2023 - VOLUME 35 ISSUE 1

# ISBE Newsletter

Supplement to *Behavioral Ecology*
www.behavecol.com

## CONTENTS



## THE ISBE EXECUTIVE

## FROM THE NEWSLETTER EDITOR

**Behavioural Ecology in the age of AI**

November 2022 saw the release of ChatGPT, a Large Language Model Artificial Intelligence. Everyone seems to be talking about it, at least at my University. What does this mean for written student assignments? Yes, ghostwriters have been around for ages and are readily available online. But they are rather expensive, and slow. The new "chatbots" produce decent texts in seconds at no or low cost. If anything, they have democratized the students' abilities to cut corners. We now have intense discussions on how to best assess students, which in itself is a good thing.

We academics often write texts that, to be honest, feel like a waste of our time. We may have to rewrite an animal welfare permit application only because someone has redesigned the application form. Or formulate a polite email declining an invite due to scheduling clashes. Imagine having chatbots write these texts for you, freeing up time for more meaningful matters. But where should we draw the line? Which texts do we consider OK to produce this way? Parts of papers? Entire papers?

One colleague admitted he already uses chatbots to write grant proposals. AIs are quite good at producing that vague scientific gobbledygook that grant referees seem to like, especially the cringier sections like "benefits for greater society", or just the uncomfortable task to formulate research outcomes ahead of time.

The chatbots can also help us assess texts written by others, which could save time grading exams (or reviewing grant proposals). But how pointless will it be to end up with AIs evaluating scientific texts written by other AIs?

Will the new AIs change the way we think? Probably. We tend to define human intelligence partly based on what machines happen to be good at. Such as remembering lots of facts, or being good at math. If intelligence equals the ability to quickly formulate an acceptable summary of a scientific topic, then chatbots are already smarter than us. But isn't intelligence more than that? What, then, is it?

Like all tools, chatbots steer and limit our thinking. I recently asked 30 students: "What can prevent organisms from becoming perfectly adapted to their environment?". The group discussions led to a list of seven answers. We then put the same question to chatGPT. It (rather eloquently) formulated *three* of those answers. It was good, but incomplete. Now, if we'd asked chatGPT first, chances are we all would have focussed our discussion on those three answers, missing the other four.

The LLM chatbots are trained on enormous amounts of published texts. They become, per definition, experts on thinking *inside the box*. But what about creativity? Real scientific breakthroughs require *new* thoughts. We already seem to have a pattern of declining scientific novelty[1]. I wonder if AIs will accelerate this trend of "more of the same"?

**P. Andreas Svensson**
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[1] Park, M., Leahey, E., & Funk, R.JU. 2023. Papers and patents are becoming less disruptive over time. Nature, 613: 138-144

## CONTRIBUTE TO THE NEWSLETTER!

# Your contribution is important!

The ISBE Newsletter publishes Book Reviews, Conference/Workshop Reviews, Job postings and other advertisements, as well as Commentary Articles of interest to the International Society for Behavioral Ecology and Obituaries for recently deceased colleagues. The ISBE Newsletter will only consider work that is not already published or intended to be submitted for publication elsewhere.

**Book Reviews:** Persons involved in the publishing of books who would like these to be considered for review in the Newsletter should contact the editor so that they can be added in the books-for-review list. Authors may submit a list of possible reviewers. Members who wish to review a particular book should contact the editor. The editor will provide reviewers with instructions. Reviews are typically 1500-2000 words. For suggestions of books currently available for review, see the end of this Newsletter.

**Workshop/Conference Reviews:** Workshop and/or Conference reviews can be prepared in one of the following formats: *Brief synopses* (around 1500 words) and *Longer reports* (around 3000 words). Graduate students and postdocs are strongly encouraged to consider contributing to writing these reports.

**Cartoons:** Cartoonists and other artists are encouraged to submit artwork, either in hardcopy, or as TIFF or high resolution (>300 dpi) gif or jpg files. All cartoons published in the Newsletter will be credited to the illustrator.

**Spotlight on young scientists**: Early career members (PhDs/ postdocs) are encouraged to participate in the section "Spotlight on"; please provide name, education, current address, research interests and selected papers in an email to the editor.

**Upcoming conferences and events:** Please submit information about events that are relevant to the Society. Do this by emailing the Newsletter editor so that it can be included in the "Conference calendar"

**The deadline for contributions to the next issue is Sep. 30, 2023**

# CONFERENCE CALENDAR

**International Conference on Animal Ecology and Behavior (ICAEB)**
April 3-4, 2023, Venice, Italy
https://waset.org/animal-ecology-and-behavior-conference-in-april-2023-in-venice

**Conference for the European Human Behaviour and Evolution Association**
April 18-21 2023, University College, London
https://ehbea2023.wixsite.com/ehbea-2023

**Human Behavior & Evolution Society**
May 31-June 3, Palm Springs, California.
www.hbes.com/conference

**2023 International Conference on Pollinator Biology, Health and Policy**
June 3-6, 2023 Penn State
https://web.cvent.com/event/c21acf50-b587-4d7c-b0bc-55cbecd97098/summary

**Evolution 2023 (ASN/SSB/SSE)**
June 21-25, 2023 Albuquerque, New Mexico
www.evolutionmeetings.org

**International Student Symposium on Animal Behaviour and Cognition**
21-23 Jun 2023 in UNAM, Mexico City, Mexico
https://www.applied-ethology.org/International_Student_Symposium_on_Animal_Behaviour_and_Cognition_2023.html

**The International Conference "Defense Strategies in Early Human Evolution"**
23-26 June 2023, Tbilisi, Georgia
If you have questions, please contact the organizers:
Joseph Jordania: josephjordania@yahoo.com.au
David Lordkipanidze: dlordkipanidze@gmail.com

**The Animal Behavior Society (ABS) conference**
July 11-15, 2023 Portland, Oregon
www.animalbehaviorsociety.org

**ESEB, ASN, SSE & SSB joint conference.**
July 26 – 30 July, 2024, in Montreal, CA.
https://eseb.org/congresses/

**The American Ornithological Society (AOS) and the Society of Canadian Ornithologists (SCO–SOC).**
8–12 August 2023 in London, Ontario, Canada.
https://americanornithology.org/meetings/annual-meeting

**Behaviour 2023**
Aug 14-20 2023, Bielefeld Germany
https://www.uni-bielefeld.de/fakultaeten/biologie/forschung/veranstaltungen/behaviour2023

**14th European Ornithologists' Union Congress**
Aug 21-25 2023 in Lund, Sweden
*The biennial congress of the European Ornithologist Union, EOU, will be hosted by Lund University 21-25 August 2023. Everyone who is interested in ornithology is most welcome. The conference website with more information can be found at: www.eou2023.event.lu.se and the EOU website at: EOU - European Ornithologists' Union (eounion.org).*

*For the organizers, Anders Brodin*

**SORTEE virtual conferece**
The third conference of the Society for Open, Reliable, and Transparent Ecology and Evolutionary Biology (SORTEE)
17-18 Oct 2023 online, se also p9 in this issue
hwww.sortee.org/

**Australasian Ornithological Conference**
28-30 Nov 2023 in Brisbane (Meaanjin), Queensland, Australia
https://2023aoc.com/

**WCH10 10th World Congress of Herpetology**
August 2024, in Kuching, Malaysia
www.worldcongressofherpetology.org/

**Cultural Evolution Society**
9-11 Sep 2024, Durham (UK) hosted by Durham Cultural Evolution Research Centre (DCERC).
https://culturalevolutionsociety.org/story/Conferences

**ISBE 2024**
29 Sep - 4 Oct, 2024 in Melbourne, Australia
https://twitter.com/ISBE2024

**European Society for Evolutionary Biology**
18-22 Aug 2025, Barcelona, Spain,
https://eseb2025.com/

## In a desert garden
## The life and passing of John Alcock

On 15 January 2023 the field of animal behavior and behavioral ecology lost one of its champions with the passing of John Alcock. Through his prolific writings for scientific and popular audiences and his teaching, John drew his readers and students into the field though infectious enthusiasm and passion for animal behavior, natural history, natural selection, adaptationist hypotheses, and field work that were the hallmarks of his career.

John's passion for nature started at an early age in Pennsylvania as a deep love of birdwatching, a love that persisted throughout his life although his interests later expanded to include the natural history of all things. As an undergraduate at Amherst College, he was mentored by the eminent chemical ecologist and Monarch biologist, Lincoln Brower. A formative experience at that time was a field trip to Trinidad with Brower who coached John on how to design rigorous experimental work on bird feeding. John went on to graduate school at Harvard University where his Ph.D. advisor was Ernst Mayr, a leading evolutionary biologist of the time. John's commitment to the power of evolutionary concepts, especially that of natural selection and adaptation, grew out of his interactions with Mayr. His doctoral dissertation research was on learning in birds.

Upon graduating from Harvard in 1969, John immediately took a faculty position in the Department of Psychology at the University of Washington. There he was invited to join a field trip with Robert Lockard to the Chiricahua Mountains in Arizona. This trip was formative, and during it John discovered his intense love of the Sonoran Desert and its denizens. This led to two major changes in John's career trajectory. One was his move in 1972 to join the faculty at Arizona State University where he remained even after retirement in 2008. The other was a shift in the focus of his research program from birds to insects.

At ASU, John was fully committed to both teaching and research. Early on he wrote his widely used and engaging textbook, Animal Behavior: An Evolutionary Approach. This book featured an approach that was a hallmark of virtually every book he wrote, that is, an enthusiastic use of testing of hypotheses for the adaptive function of traits to unravel the complexity and hidden secrets of the natural world, especially the behavior of animals. His textbook and lectures walked students through scientific analyses of behavior in a way that was understandable, empowering, and exciting. His skills and excellence in teaching were recognized through awards from ASU's College of Liberal Arts and Sciences (1974) and the Animal Behavior Society (2007). John regularly revised his textbook ultimately producing an astounding 10 editions, the last printed in 2013 before he enlisted Dustin Rubenstein as a coauthor for the 11th (2018), the last edition that John coauthored. Thus, his writing drew students into the field and shaped their thinking about the process of science and animal behavior for over 40 years.

John's textbook was also notable for promoting the application of an adaptationist approach to understanding the behavior of humans as well as non-human animals. This perspective on human behavior has been controversial since the publication of E. O. Wilson's Sociobiology in 1975. It was a perspective that John, in the face of ardent criticism, wholly embraced and defended in a variety of his writings. The Triumph of Sociobiology (2001) is John's compelling, clear, and full-throated defense of human evolutionary psychology.

Research was also a passion for John at ASU. He wholly embraced insects as tractable study organisms with a special focus on their mating systems. He recurrently worked on several taxa especially burrowing bees both in the US and Australia, tarantula hawks, and damselflies, producing detailed and insightful studies of the strategies, such as hilltopping, used by males to maximize their chance of encounters with receptive females. All told, his efforts yielded over 200 peer-reviewed publications and his widely cited book with Randy Thornhill, The Evolution of Insect Mating Systems (1983).

John was also very active in presenting natural history to a broader audience. In addition to 57 articles in the popular press, he wrote eight books on topics ranging from gardening and insects in the desert to orchids. One of those books, In a Desert Garden: Life and Death Among the Insects, received the John Burroughs Medal as the best natural history book of 1998.

This is not the only accolade John received that recognized his contributions to the fields of animal behavior and natural history. The US-based Animal Behavior Society elected him a Fellow in 1990 and he received their Exemplar Award (1996) and the 2007 teaching award mentioned earlier. In Britain, the Association for the Study of Animal Behavior presented him with their ASAB Medal recognizing his contributions to the science of animal behavior. At ASU, he was honored in 1988 with a Regents Professorship. He was in the first group of faculty to receive this honor. Clearly,

John was a significant contributor to the development of the field of animal behavior and behavioral ecology for the last 50 years.

A picture of John and his life would not be complete without a few words about his personality that were well known to his friends. First, John was a staunch, if not obstinate, liberal. He regularly expressed his liberal views in no uncertain terms to those around him, to his elected representatives through letters and phone calls, and through regular contributions to liberal causes, especially those focused on the environment and conservation. His book, The Masked Bobwhite Rides Again, is perhaps his clearest statement of his environmental ethic. Second, John was a creature of habit. This is illustrated best by his multiple repeated visits to favored field sites in the Sonoran Desert such as Usery Mountain where he worked for decades on hilltopping insects, and Carnarvan in Western Australia which he visited 18 times to study burrowing bees. While not the most adventuresome lifestyle, it gave him a long-term perspective on his favorite haunts that is featured in some of his popular writings such as After the Wildfire: Ten Years of Recovery from the Willow Fire (2017). Third, John followed sports closely, especially the teams from Philadelphia near where he grew up and Phoenix-based teams. As a rule, he placed small bets with friends against these teams figuring that either outcome was a win for him. Lastly, the word game Boggle and ping pong were two of John's very favorite leisure, albeit fiercely competitive, activities.

In 1968 John married Sue Coates and together they created a home on East Loyola Drive in Tempe where they hosted hundreds of memorable dinner parties with very lively discussions for local and visiting friends, colleagues, and family. They also raised two sons, John and Nick, who have become respected and accomplished practitioners in medicine and law, respectively.

For the last several years John dealt heroically with the physical and mental decline brought on by what was diagnosed in 2019 as Parkinson's Disease but then later as Progressive Supranuclear Palsy. It was complications from this disease that ended his productive and rich life at the age of 80. He will be greatly missed by family, friends, and his profession.

The family asks that remembrances be in the form of donations made in John's name to the Center for Biological Diversity or the Nature Conservancy of Arizona. The memorial service live stream and other information may be found at JohnAlcock.com

Ronald L. Rutowski
Arizona State University

## MARC THÉRY MEMORIAL FUND

As mentioned in ISBE Newsletter Vol 34(1), a fund has been created in memory of behavioural ecologist Marc Théry (Fond Marc Théry en faveur du Coq de Roche). The object is to protect the cock-of-the-rock and its forest in French Guyana. Information about this fund and how to make contributions can be made at:

https://www.helloasso.com/associations/gepog/formulaires/2/en

Jack Bradbury
Cornell University

## FUNDING OPPORTUNITY

The National Geographic Society is launching a rigorous global effort to find three of the best scientists doing field research on animal behavior and cognition. Ideal candidates must have at least three (3) years of relevant work experience after the award of their Ph.D. We welcome applications from all career stages beyond that, but preference will be given to early-career scientists.

If selected, each individual will receive direct funding of $800,000 ($200,000/year), as well as substantial additional resources and services over four (4) years (with the possibility to extend an additional six (6) years, totaling a project length of 10 years).

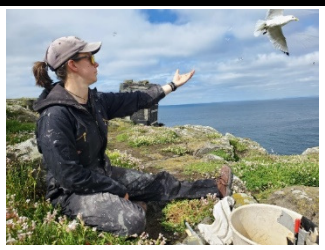
Here is the web link for the information on this funding opportunity.

https://www.nationalgeographic.org/society/grants-and-investments/animal-behavior-and-cognition-funding-opportunity/

Deadline April 12, 2023

Jasmin Chan
National Geographic Society

## Sophie Bennett



**Education**: PhD in seabird ecology at the UK Centre for Ecology & Hydrology and the University of Liverpool, UK

**Address**: Centre for Conservation Science, Royal Society for the Protection of Birds, Edinburgh, UK. Email: Sophie.Bennett@rspb.org.uk

**Research Interests**: My main academic interests are the population ecology, behaviour and conservation of seabirds and the marine environment. I am currently developing bioacoustics techniques to monitor remote seabird populations.

**Selected papers:**

Bennett, S., Harris, M.P., Wanless, S., Green, J.A., Newell, M.A., Searle, K. and Daunt, F. 2022. Earlier and more frequent occupation of breeding sites during the non-breeding season increases productivity in a colonial seabird. Ecology and Evolution, 12:e2913.

Bennett, S., Wanless, S., Harris, M.P., Newell, M.A., Searle, K., Green, J.A. and Daunt, F. 2022. Site-dependent regulation of breeding success: evidence for the buffer effect in the common guillemot, a colonially-breeding seabird. Journal of Animal Ecology, 91: 752-765

Bennett, S., Girndt, A., Sanchez-Tojar, A., Burke, T., Simons, M.J.P. and Schroeder, J. 2022. Evidence of paternal effects on telomere length increases in early life. Frontiers in Genetics. 13.

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## Tobit Dehnen

**Education:** Integrated Master of Biological Sciences (Zoology) from the University of Sheffield (2015–2019), PhD student at the University of Exeter (2019–present)

**Current Address:** Centre for Ecology and Conservation, University of Exeter, Penryn Campus, Penryn TR10 9FE, UK.
Email: td430@exeter.ac.uk

**Research Interests:** I am broadly interested in social behaviours in group-living species, with a particular interest in the causes and consequences of social dominance in animal groups. I am currently working on whether and how reproductive effort affects social dominance in female vulturine guineafowl, a plural breeder native to Eastern Africa.

**Selected Papers:**

Dehnen, T., Arbon, J.J., Farine, D.R. Boogert, N.J. 2022. How feedback and feed-forward mechanisms link determinants of social dominance. Biological reviews 97: 1210-1230

Dehnen, T., Papageorgiou, D., Nyaguthii, B., Cherono, W., Penndorf, J., Boogert, N.J. and Farine, D.R. 2022. Costs dictate strategic investment in dominance interactions. Phil.Trans. R. Soc. B 377: 20200447

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## Olivia S.B. Spagnuolo

**Education**: PhD, Integrative Biology and Ecology, Evolution, and Behavior, Michigan State University, U.S. (anticipated October 2023). Graduate Certificate in Spatial Ecology and Master of Science, Natural Resources and Environment, University of Michigan. Bachelor of Science, Michigan State University, U.S.

**Address**:
Natural Science Building, 288 Farm Lane, Room 203, Michigan State University, East Lansing, MI, U.S.A. Email: oliviaspagnuolo11@gmail.com

**Research Interests:** My research focuses on advancing methods in Geographic Information Systems (GIS) and understanding anthropogenic effects on large carnivore behavior. I specialize in spatial ecology and am currently investigating the effects of livestock grazing on the space use and diel activity patterns of apex and mesocarnivores in Kenya. My long-term goal is to aid in the conservation of large carnivores in multi-use landscapes by identifying threats to survival, reproduction, and dispersal; predicting spatial and temporal patterns of human-carnivore conflict; and testing the efficacy of mitigation strategies.

**Selected papers:**

Spagnuolo, O.S.B., Lemerle, M.A., Holekamp, K.E., Wiesel, I. (2022.) The value of individual identification in studies of free-living hyenas and aardwolves. Mammalian Biology 102, 1-24.

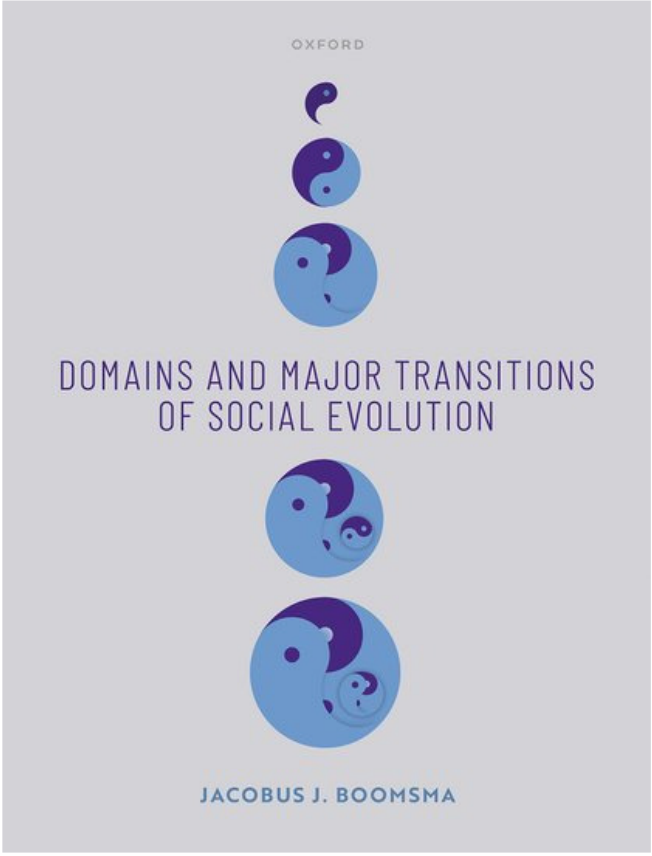
Spagnuolo, O.S.B., Jarvey, J.C., Battaglia, M.J., Laubach, Z.M., Miller, M.E., Holekamp, K.E., Bourgeau-Chavez, L.L. (2020). Mapping Kenyan grassland heights across large spatial scales with combined optical and radar satellite imagery. Remote Sensing 12, 1086.

Lehmann, K.D.S., Montgomery, T.M., MacLachlan, S.M., Parker, J.M., Spagnuolo, O.S., VandeWetering, K.J., Bills, P.S., Holekamp, K.E. (2016). Lions, hyenas, and mobs (Oh my!). Current Zoology 63, 313-322.

# Domains and Major Transitions of Social Evolution

By Jacobus J. Boomsma

*Oxford University Press*
*DOI: 10.1093/oso/9780198746171.001.0001*
*ISBN: 9780198746171*




The first three chapters of this book by Jacobus (Koos) Boomsma are an ambitious and comprehensive historical account of how Darwin's theory of natural selection navigated after inception to the prominent position that adaptationist thinking and inclusive fitness paradigms hold in evolutionary biology today. This then leads into Boomsma making his case over the last five chapters that inclusive fitness maximization is key to understanding Major Transitions in Evolution (MTEs); from eukaryotes to eusocial insects and possibly humans.

Boomsma begins by detailing how early on natural selection and genetics were alternative rather than complementary streams within the emerging field of evolutionary biology. Champions of adaptation such as August Weismann, William Morton Wheeler, and the young Julian Huxley observed that species could be arranged according to increasing levels of organismal complexity. However, pursuing questions about organismal and social complexity were often considered secondary to studying genomes, with the assumption that evolutionary history would become self-evident once the functioning of genes was fully understood. Interestingly, this early split had a geographic component with North American science (e.g., the Chicago school) focusing on genetics and systems, while European science (e.g., the Oxford school) did at least maintain natural selection as an ongoing concern. To the extent that the modern synthesis of Fisher, Haldane, Wright, Simpson, Mayr and Stebbins brought the schools together, Boomsma notes, it did not adequately incorporate social evolution. It is not until the seminal works of Nico Tinbergen, George Williams, William Hamilton, Robert Trivers and Richard Dawkins that adaptationist viewpoints on behavior and sociality were significantly integrated into evolutionary theory. The field of evolutionary biology finally came to realize that extant genes alone could not explain why traits come into existence, spread through populations, and cause adaptive radiations. Only the theory of natural selection provides the tools to do so.

At this point Boomsma introduces who I might call a 'villain' to the story – E. O. Wilson and his "shallow analogies" (pg. 30) as the basis of sociobiology. Many view Ed Wilson as one of the giants in promulgating an approach to the study of social behavior that seamlessly incorporates genes and adaptation. (I do note that reading his 1975 book instantly converted me as a young undergraduate!) Boomsma, however, takes issue with Wilson's 'continuity' view on social evolution: i.e., solitary life, to occasionally cooperative, to facultatively cooperative, to obligately cooperative. Along this pathway, reproductive division of labor incrementally increases until absolute. The driving process is that more cooperative groups have greater ecological success than their less cooperative antecedents.

Boomsma instead champions a more episodic view of social evolution – that, for example, the vespine wasps with morphologically-differentiated queen and worker castes could not have gradually evolved from a polistine-type ancestor where same generation females cooperate and where every 'worker' could become a queen should an opportunity arise. In Boomsma's view, Wilson's sociobiology delayed the acknowledgement and appreciation of Wheeler's original insight that superorganisms are fundamentally different from cooperating groups in having passed through a window of evolutionary irreversibility (Pg. 100, Figure 4.6).

The crux of Boomsma's argument is that social evolution follows Hamilton's rule where inclusive fitness governs ($r_xb - r_oc > 0$; with $r_o$ = relatedness to lost own offspring, $r_x$ = relatedness to recipients' gained offspring). There are two special situations where $r_o/r_x = 1$, and Boomsma argues this ratio is essential in creating a needed precondition for an MTE. One situation is in interactions between cells resulting from mitotic division (with $r_o = r_x = 1$). The second is in monogamous families where the genetic worth of an offspring is equal to that of a full sibling ($r_o = r_x = 0.5$). Only through the "window" of $r_o/r_x = 1$, might it be advantageous for altruists to enter into a lifetime commitment of sterility. In multicellular clones,

this commitment allows the evolution of altruistic and sterile somatic tissue. For social insects, an altruistic and obligately sterile worker caste can evolve. Boomsma emphasizes such events may be irreversible, with their specific and measurable traits defining that an MTE has occurred.

At this point, I do need to acknowledge my disagreements with Boomsma on the issue of how important monogamy is for evolving cooperation. Specifically, I have published several papers using population simulations showing cooperation and obligate castes can evolve without monogamy – and under some situations monogamy actually reduces the spread of a cooperative trait. None of these models or results have been refuted. Moreover, the increasing evidence for offspring being manipulated through diet into assuming helper roles with diminished fitness makes the matedness status of mothers irrelevant. Indeed, I eagerly expected a cogent rejoinder to these findings somewhere in this book. There is none. In essence, Boomsma writes this section of the book as a lawyer might initially prepare a court case, where there is no requirement to rebut the other side, or even acknowledge that an alternative viewpoint exists. This approach extends to broader issues than monogamy, *per se*.

In 2010, the infamous 'Nowak et al.' took a very aggressive tone towards kin selection; sparking a series of heated responses (with both Boomsma and I contributing to critiques on different aspects!). Despite the generated heat, significant issues were left unaddressed. Martin Nowak and colleagues, for example, acknowledge kin selection as one of five mechanisms for the evolution of cooperation. They, however, take strong issue with inclusive fitness as a modeling technique because of the ambiguous and malleable ways in which benefits and costs can be assigned and measured. A different critique is raised by Wilson, arguing that kin selection is a dissolutive process in which the directing of benefits towards kin requires exclusionary efforts towards non-kin that may use up whatever gains group living provides. Hence, its ubiquity as an explanation for social evolution needs reassessing. It is not possible to fully represent all the dissents in a book review. Readers just need to be aware that this book declines to engage with criticisms of its proposed causative agency – inclusive fitness – in any substantive way. It is a one-sided viewpoint from an author who has devoted much of his distinguished career to promoting kin selection. Granted, he does an unarguably excellent job of presenting his case; and he may well be right. But also, maybe not.

Boomsma views inclusive fitness maximization as a first principle cause for natural selection, for which MTEs would be no exception. A problem with this is that inclusive fitness, as commonly understood, is as a within-species, between-kin thing. Thus, among the variety of MTE's proposed in the literature, it obviously applies to only the evolution of multicellularity and eusociality. Boomsma attempts to add the evolution of mitochondria and other interspecific obligate mutualisms (maybe because with $r_x = r_o = 0$, their ratio is kind of like being equal to one?). Hence, such relationships can evolve when both c and b > 0. I confess to not entirely follow the argument here. It seems akin to proposing celibacy is a kind of sexual act. For me, inclusive fitness by Hamilton's rule seems unneeded and adds nothing towards understanding why mutualism occurs across species or between unrelated individuals. However, I do encourage readers to check for themselves.

The final chapter is on humans, and Boomsma acknowledges that if we are an MTE, it was not driven by his first principle. In his words, the MTE is an "endosymbiosis between individual brains and sets of self-organizing algorithmic symbionts" (pg. 194). Make of that what you will. The key point seems that human cumulative culture is like other species' cultures only in the broadest of generalizations, and far exceeds all others in almost any quantitative measure chosen. The difficulty with this is where and when does the MTE happen? With *Homo erectus*? With *H. sapiens*? When *H. sapiens* shifts from hunting and gathering to living in cities and writing books? How do we test if our brains coexist with sets of self-organizing algorithmic symbionts, or that other species' brains do not?

To his credit, Boomsma addresses the question of testability by closing with five predictions (Box 8.3) that would be consistent with his conceptualization of MTEs. However, they seem to me to be either biased to support his conjectures or inherently untestable.

**1. "MTEs do not just emerge".** Lower level selection does not gradually give way to higher level selection. [Seems untestable as "gradual" is an arbitrary label in the eye of the beholder. *E.g.,* did or did not the mitochondria gradually give up its independence?]
**2. "MTEs are strictly hierarchical".** [It is unclear how it could be otherwise and how a definitely non-hierarchical MTE would look.]
**3. "Groups cannot evolve MTEs".** Traits cannot evolve in one group for the express benefit of descendent groups. [Given the paucity of evidence that non-MTE traits can evolve in individuals when the traits' fitness benefits are only realized at the group level, this seems a fairly safe prediction.]
**4. "MTEs have unique GNRs".** [Is one gene regulatory network enough? What if there are also one or multiple shared GRNs across species on either side of the MTE boundary?]
**5. "Ectosymbionts and MTEs".** The former cannot produce the latter. [Cannot all the cells of a multicellular organism be considered ectosymbionts of each other? Or, workers and queens as ectosymbionts of the other?]

Certainly, isolated failures of inclusive fitness theory predictions would not invalidate it either as explanatory for other phenomena or for playing a definitive role in a given MTE. Indeed, Boomsma's arguments would be more impactful with a more balanced presentation rather than a lawyerly ignoring of "explicit tests" (pg. 184) where inclusive fitness theory predictions have failed – and to draw lessons from those failures. Reflecting multiple authors and studies, the list of failing ideas or contradictory results includes examples such as: reproductive skew theory; haplodiploidy explicitly driving eusociality; unicoloniality with no effect on cooperation; a general lack of genetic kin recognition mechanisms; workers drifting into unrelated nests; and worker policing occurring with the wrong relatedness relationships, to name a few. Inclusive fitness apologists may present explanations for why each one is actually consistent with theory (thereby supporting Nowak's

contention that inclusive fitness is an unfalsifiable, amoeboid concept). As a thought problem, consider what if the failures had instead produced results unequivocally and only supportive of inclusive fitness maximization. Rather than ignored, they then would be glowingly presented in books like this one.

In summary, this book is valuable for anyone interested in the history of evolutionary thought and theory. It is valuable to those considering the entire sweep of evolution of life on Earth and the processes driving it. It is a must have for anyone for whom kin selection and inclusive fitness maximization is their scientific guiding lodestar. It is also a must have for those for whom kin selection and inclusive fitness maximization is the bane of their existence – to see the best case the other side can muster. *Domains and Major Transitions of Social Evolution* is a book for the serious evolutionary biologist seeking an intellectual challenge. I found it both enlightening and worthwhile, if not entirely persuasive.

**Peter Nonacs**
Department of Evolutionary Biology and Ecology
University of California, Los Angeles

## VIRTUAL CONFERENCE

SORTEE
Society for Open, Reliable, and Transparent Ecology and Evolutionary Biology

The third conference of the Society for Open, Reliable, and Transparent Ecology and Evolutionary Biology (SORTEE) will be held virtually in October 2023 (continuously from 17 October 0700 UTC to 18 October 0700 UTC, in order to cover all time-zones).

The conference is a forum to discuss and develop ideas for improving research in fields related to ecology and evolutionary biology. If these topics interest you then please consider becoming a member:
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**Unconferences**: Facilitated discussions of ideas for how to make ecology, evolutionary biology, and related disciplines more open, reliable, and transparent. Facilitation involves moderating the conversation with ideas and examples, but there are no formal presentations.

**Hackathons**: Group projects with well-defined goals (papers, techniques, software, protocols, organizations, etc.).

**Workshops**: Facilitators will teach tools for implementing open, reliable, and transparent research practices.

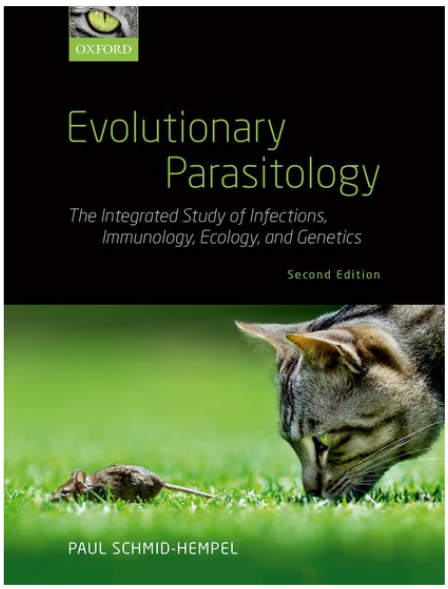
Conference registration and content submissions will soon open (content submission will close on June 1st) on the SORTEE webpage:
https://www.sortee.org/upcoming.

For more information on the conference, please contact us at conf.sortee@gmail.com

We hope to see you in October!

**Matthieu Paquet**
The SORTEE Conference Committee

# Evolutionary parasitology:
## The integrated study of infections, immunology, ecology, and genetics. 2nd edition




## By Paul Schmid-Hempel

*Oxford University Press*
*ISBN: 9780198832140*

As a behavioral ecologist with limited training in classical medical and veterinary parasitology, I designed my parasitology course in 1998 to quickly review taxonomy before emphasizing the emerging explosion of ecological and evolutionary developments, inspired largely by Hamilton and Zuk (1982). Unfortunately, all existing texts were largely details of taxonomy and life cycles. Eventually, I resigned myself to sacrificing my first sabbatical to write a text that met my students' needs. I landed in Heathrow on the September 11 to attend a meeting of the British Parasitological Society. On my way to the room where Darwin and Wallace gave their joint presentation (neck hairs standing), I was greeted by galleys of Bush et al. (2001, revised as Goater et al. 2014), and was immediately relieved to find a text that melded taxonomy, ecology, and evolution; my sabbatical was saved!

I had found a few specialist books that eschewed taxonomy and focused on ecology and evolution (e.g., Poulin 1998 revised in 2007, a translation of Combes in 2001), but my students first needed a taxonomic grounding. Schmid-Hempel's book (I did not see the 2013 edition) is an exceptional addition to this side of the spectrum that I would have leaned on for teaching; it provides reviews of both empirical and theoretical developments in ecology and evolution. Because of its limited attention to taxonomy, this book would not be suitable for a traditional parasitology course or as the sole reference for the course I taught, but would serve admirably for an upper level course that could last multiple semesters. The wealth of examples alone is worth the price of admission and the 76-p. bibliography contains ~2500 up-to-date references, which doesn't even include many others cited in Tables. This review scratches the surface of the book's contents.

Before starting, you may want to photocopy the 3 p. of abbreviations that are not comprehensive. In the preface, Schmid-Hempel notes that tables of examples are not complete; this won't matter to most readers because there are still plenty. He also notes that he mostly overlooks plants, but one will encounter some interesting botanical examples. Overall, the book is full of illustrations that range from simple to overwhelmingly complex. The text mostly does not burden readers with specialized jargon and terminology (but wait until Chapter 4!). Exceptions to almost every idea are provided throughout.

The opening chapter is about the significance of parasites, and Schmid-Hempel weaves the tale of yellow fever killing a staggering 30,000 of 80,000 workers on the Panama Canal. He uses this history to illustrate themes to follow.

Chapter 2 provides a framework for studying ecological and evolutionary questions, beginning with an overview of conditions that must be met to satisfy Darwin's framework for natural selection, among these being heritable differences in phenotype that affect both hosts and parasites. Schmid-Hempel then introduces us to "The disease space", a concept developed in David Schneider's lab (Torres et al. 2016) to visualize host-parasite outcomes, illustrating temporal trajectories of parasite intensity laid over host health; hosts begin healthy, become sick, and either die or recover. Schmid-Hempel uses disease space plots throughout the book to crystallize numerous concepts.

In the third chapter, Schmid-Hempel reviews the ubiquity and staggering diversity of parasites. Not surprisingly, current information is highly biased to economically important species. The problem of cataloguing this diversity is gradually succumbing to molecular advances, but the end is not nigh. There is a brief 14-p. review of parasite taxonomy and an overview of parasite natural history. We are walked through origins of parasite life histories that have evolved independently more than several dozen times (18+ times in nematodes alone), and the diversity of life cycles, including modes of transmission and numbers of hosts required to complete a cycle. Parasitologists often wax about how complex life cycles expose parasites to multiple immune systems, multiple physical conditions (pHs, temperatures, etc.), and so on. Accordingly, one might predict a complex genome to contend with these challenges, so it may come as a surprise that parasitism is actually associated with reduced genomes.

Chapter 4 is about host defenses, principally immunity; this is both the longest chapter (55 vs. $\bar{x}$ 27.3 ± 11.7 SD p.) and, unsurprisingly, the most complex with the most acronyms. Schmid-Hempel starts simply by

distinguishing pre- (e.g., don't walk in sewage) versus post-infection defenses. Trade-offs in investment in immunity versus other traits are introduced, as is potential tissue damage caused by overzealous investment in the former. Here and elsewhere, Schmid-Hempel draws on his Hymenoptera research to consider social immunity versus transmission risks at high densities. Arms of the immune system (innate vs. acquired, humoral vs. cellular) are distinguished. Eventually, we are plunged into the molecular maelstrom that will leave many dazed with descriptive detail. We are introduced to regulatory micro-RNAs, [one of] "… the most dramatic discoveries during [recent] decades". miRNA molecules have a wide range of previously undetected cellular functions (O'Brien et al. 2018). The delicious capacity for immune systems to recognize and respond to myriad variants of antigens is detailed, as is the genetic machinery needed to generate these responses. There are then sections on unique elements of immunity in invertebrates versus vertebrates. Immune memory is described, and elements of it mapped onto an animal phylogeny. We are reminded that immune systems are influenced by other metabolic processes; everything is connected to some degree. One of my favorite quotes was "evolution of immune systems was anything but orderly and directed; it was more the work of a tinkerer than of a brilliant engineer." The controversial "hygiene hypothesis" is discussed, and we are introduced to contributions to immunity from microbiomes, an area of research that has exploded with advanced molecular technologies.

Chapter 5 reviews the newly separated field of ecological immunology. The phenomenon of non-random distribution of parasites among hosts arises from various causes (e.g., diet, interaction of diet with microbiota), and throws a wrench into simple epidemiological modelling. A few exceptions are cited where intermediate, rather than maximum, Major Histocompatibility Complex (MHC) diversity is associated with lower parasite intensities. Measurement of investment in host defenses can quickly become an enormous and complex task. Trade-offs are described for many investments (e.g., smaller Drosophila are less fecund, but are safer from parasitoids). Experimental manipulations of hosts can provide compelling evidence of trade-offs. The squabble-worthy terms tolerance versus resistance are discussed. We learn that stochasticity can intervene to limit evolution toward optimal host defenses.

In Chapter 6, Schmid-Hempel provides a surprisingly brief 16-p. review of parasites and sexual selection. The chapter starts by covering the messy pattern of higher male susceptibility to parasites (including in plants!). A significant jump in interest in parasites arose from Hamilton and Zuk (1982), partly as a way to explain the "Paradox of the Lek"; all of this remains controversial, in part because of aforementioned stochasticity. Folstad and Karter (1992) injected more grief into our research programs by adding endocrinology and immunity into things we should be measuring. Again, we are reminded that MHC diversity is not always the Holy Grail of mate choice; one explanation is that too much antigenic diversity increases risks of autoimmunity. I reiterate; it's complicated.

Chapter 7 tackles trade-offs between specialist versus generalist parasitism, and the tricky minefield to empirically categorize them (e.g., the difficulty of determining whether a parasite is paratenic). If one survives a study system's minefield, numerous indices are explained. Combes' (2001) concept of filters to parasite establishment is laid out as a way the generalist-specialist continuum arises. On the one hand, minefields may be navigated with molecular methods, but on the other hand reveal additional diversity of cryptic parasites. Experiments are another logical way of navigating minefields, but are for most study systems impractical. Specialization is a risky evolutionary pathway if there is temporal or spatial stochasticity in host density, whereas a generalist strategy is apt to reduce parasite competitiveness. Schmid-Hempel covers an interesting and broad set of influences on how the trade-off can see-saw. We have known about transgenerational immune priming since 1900 (!); it can even include seminal fluids. Another observation is that one binding region of MHC I can differentiate 99.8% of self from non-self.

The next chapter is about how parasites both evade immune systems and manipulate host phenotypes. The latter has traditionally emphasized behavior, but appearance and odors are attracting increasing attention. The remarkable cyclic antigen variation of trypanosomes (agents of sleeping sickness and other diseases) is reviewed. Manipulations may arise as exaptations that passively defeat host defenses, such as by releasing toxic waste products. Mechanisms of both evasion and manipulation are extremely diverse. The chaos in how investment in these two aspects occurs is only notched up by carrying multiple parasite species (e.g., hitchhiking).

Chapter 9 explores steps needed to complete parasite life cycles, and how optimal virulence is subject to the same stochasticity that interferes with good clean theory in many of the chapters. Trade-offs are reviewed for vertical versus horizontal transmission and passive versus vectored transmission, and how they affect optimal virulence. Parasite synergies versus antagonisms are covered. Proximate mechanisms of pathogenesis are distinguished from virulence, and many additional facets of humoral and cellular invasion and defense are detailed.

The immensely complex topic of host-parasite genetics follows. This may be too molecular for some, but this battleground is laid out so that most should glean something. Schmid-Hempel illustrates how different hosts have different disease spaces, and how different parasites have different trajectories within those disease spaces. Empirical investigation of these is being aided by advances in genomics, bioinformatics, and computation. Schmid-Hempel suggests that the overview he provides of this fast-moving field will soon be obsolete. Nonetheless, the staggering genetic diversity revealed by new developments (e.g., Salmonella enterica) has >2600 "species" is overwhelming.

The 11th chapter, on epidemiology, opens with some statistics: 228 million people with malaria and close to half a million deaths (mostly children), 71 million with Hepatitis C and 1.4 million deaths, and so on. Some of

the earliest modelling in this field can be traced to none other than Bernoulli, who did so with smallpox and vaccine efficacy. Much later, susceptible, infected, and resistant (SIR) models were developed in a series of papers by Anderson and May; they convinced many that, contrary to the prevailing literature, parasites were important to regulating populations. Vaccination skepticism and its consequences are discussed, as are super-spreaders, and stochasticity in host encounters and how these affect modelling. The topics of network theory being used to study epidemics, phylodynamics, and immunoepidemiology round out the chapter.

Disease dynamics within hosts are subsequently covered. Signaling theory is used to investigate how false infections are distinguished from true infections by hosts, and how parasites are selected to interfere in this interface. The delicate balance between under- and over-reacting by a host is re-visited, as is selection for parasites to time when they cause the most damage to maximize transmission. Within hosts is where most horizontal gene transfer occurs for parasitic microbes, a process complemented by mutation. Both processes contribute to antibiotic resistance, something recognized only two years after Fleming discovered penicillin; antibiotic resistance is a growing source of panic in medicine. Microbiomes may rely on cues to assess community makeup (quorum-sensing) as an adaptation to rebuff competitors and hitchhikers.

In the 13th chapter, the evolution of virulence is confronted in more detail; this is viewed as a "negotiation" that co-evolves so that hosts do not invest or lose too much, and parasites do not get out-competed while limiting harm. For reasons given above, this can be a fragile, dynamic, and chaotic arms race that is probably at its most unpredictable when a parasite initially establishes in a new host species. The idea that virulence always starts high is dismissed with empirical evidence. The classic story of oscillations in virulence and resistance in myxomatosis and European rabbits (Oryctolagus cuniculus) is reviewed, and modelling to understand how it happened is presented. Additional influences on virulence are reviewed, including genetic structure of populations, horizontal versus vertical transmission, intra-host competition, host longevity, etc. The balance of supporting versus contrary examples varies for each. The controversy over whether vaccines affect virulence is among chapter topics.

Schmid-Hempel follows with an exploration of co-evolution; does co-speciation lead to congruent phylogenies of hosts and parasites? When I taught this topic, I was always amused that researchers judged by eye whether congruence was the outcome, until the math was developed in 1994. A more formal body of science followed to evaluate the relative frequency of co-speciation, host-switching, duplications, missing the boat, or drowning on arrival. Negative frequency-dependent selection and the Red Queen are explored, as is the importance of parasites to maintaining genetic diversity by favoring sexual over asexual reproduction. The notion that parasites always evolve faster than their hosts is generally supported, but there are exceptions.

The 15th, closing chapter is about ecology. Schmid-Hempel focuses on a few topics, such as how host body size relates to various aspects of parasitism (e.g., Harrison's rule that parasite body size increases with host body size is generally supported). There are also descriptions of complex consequences of parasitism for communities, including a case history on rinderpest in Africa that allowed vegetation to establish, and how this triggered an upsurge in tsetse flies and thus sleeping sickness. He builds to how humans have contributed to parasite introductions (including yellow fever), and how climate change threatens to stir the pot even more, costing billions in medical and veterinary interventions. Layered on intuitive theory, we are again regularly greeted with empirical disobedience: "The search for general laws in parasite ecology has … remained difficult."

A brief sample of fun nitpicks, of which I had few. I stumbled over "inducing a carving for a diet". The caption to Fig. 11.3 implies that Vancouver is an American city! In one of two of my papers that are cited, I am promoted to D. Schluter!

If I were to interview Prof. Schmid-Hempel, I would ask how much his interests versus those of a target audience influenced the book's content? Related to that, how did he settle on relative emphases in content? Was he disappointed with how so much wonderful theory is tainted by ecological and evolutionary complexity? Personally, seeing the exceptions reminds me that the more I think I know, the less I know.

My executive summary is that this a wonderfully executed book, full of rich detail both empirical and theoretical. If you dabble in parasites as part of your teaching or research, this book is certainly one to add to your collection.

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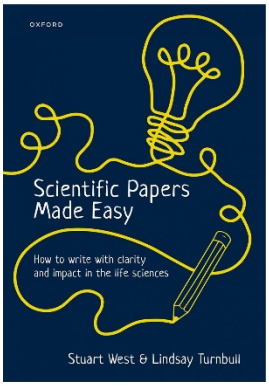

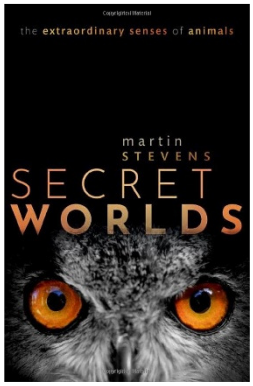

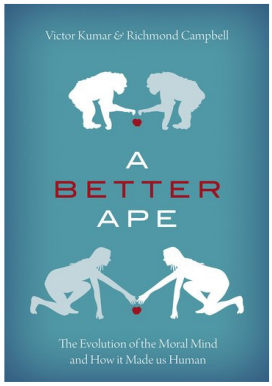

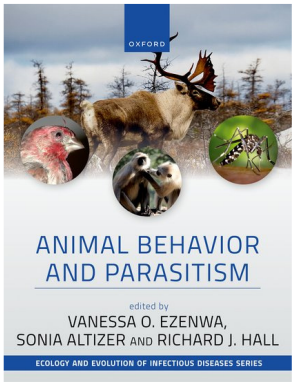

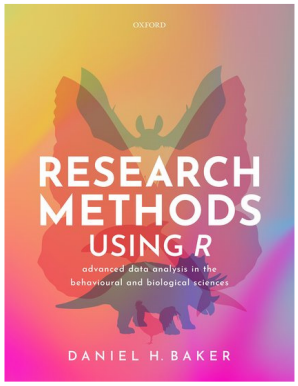


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