeoffs, developmental trajectories, fecundity, and lifespan), which declined from 11% in 1994 (3rd) to 6% in 1998 (6th).

What organisms do behavioral ecologists study? At Asilomar, the majority of presentations (70%) were about vertebrates. Relative rankings

by specific taxa were: (1) birds (34%), (2) mammals (21%), (3) insects (15%), (4) fishes (11%), (5) herps (4%), (6-8) spiders, crustacea, and "other" (3% each); the remaining 6% were purely theoretical. A perusal of programs from previous ISBE Congresses indicate a perennial focus on vertebrates (especially birds and mammals), but Gross (1994) did not make quantitative taxonomic comparisons.

A striking aspect of the Asilomar program was that although only 4% of presentations were on applied topics (including conservation, animal welfare, and studies of humans), two of the three Plenary lectures (John Crook and Paul Sherman) and Stephen Emlen's Presidential Address fit into this category. Crook discussed the behavioral ecology of polyandry among agriculturalists in high Himalayan valleys and the stresses young women endure when they marry groups of men. Knowledge of the costs and benefits of polyandry enabled him to interpret the various mechanisms wives and their communities use to deal with such mental trauma. Emlen argued that behavioral ecology research is relevant to solving real world problems, and that behavioral ecologists are responsible for applying our knowledge in the public arena. As examples he discussed how understanding the navigational aids used by migrating birds enables controllers to predict peak migrations and divert commercial flights, how changes in patterns of land ownership may destabilize the structure of a resource-based African society, and how dysfunction in step-families is a predictable outcome of associated asymmetries in kinship.

My own talk was meant to illustrate how cost/benefit analyses are helping resolve a

management dilemma. I investigated the circumstances under which more than one female wood duck lays eggs in the same nest. I found that "parasitism" actually is a manifestation of competition for safe, well-hidden nesting cavities, which females locate by returning to their own (natal) cavity or by following a conspecific home. When boxes are erected in clusters in the open (a standard management practice), cavity-finding becomes so easy that "dump nesting" (16-70 eggs/clutch) occurs. Super-normal clutches seldom are properly incubated, so individual reproductive success and population productivity decline. A possible solution is to return the birds to more normal nesting densities and circumstances by hiding boxes in the woods. I've done it at three study sites, and it always works! Apparently the costs of cavity-finding are reestablished, resulting in decreases in clutch sizes, increases in egg hatchability, and population stabilization.

These three "non-traditional" lectures had several common themes. First, the line between basic and applied research in behavioral ecology is blurry. Second, insights gained from basic research in behavioral ecology can help in solving real world problems that involve the behavior of animals, including humans. Third, social and wildlife management programs must be developed in light of, rather than in spite of, each organisms' natural history and behavioral ecology. Finally, because findings of behavioral ecologists are readily comprehensible and interesting to the lay public (unlike some other biological disciplines), we have a unique opportunity to communicate insights gained by applying natural selection theory to study behavior in relation to ecology and to use those insights to help develop conservation strategies and

social policies. Actually, these four explicit "take home" messages were implicit in many of the presentations at Asilomar. Therefore I am optimistic that public knowledge about and perception of the value of behavioral ecology will increase in the 21st century. I think 7 was a lucky number for ISBE!

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ISBE98: A Scandinavian View

The 7th biannual Behavioral Ecology Conference was organized by Walt Koenig, Janis Dickinson and Joey Haydock at the Asilomar Conference Center, in Pacific Grove from 27 July to 1 August 1998. About 600 delegates participated in this meeting in the beautiful area of Monterey Bay and its natural treasures. It is almost impossible to make a complete summary of such a diverse meeting with so many parallel sessions. In fact, there were 4×10^{51} possible conference experiences from the number of ways one could combine the talks. This note reflects our personal views on where our field is going, and we are well aware of the fact that other delegates may disagree with us.

When we interviewed individual delegates about what they thought was the main new subject at this meeting, almost every one said: "immuno-competence". Indeed, there were two complete sessions devoted to talks about the relationships between immuno-competence, mating behaviour and honest signaling. The popularity of this subject has its roots in the hypothesis by Folstad & Karter

(1992) who suggested that costly secondary sexual traits that are testosterone-mediated, are held in balance (that is, kept honest) by the fact that testosterone also suppresses immune function (or at least is assumed to do so). Many behavioural ecologists interested in the honesty of secondary sexual traits, were soon attracted to this elegant idea. Folstad & Karter saw their hypothesis as a proximate extension of earlier models dealing with parasite-mediated sexual selection (Hamilton & Zuk 1982) and honest signaling (Grafen 1990). Within a few years, Folstad & Karter (1992) became one of the most cited papers in behavioral ecology and started a bandwagon: everybody now "knew" that there was a trade-off between secondary sexual traits, testosterone and immunocompetence. The only problem was... to demonstrate it. Interestingly, not a single rigorous study published to date from any natural population has convincingly provided support for this idea. The reason could be a lack of knowledge about immunology among behavioral ecologists, and/or a lack of interest in behavioral ecology among immunologists.

Ultimately, however, all models must be confronted with reality, and the result of this has mainly been bad news for the Immunocompetence Handicap Hypothesis (ICH). Two talks presented negative evidence, that is, absence of significant relationships between natural and/or experimentally elevated testosterone levels in red-winged blackbirds (Dennis Hasselquist et al.) and capybaras (Emilio Herrera and Carolina Galindez). Furthermore, Tim Birkhead found no significant relationships between experimentally manipulated body condition, secondary sexual traits and humoral immunocompetence in laboratory studies

of zebra finches. The enthusiasm for the ICH among these contributors was not overwhelming. David Westneat and Tim Birkhead also discussed some alternative hypotheses for the links between the immune system and mate choice. They pointed out the methodological difficulties in testing the ICH, its internal inconsistencies, and the fact that the trade-offs may be based on energy or nutrient limitation or autoimmunity risks, all of which give rise to different predictions in empirical tests. It now seems obvious that there is a long way to go before the role of the immune system in sexual selection is clarified. Investigators in this field should prepare themselves to cooperate with medical immunologists and not expect to get any clearcut results on a short time-scale, neither in the field nor in the laboratory. If immunopathology/autoimmunity is important, as Westneat suggests, it will become even more difficult and this field may therefore evolve into a new branch of ecophysiology. ICH, in its original form at least, does therefore seem to be in bad shape at the moment. A lesson from this story could perhaps be that our enthusiasm for physiological mechanisms should be balanced with a more critical attitude, especially against mechanistic models that are built upon weak inferences from other fields.

Another field that currently seems to be very active is the study of sperm competition in insects. Several technically sophisticated studies were presented during the conference in which the workers had used advanced histological and physiological methods to describe and characterize the structure of sperm tubuli and other aspects of the female reproductive tract, as well as sperm morphology. Workers are now discussing various mechanistic models for sperm displacement and

sperm removal. As outsiders of this culture, we found these talks fascinating but difficult to follow, and we got the impression that this field may soon also evolve into a discipline of its own. After the heyday of the "adaptationist programme", physiological mechanisms seems to be the new dogma of behavioral ecology.

Sexual selection continues to be one of the core areas in behavioral ecology, and in particular the underlying causes of the evolution of female mate preferences is far from solved. The Fisherman school that has had many supporters in the past seems now to have lost most of its territory to the proponents of "good genes"-models. In particular, the Hamilton and Zuk - model has been popular since it provides a solution to the problem of maintenance of high levels of additive genetic variation in secondary sexual traits (see also section about Westneat's talk above). By choosing males with extravagant traits, it has been suggested that females will obtain good genes that enhance offspring survival through e. g. increased resistance towards diseases and parasites. In spite of the extreme (uncritical?) popularity of this idea among behavioral ecologists, there are few studies that have shown any convincing evidence for this process in natural populations. Moreover, the Hamilton and Zuk - model may actually be superfluous for its original purpose (that is, to explain how additive genetic variance is maintained in spite of selection); many population geneticists argue that for condition-dependent secondary sexual traits the levels of mutational input is sufficiently high to maintain the genetic variation (Rowe and Houle 1996).

A further complication for both the Hamilton and Zuk-model and for good genes

models in general, is the findings by several workers that there may be significant costs to female mate choice and participation in multiple matings. Three talks presented evidence for such costs. Simon Griffith and coworkers presented evidence from an insular island population of house sparrows that males with large badges feed their offspring less often than small-badged males and that the offspring of the former had lower recruitment success to the breeding population. Andy Cockburn and coworkers showed that illegitimate offspring in superb fairy wrens did not have higher survival rates than legitimate ones, and illegitimate daughters could actually have lower survivorship than legitimate daughters. Among sons the pattern was more complicated; data indicated a higher variance in the reproductive success of illegitimate sons than of legitimate ones, suggesting an opportunity for selection on offspring variance rather than the mean. Finally, Brett Holland and William Rice showed that experimentally enforced monogamy in fruit flies reversed the well-known antagonistic co-evolution observed in previous studies of this species. After 38 generations of selection, the sexes had evolved more mutualistic relationships and female survival rates were enhanced, compared to the polygynous situation when she mates with several males. Although none of these three studies provide any evidence against good genes, they complicate the issue somewhat, by suggesting that fitness costs to females could restrain the sexual selection process, and they point to some interesting possibilities for future investigations.

There were several sessions on signaling and communication, including talks on the handicap hypothesis. Two different theoretical analyses (Seth

Bullock, and Thomas Getty) showed that costly signals may evolve under a broader range of conditions that was previously thought. The provocative title "Why the handicap principle is superfluous" of Thomas Getty's talk turned out to be a question of semantics. Getty was the advocate of the sports-oriented definition as it is used in horse racing and golf. Here, handicapping equalizes the differences between individual players or horses. Most of us however, would probably stick to a more relaxed definition where a handicap is a trait that in some way impair the fitness of its carrier. The perhaps most refreshing talk of the conference was given by John McNamara (coauthored by C. Gasson & A. I. Houston). He showed that when individuals need to negotiate on a level of cooperation, the ESS will be a negotiation rule, not a cooperation level rule. Workers have traditionally stuck to the latter, but the former approach will not yield the same result. The implications are that all negotiation games, such as parental effort negotiations, parent-offspring conflicts, etc... will have to be reanalyzed.

In summary, the conference participants displayed the great variety of the present status of behavioural ecology. It is fascinating to be part of this diverse and dynamic field. It will be very interesting to see where the field has moved at the next meeting, which will be held in Zürich, Switzerland in two years.

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Book Reviews

Partnerships in Birds: The Study of Monogamy. Edited by Black, J.M. 1996. Oxford University Press, 420 pp. \$55 paper, \$125 hardbound @amazon.com; £27.50 and £62.95@nhbs.com

When Emlen and Oring presented an ecological classification of mating systems in 1977, they distinguished four types and two sub-types of polygyny and two types of polyandry. Monogamy, by contrast, was classed as a monolithic entity, favored by synergistic fitness benefits from biparental care, and, in a few long-lived birds, increases in such benefits with the duration of a partnership. In subsequent papers, Wittenberger (e.g. Wittenberger and Tilson, 1980) distinguished several ecologically distinct types of monogamy, and a symposium in 1984 entitled "Avian Monogamy: the Neglected Mating System" (Gowaty and Mock, 1985) further stimulated theory and empirical studies in birds. However, 1987 was a pivotal year for this field, when twin papers in *Nature* showed surprisingly high levels of multiple paternity in socially monogamous House Sparrows. Suddenly, the reproductive opportunity costs incurred by providing parental care, and of prolonged association with a single mate, seemed even greater than previously thought. This emphasized the need to measure the offsetting benefits, or identify other contingencies, that stabilized the interactions that result in "pairs". In the aptly titled "Partnerships in Birds", Jeff Black has brought together contributions by 43 authors

that cover much of the data obtained and theory developed since that year, and take the field a step further along. The book, and specific chapters in it, offer novel perspectives that will be widely cited in future research.

"Partnerships in Birds" consists of three broad theoretical introductory chapters, 14 accounts from long-term "case studies" of species or small groups of related species, and two summary chapters. The case studies are loosely grouped into species with "continuous partnerships" meaning year-round associations and those with "part-time" partnerships, being the breeding season only. Editor Black challenged the authors of these chapters to address four common questions: (1) what factors influence the probability of repairing (or remaining paired) from season to season; (2) is seasonal (or lifetime) reproductive success affected by repairing; (3) do the effects of repairing change with the duration of an association, and (4) what affects the probability of being paired with a "preferred" mate? Most of the authors provide information on most of these points. The introductory and summary chapters utilize the results of the case studies, and interactive discussion among the summary chapters themselves gives the book much more the feeling of a coherent research enterprise than the hodge-podge of chapters often found in comparable compendia.

Mock, Schwagmeyer, and Parker's introductory chapter is a lively, if conventional, recapitulation of issues in family values: male-female, parent-offspring, and sib-sib. (My feeling of familiarity with their thinking may arise because Doug Mock, as a graduate student, taught the first

ethology class I took.) Mock et al. largely avoid the extra-pair paternity issue, and concentrate instead on the intrinsic complexities of even the simplest idealized “model family”. The authors stress the heuristic value and predictive value of modeling questions in each of the three dimensions considered, and present useful versions of such models as simply as possible.

Patty Gowaty’s introductory chapter “Battles of the Sexes and the Origins of Monogamy” presents, characteristically, the most novel views in the book. First, she decomposes questions about the maintenance of “monogamy” into a set of simpler questions, and shows that most theories address the question of “why do males stay” rather than “why one male”, “why one female”, or other questions. She then develops a model to account for variation in rates of extra-pair mating behavior, flowing from the general mating systems dogma that resource distribution predicts female behavior, from which male behavior largely follows.

Starting with the assumption that selection favors females who obtain “good genes” from males for their offspring, Gowaty considers the range of potential impediments to their doing so, under the rubric of the “Constrained Female Hypothesis”. In this model, females are predicted to be genetically monogamous in two entirely different situations: (1) when their mate choice is totally unconstrained (e.g. as in an idealized lekking species) and they can thus readily obtain “good genes” from a preferred male, or (2) when female reproductive potential is highly controlled by males by coercion, or if female extra-pair mating behavior is completely constrained because males provide essential support that females cannot risk losing.

Mixed paternity is predicted to occur when females have partially constrained choice. The level of a female’s control of her own reproductive potential— total for (1); none for (2) — thus becomes the focal variable of interest in accounting for the level of mixed paternity. Females of different social or genetic “quality”, and/or those in richer or poorer environments, will also differ in their level of control, ability or need to resist male control, the potential costs of male retaliation, and thus in their opportunities to pursue “good genes”.

The model can be considered, and tested, at both intra- and interspecific levels. In addition to presenting their own view of the social and ecological correlates of genetic monogamy, Anders Møller and Tim Birkhead do some preliminary interspecific tests of predictions from Gowaty’s model in their summary chapter, with supporting results. The greatest weakness in this entire area of sexual selection, remains, in my opinion, quantifying the strength of indirect benefits, that is, quantifying the degree to which, or situations in which, a female’s offspring benefit from her mate choice.

The case studies of this book, by contrast, concentrate on the more readily measured direct benefits favoring social monogamy, as largely summarized by Black’s four questions. The 14 case studies chapters are sharply focused on their species or groups, as evidenced by their first lines: “The mallard-size Blue Duck”, “Barnacle Geese”, “Of the three swan species that occur in Britain”, “Two New World Jays”, “Splendid Fairy-wrens”, “The Blackbird”, “Ptarmigan”, “Cassin’s Auklets”, “Short-tailed Shearwaters”, “The Great Tit”, “The Sparrowhawk”, “Penguins”, “The Red-billed Gull”, and finally, “In late spring and through the summer,

the song of the Indigo Bunting". These chapters appropriately minimize recapitulation of general issues, preventing redundancy that readers would encounter had they been published as 14 separate papers, an efficiency that is one argument in favor of producing specialized compendia such as this book. The case study authors do present their favorite hypotheses in their discussions, and, predictably, there is a diversity of opinion with respect to the applicability, for particular species, of the leading general hypotheses for the maintenance of social monogamy for in birds.

I have two general caveats on the data chapters. First, most authors take a multivariate approach to disentangling the potentially independent effects of "age" versus "pair bond duration" on annual reproductive performance, attempting to demonstrate a genuine pair bond effect. Many find significant effects. However, the data matrices these analyses are based on are systematically incomplete, since birds of age 'n' can only have been paired for 'n-1' or fewer years. One can avoid potentially misleading results in such cases by doing the analyses age by age, as was done in at least two chapters, or by restricting the analyses to a saturated rectangle of ages x duration, in which case the analysis applies only to those ranges of pairs. Other approaches to demonstrating the advantages of continuing associations are possible, such as comparing success in the last year of a long-term pair bond with the first year of a newly established one, but these comparisons have other difficulties, such as the non-comparability of partners ages in such situations. Bruno Ens, Sharmilla Choudhury, and Black present a balanced discussion of the value and limitations of these and other analyses in their

thoughtful summary chapter, "Mate fidelity and divorce in monogamous birds", which focuses on answering Black's questions and draws heavily on the book's case studies. Despite the statistical and theoretical caveats mentioned above, we can make a far stronger case for genuine positive fitness effects of maintaining pair bonds than was possible twenty years ago.

My second, more conceptual caveat, is that no study in the book tests for a relationship between pair-bond duration and individual (or mate's) survivorship. The analyses are restricted to fecundity components of fitness. Marzluff et al.'s analysis of life-span of Pinion Jays as a function of mate's body size, based on previously published work, is the sole exception. Amidst 15 plots of relative annual reproductive performance as a function of pair bond duration, there is none of annual survivorship as a function of same, or even simple tabulations of the probability of an individual surviving or returning with respect to maintenance or establishment of a new pair bond the previous season. Might we expect to find more significant effects of pair-bond breakage on survivorship among species with continuous pair bonds than those with part-time partnerships? A potential survivorship consequence of breaking a partnership was apparently overlooked, even by the deep-thinking Bruno Ens et al., except as a passing reference to its inclusion as a potential cost in a model by McNamara and Forslund (1996). That model, unpublished when the book went to press, suggests that substantial mortality costs of pair bond breakage would affect divorce decisions more strongly in long- than short-lived species. The omission of this question does not reflect a lack of data, but may result from the authors' emphasis on

the causes of divorce, since such analyses consider only cases of pair breakage when both partners survived.

Hypothetically, the constraints of maintaining a pair bond might shorten life times, in which case currently unrecognized fitness tradeoffs should be added to the cost-benefit calculation. Many waterfowl species pair during the winter, but do so late in the season, suggesting that maintaining a pair prior to that time has no net benefit for some party, despite strong competition for mates at the same sites a few months later. On the other hand, as insurance companies know, married human men (at least), live longer than unmarried men (controlling for age). Extrapolating across taxa, adding in effects of pair maintenance on survivorship would likely increase the lifetime fitness benefits of social monogamy for many of the species considered.

Topical collections such as this are expensive, but in this case, the editors and authors were sufficiently cooperative to produce a coherent message, one that strikes a balance between recognizing the diversity of life, yet seeking the general explanations for such patterns as may be recognized within it. References are conveniently included after each paper, rather than being compiled in a single list, a luxury justifiable in part because of the minimal overlap among the case studies. A second luxury are 19 well-informed and executed species illustrations, by Mark Hulme, placed at the start of each chapter. It also is nice to see that Oxford University Press has relaxed the previously uniform cover style of its Ornithology Series.

Together, the chapters illustrate the power of complimentary approaches— deductive and

empirical, intraspecific and comparative— towards improving our understanding of complex problems. Finally, however, as Ens et al. stress, in this field as in others, experiments are needed to strengthen conclusions based on inference.

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Behavior and Ecology of the Northern Fur Seal. R.L. Gentry. Princeton University Press, Princeton, New Jersey. 392 pp.

Behavioral ecology would be incomplete without the monograph. Such works have been central to the development of the field because the complex sets of interactions that determine fitness are often difficult to distill into highly focussed scientific papers. They also represent a corpus of work from a single individual or a research group that connects many disparate pieces of information into a cohesive whole. Roger Gentry's monograph on northern fur seals is one such book; the culmination of one man's vision of a holistic view of the

behavioral ecology of one of the most scientifically significant large mammal species.

It is probably true that some of the greatest insights about the physiology, behaviour and autecology of species can be found in those examples that inhabit extreme environments. As air-breathing endotherms, marine mammals certainly occupy a challenging environment. Maintaining heat balance in cold, polar seas might require high metabolic rates but paradoxically these animals are faced with feeding in what is to them an anoxic environment in which they mainly use aerobic metabolism. Such physiological challenges limit the degree to which marine mammals can exploit their environment but are met with a range of novel anatomical, physiological and behavioral adaptations. Although many of the fundamental features of marine mammal anatomy and physiology are well understood as they related to the challenges presented by a marine existence, there is a less complete view of how behavior and social structure relate to these challenges.

Over a period of almost 20 years, Gentry and colleagues (some of whom have co-authored chapters within the book) examined the detailed behavior of northern fur seals mainly on the Pribilof Islands in the Eastern Bering Sea. This study was stimulated both by the fundamental interest there was in examining the breeding and foraging behavior of a marine mammal and by the pressing need to understand the ecology of a species that was the subject of commercial exploitation. After the cessation of exploitation, the study evolved into an examination of a critical component species within the rich marine ecosystem of the Bering Sea.

The book is presented in five parts. Part one provides the background to the work including

general information about pinniped mating systems, behaviour and distributions and then more specific information about the population dynamics of northern fur seals throughout the period covered by the studies in this book. It also shows the phenology of the annual cycle in the species which is essential to understanding subsequently experimental studies described in the book. Part two deals with mating behavior. Like much of the book, it shows an experimental approach to examining the processes governing the observed patterns of behavior. For example, removal experiments showed that males had high fidelity to particular territories on the breeding beaches. Studies of both male and female behavior suggest that the concept of males holding harems does not apply but nor does that of the lek. Males control access to a female resource in the form of sites for parturition.

Part three investigates the detailed processes that are necessary to maintain the mating system. This includes site fidelity in adults and philopatry, both of which are present in both sexes. The fabric of the mating system appears to depend upon long-term associations of individuals with particular sites and, even amongst males, many years may be spent during the breeding season in the vicinity of territories before a territory is eventually gained. We are presented with the intriguing possibility that male dominance is already well established years in advance of territory tenure. Part four deals with maternal strategies. Amongst otariid pinnipeds like northern fur seals, food is located at distances of up to several hundred kilometres from the pup. Mothers must alternate foraging at sea for several days with periods spent attending and feeding the pup. The

book explores how this behavior is influenced by temporal and spatial variability in environmental conditions and also how this ultimately affects offspring growth.

The final part of the book addresses explicitly some of the applied questions that first stimulated the study. In many cases clear answers are given based on the research but in others the author is less sure. Recommendations for management are provided. This section also provides a synthesis which highlights the close interaction between the behavior of these animals, especially adult females feeding pups, and local to large-scale environmental processes. It also identifies many intriguing and, as yet, unanswered questions. For example, why do males appear not to compete openly for territories on the breeding grounds?

This book contains a wealth of information presented in a clear and concise style. It should be essential reading for all researchers in marine mammalogy and it will also provide important information for those studying mammalian behavioral ecology and marine ecology. As is inevitable with any study lasting 20 years, many of the ideas and results presented in the book seem to have been around for a long time. Often spoken of at informal meetings, they had become part of the folklore of pinniped biology. Now that they have been set down formally they have attained their rightful and lasting place within the scientific literature.

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The Ecology of Migrant Birds. A Neotropical Perspective. J.H. Rappole. 1995. Smithsonian Institution Press, Washington, D.C. 269 pp., 18 figures, 27 tables, 5 appendices. ISBN 1-56098-514-3. Cloth, US\$35.00.

Over 50% of the species that breed in North America spend the winter months south of the Tropic of Cancer. The prevalence of migratory behaviour in the North American avifauna has inspired a massive body of research. Rappole's effort represents a synthesis of work to date and is an update of the 1993 U.S. Fish and Wildlife Service publication, *Nearctic Avian Migrants in the Neotropics*, authored by Rappole, Gene Morton, Tom Lovejoy and Jim Ruos. The book is divided into 9 chapters and 5 appendices, each designed to give the reader a feel for the complexity of migration and migratory behaviour.

In the introductory chapter, Rappole attempts to prepare the reader for obvious biases that appear throughout the book (e.g. towards passerines, towards winter ecology). However, even with his caveat, the book displays a disheartening bias towards eastern North American passerines and, perhaps more telling, eastern research and conservation organizations. In addition, while reading this book, it is important to remember that there has been significant research progress since 1995 in the areas of migration and migratory behaviour.

Chapters 2 and 3 focus on habitat and resource use by Neotropical migrants during the winter. On the wintering grounds, migrants are not under any serious reproductive constraint. This

freedom from reproduction appears to result in a degree of behavioural plasticity not observed on the breeding grounds. The amount of plasticity is influenced by a variety of factors (e.g. season, body condition) and makes it very difficult to accurately determine habitat and resource needs. The main conclusion of this chapter is that the traditional approach of treating Nearctic-Neotropical migrant species as a group may be misguided. The diversity of habitat and resource use patterns and behaviours is such that an "individual species approach" is likely to bear more fruit.

Despite the author's recognition of the ecological diversity of migrants, a disproportionate amount of time is spent on migrant use of forested habitats. This is in direct contrast to the author's conjecture that "less than one-third of all migrants use forests during the nonbreeding season". Further, very little time is spent discussing actual habitat use; most of the chapter focuses on habitat use hypotheses. Perhaps the most useful discussion in this section is on intraspecific territoriality of migrants on the wintering grounds. Individual species show an array of behavioural responses often dependent on resource and habitat availability; a species that is intraspecifically territorial in one habitat may join mixed-species flocks in another. An understanding of the social dynamics of long-distance migrants is currently lacking for most species and is a key component of any conservation strategy.

Chapters 4 and 5 are the strongest chapters in the book. Possibly the single most important line of migrant research in either the Old or New World is to understand the migrant's role in tropical communities. In Chapter 4, the author discusses the

existing paradigm that migrants are "nomadic ecological generalists". In his exploration of six ideas that support the paradigm, Rappole makes it clear that many, if not most, Neotropical migrants do not fit the mold. We are again faced with the conclusion that the behaviour of migrant birds needs to be explored on an individual rather than group basis.

The general conclusion of Chapter 5, a study of migration, is that while researchers have thoroughly studied navigation, orientation, and the physiology of migration, the exploration of how they relate to what an individual bird is doing during migration has fallen behind. Migratory behaviour is intensely variable and can depend on both the sex and age of an individual as well as the natural and genetic selective forces acting on a given species. Perhaps the most glaring gap in our knowledge of migration is an understanding of stopover behaviour and ecology. These areas are pivotal from both a conservation and ecological perspective.

If migratory behaviour is as variable as research to date would indicate than the evolution of migration is likely equally complex. In Chapter 6, Rappole details the following explanations for the evolution of migration: ancient environmental changes, availability of resources elsewhere, proximate factors (eg. photoperiod), climatic changes, seasonal use of nectar or fruit resources, seasonality and interspecific competition, seasonal change and dominance interactions and Baker's migration threshold hypothesis. Not surprisingly, no one of these explanations covers all migrants. Rappole proposes a ninth hypothesis that migration arises from intense interspecific competition for breeding sites.

Chapter 7 compares and contrasts Old World and New World migration systems and attempts to capitalize on good research on both sides. The author acknowledges that much more is known about Old World migration systems but recognizes that the Palearctic-African migration system is very different from Asian and Neotropic systems. Rappole states that viewing migration as a filtration process may allow for generalization across systems. The primary filter is the material available for natural selection to act upon, a second filter is the heterogeneity of subtropical habitats available as stepping stones, a third filter is the heterogeneity of temperate habitats available, and a fourth filter may be the existence of isolated breeding and wintering sites that could engender rapid speciation.

Much of the recent focus on Neotropical migrants has been the result of reports that breeding populations of many of these species are declining rapidly. Chapter 9 deals with ways such population declines are diagnosed (eg. North American Breeding Bird Survey), potential causes for these declines and reasons why migrants may be more vulnerable than non-migrants. Rappole provides a list of flaws inherent in many commonly-used census methods that highlights the lack of basic behavioural and natural history information (eg. singing behaviour of unmated or immature males) crucial to the understanding of population structure and change. Despite these flaws, Rappole feels that detailed investigations can highlight where in the annual cycle migrant populations are being limited. Unfortunately, this chapter was very unbalanced, paying short shrift to a very large body of literature that exists on

migrant population change and virtually ignoring western North American migrants.

The final chapter focuses on conservation issues facing Neotropical migrants on the wintering grounds. Rappole recognizes that the conservation of migratory birds may not be the first priority for most of the human population living in the Neotropics and offers a variety of research and education goals centred on increasing involvement on a local scale. To further these goals, this book has also been published in Spanish.

Despite the biases outlined, this book is a welcome addition to the literature and I highly recommend it. Although this book focuses on the Neotropical migration perspective, there is sufficient emphasis on behaviour to make it a worthwhile acquisition for avian and behavioural ecologists everywhere.

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