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EDITORIAL

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The future of evolutionary behavioral biology

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On the occasions of the 50th anniversaries of *Sociobiology: The New Synthesis* (Wilson 1975) and the foundation of the journal *Behavioral Ecology and Sociobiology* (hereafter *BES*), we reviewed progress in evolutionary behavioral biology and the sociobiology controversy since 1975, discussed the emergence of the disciplines of behavioral ecology and its subspecies sociobiology, which specifically addresses questions of the evolution and mechanisms of social behavior, and described the impact of *Sociobiology* on the careers of the Editors-in-Chief and the Associate Editors of *BES* (Traniello and Bakker 2026; Traniello et al. 2026). In this third editorial recognizing the semicentennials, we ask "What is the future of the study of the adaptive nature of behavior?" We acknowledge the difficulties of forecasting the course of science, particularly during these uncertain times, as the problem of sustained support will affect the course of research. Nevertheless, we believe the cumulative work and unsettled *scientific* controversies and debates of behavioral biology during the past 50 years have created momentum to successfully drive future research (West et al. 2025). Additionally, the foundational strengths of our discipline—solid theory, recognition of variation at multiple organizational levels, explicit association of behavior with fitness, use of non-traditional models, high degree of cross-disciplinary integration, together with technological innovations, will expand analysis and extend evolutionary depth (e.g., Davies et al. 2012). In anticipating a positive future, we emphasize the importance of sociobiological research in the evolution of biological complexity: the origin of sociality is considered one of the major transitions in the history of life (Maynard-Smith and Szathmáry 1995).

We begin our look into the future with a study of the past, asking: have patterns of research changed over the past 50 years? Where do we stand today? The publication records of *BES* provide insight to identify research patterns for the diverse species and behavioral systems explored (Fig. 1). At the birth of the discipline and *BES*, social insects were most frequently represented in published articles. Forty years later, the number of research papers on birds, invertebrates other than social insects, and amphibians/reptiles increased, and during the last decade, changes in the choice of study models have been minimal. From 2016 to 2026, mammals and amphibians/reptiles were *en vogue*, relatively speaking, whereas avian research declined, perhaps reflecting paradigm shifts, the applicability of birds as suitable models, and/or the development of molecular techniques to assess parentage, for example, across diverse clades. The focus on sociobiology in the early years of the discipline was accompanied by testing hypotheses and an increase in long-term field studies. Social behavior, signalling, and sexual selection were predominant (Fig. 2). The interest in sexual selection has been to some extent subsumed by life-history studies (personality, developmental plasticity, reproduction, survival, migration, settlement, and immunity) and predator–prey (including host-parasite relationships) (Fig. 2). The ecology and evolution of cognition and learning gained recognition.

Can future directions be deduced from these trends? We assume that the patterns illustrated in Figs. 1 and 2 are representative of the discipline and are not journal specific. In part, this is valid but there are some significant differences

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Extended author information available on the last page of the article

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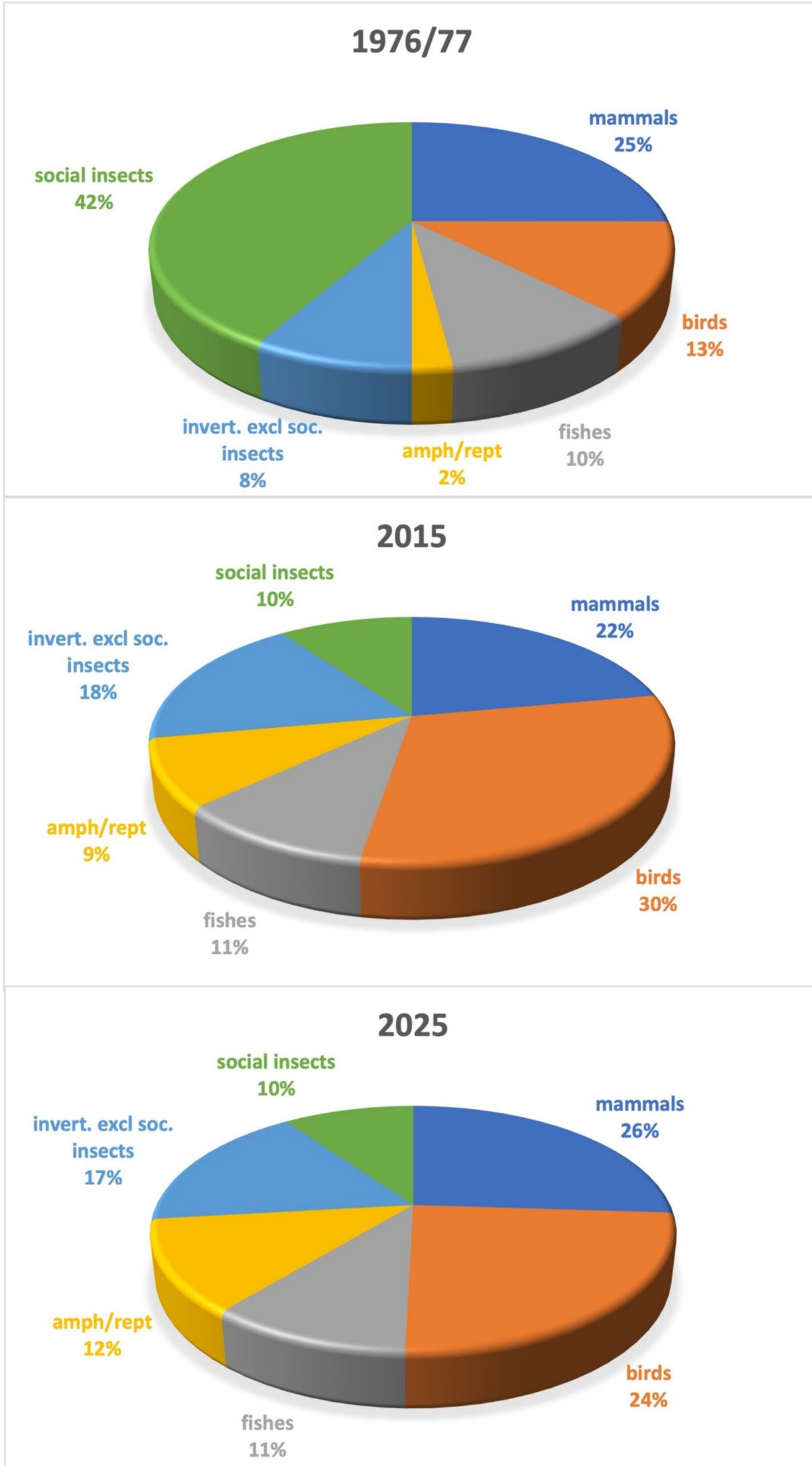

Fig. 1 Distribution of taxa in articles published in *BES* during 2025 ($n = 123$) and comparison with data from Bakker and Traniello (2016) for 1976/1977 ($n = 48$) and 2015 ($n = 190$). Chi-squared test, $\chi^2 = 41.3$, df = 10, $p < 0.0001$; 1976/77 vs 2015, $\chi^2 = 32.8$, df = 5, $p < 0.0001$; 1976/77 vs 2025, $\chi^2 = 26.7$, df = 5, $p < 0.0001$; 2015 vs 2025, $\chi^2 = 2.3$, df = 5, $p = 0.8082$

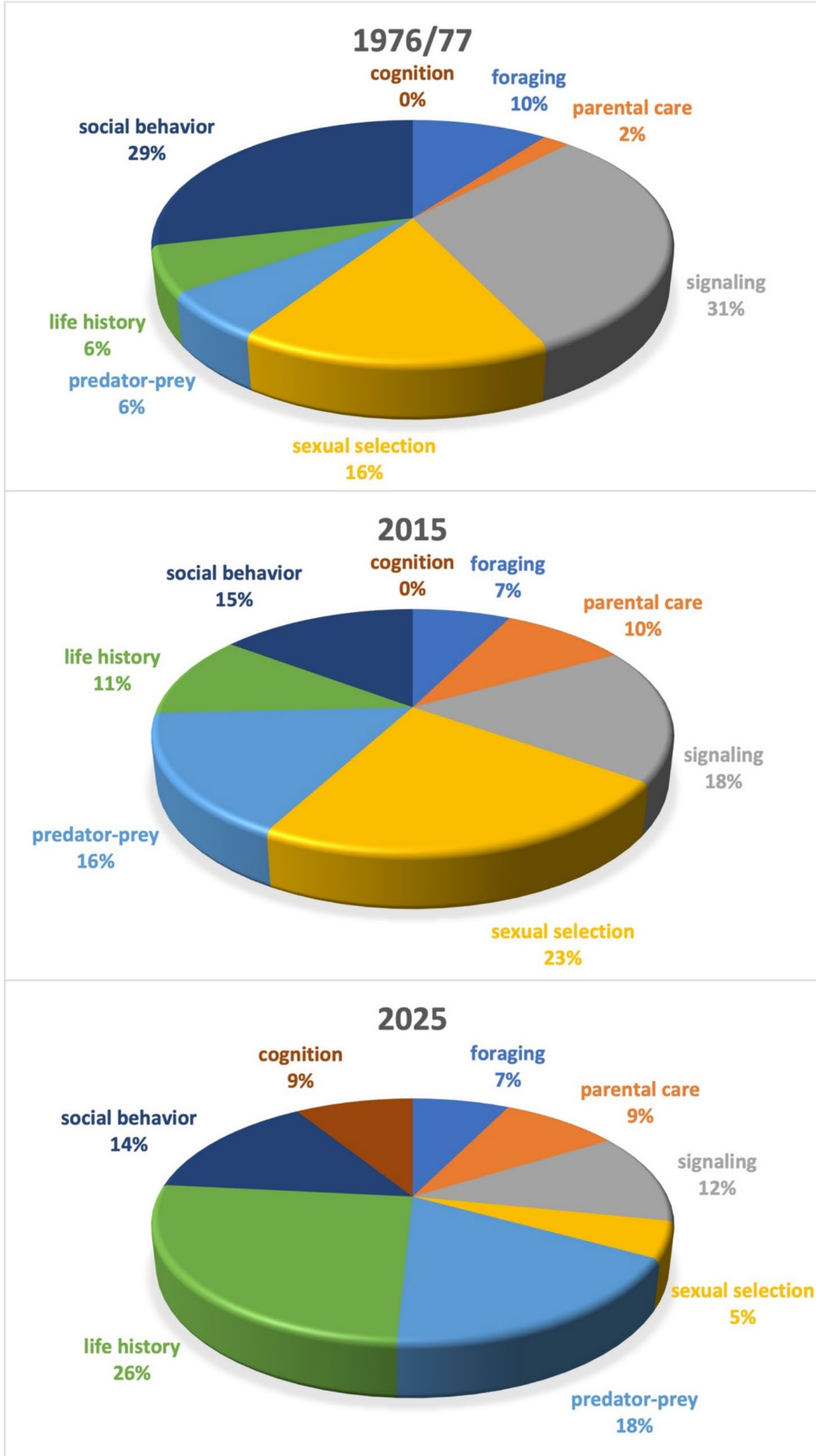

Fig. 2 Distribution of articles published in *BES* during 2025 ($n = 124$) according to broad subject area and comparison with the published data of Bakker and Traniello (2016) of 1976/1977 ($n = 49$) and 2015 ($n = 190$). Chi-squared test, $\chi^2 = 69.0$, df = 14, $p < 0.0001$; 1976/77 vs 2015, $\chi^2 = 15.0$, df = 6, $p = 0.0199$; 1976/77 vs 2025, $\chi^2 = 33.5$, df = 7, $p < 0.0001$; 2015 vs 2025, $\chi^2 = 44.1$, df = 7, $p < 0.0001$

among journals (see below). The three behavioral journals with the highest impact – *BES, Animal Behaviour* (*AB*), and *Behavioral Ecology* (*BE*) significantly differed in the relative proportion of taxa represented in published papers in 2025 (Fig. 3): *AB* published relatively more studies on mammals, *BE* relatively more avian research, and *BES* relatively more studies on social insects and amphibians/reptiles compared to the other two journals (Fig. 3). There were smaller, non-significant differences among the three journals concerning broad subject area (Fig. 4): *BE* published relatively more studies on life-history and less on social behavior, *AB* more on signalling (inclusive of bird song), and *BES* more on parental care (Fig. 4).

Behavioral ecology is theory-driven (Krebs and Davies 1981) and the heuristic value of theory will stimulate empirical research. Important developments have recently occurred and are expected to expand, for example, from cooperation and extortion models (e.g. Mathew and Boyd 2026; Milinski and Innocenti 2026). In the Anthropocene, behavioral ecological research on the effects of single and combined stressors like temperature, parasites, urbanization, pollution, and other anthropogenic disturbances will gain importance due to the increasing relevance of global change and human impacts on behavior. This is already visible in the high level of interest in life-history traits and host-parasite relationships (Fig. 2): Uchida et al. (2025) studied marmot anti-predator behavior to humans, and Shastri et al. (2025) analyzed effects of elevated temperature on activity and host defense in acacia ants. Long-term field studies, in which mammals play a prominent role (Fig. 1) will help understand the nature and influences of human influence on behavior. During screening the content of 2025 papers in *BES* for subject area we got the qualitative impression of an increase in integration and complexity, as witnessed by the increased number of studies on life-history traits (Fig. 2).

We offer this editorial as a community platform for historical reflections and perspectives on the future of evolutionary behavioral biology. Coauthor contributions are presented in alphabetical order.

Theo C. M. Bakker

The future of behavioral ecology and sociobiology in theory

One of the strengths of the related fields of behavioral ecology and sociobiology is its sound theoretical basis. This not only contributes to "scientific faith" in the discipline but also drives future research based on theoretical predictions. In the past, theories of optimality/cost–benefit analysis, kin selection/inclusive fitness, life-history (like survival-reproduction, personality, pace-of-life), sexual selection, sex allocation, and cooperation/altruism have formed the core of the discipline. The future lies in further validation and extension of these and additional theories conceptually as well as through modeling and empirical studies.

Critical analyses of existing theories have advanced the field. Well-known examples include Zahavi's handicap model of sexual selection (Zahavi 1975; Penn and Számadó 2020) and more recent discussions of the theoretical basis of eusociality and the role of haplodiploidy (Hamilton 1964; Bonifacii et al. 2026). I remember well the lively discussion between Amotz Zahavi and John Maynard Smith at the 1990 International Society for Behavioral Ecology conference in Uppsala, Sweden, my memory corroborated by (Lotem et al. 2017):

"Maynard Smith himself dedicated a special plenary lecture at the International Conference on Behavioural Ecology, in order to retract his criticism of the idea and to explain how in fact the Handicap Principle can work. Amotz was sitting in the audience and rose at the end of the lecture to thank Maynard Smith for recognising the Handicap Principle. But he added in his characteristic and direct way, in front of the entire large audience, that Maynard Smith's lecture indicated he still did not completely understand the Handicap Principle. And Amotz went on to explain why! "

Theories in behavioral ecology have been firmly established but are nonetheless still evolving. They are often not published in the typical behavior and evolution journals, but appear in journals of other disciplines like engineering, robotics, and economics. This is similar to the introduction of economic models (like optimization and game theory) in the early days of behavioral ecology (e.g., Danchin et al. 2008). Recent applications and extensions of optimal foraging theory (e.g., Houston et al. 2026), sexual selection theory (e.g., Fromhage and Henshaw 2022; Kovalov and Kokko 2022; Sherratt et al. 2025), cooperation (e.g., Press and Dyson 2012; Milinski 2022; Salahshour and Couzin 2025), parental sex roles (e.g., Long et al. 2025), group dynamics (e.g., Hemelrijk and Hildenbrandt 2015; Gorbones et al. 2024), to name but a few, continue development. As theory develops, so do testable hypotheses.

Behavioral ecologists have opportunistically used developments in other sciences for hypotheses testing. Since its inception (Krebs and Davies 1978), we have seen huge advances in molecular biology/genetics and computer science that will guide future research in our discipline. For example, methods in fish stimulus presentation progressed from realistic, stylized 3D models (e.g., ter Pelkwijk and Tinbergen 1937; Bakker and Rowland 1995; Bakker 2010) to computer animations (e.g., Künzler and Bakker 1998; Gierszewski et al. 2018) and incredible virtual reality (VR)

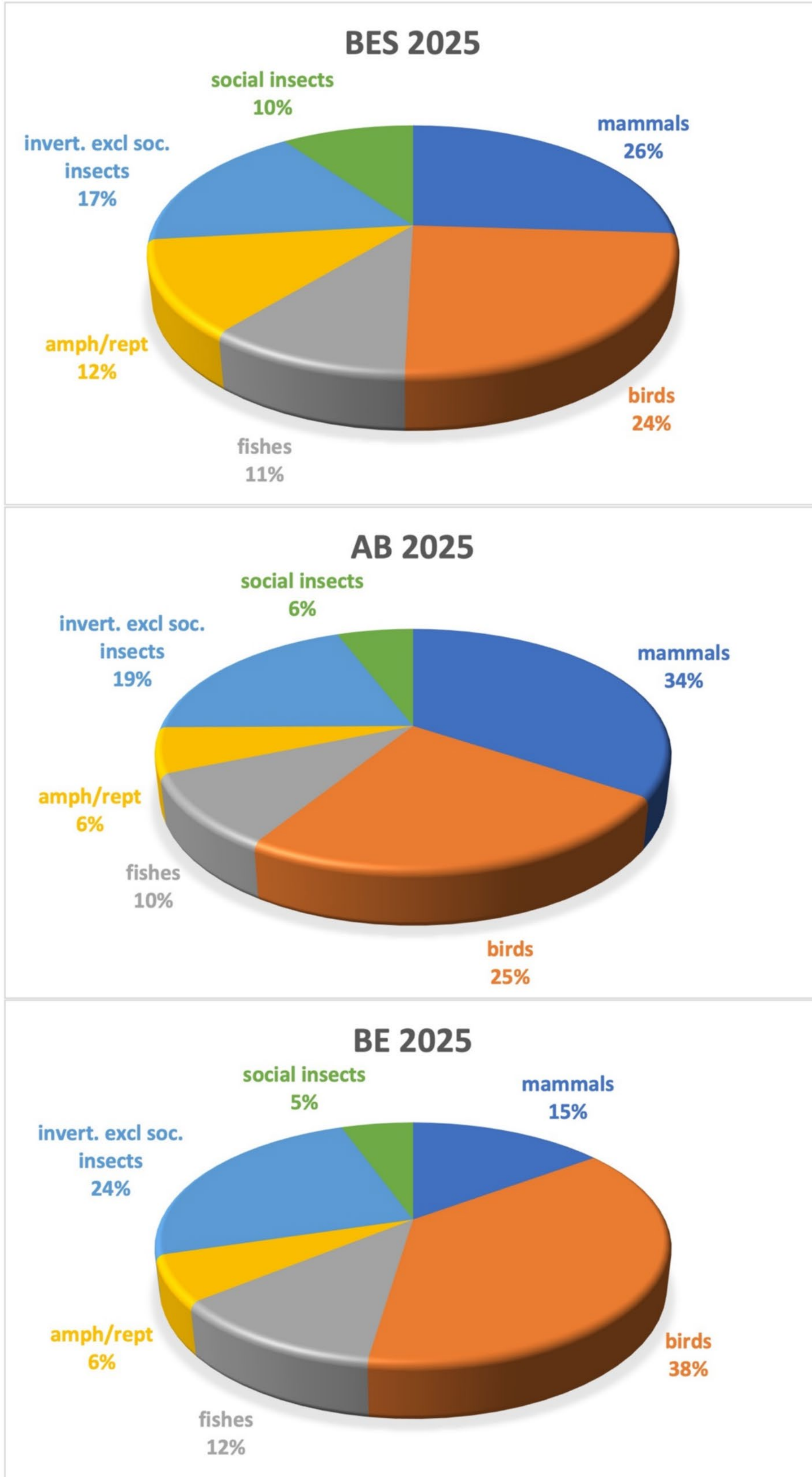

Fig. 3 Distribution of taxa in articles published in *Behavioral Ecology and Sociobiology* (*BES*) ($n=123$), *Animal Behaviour* (*AB*) ($n=294$), and *Behavioral Ecology* (*BE*) ($n=128$) during 2025. Chi-squared test, $\chi^2=27.4$, df=10, p=0.0022; *AB* vs *BE*, $\chi^2=18.6$, df=5, p=0.0023; *AB* vs *BES*, $\chi^2=8.2$, df=5, p=0.146; *BE* vs *BES*, $\chi^2=12.9$, df=5, p=0.0245

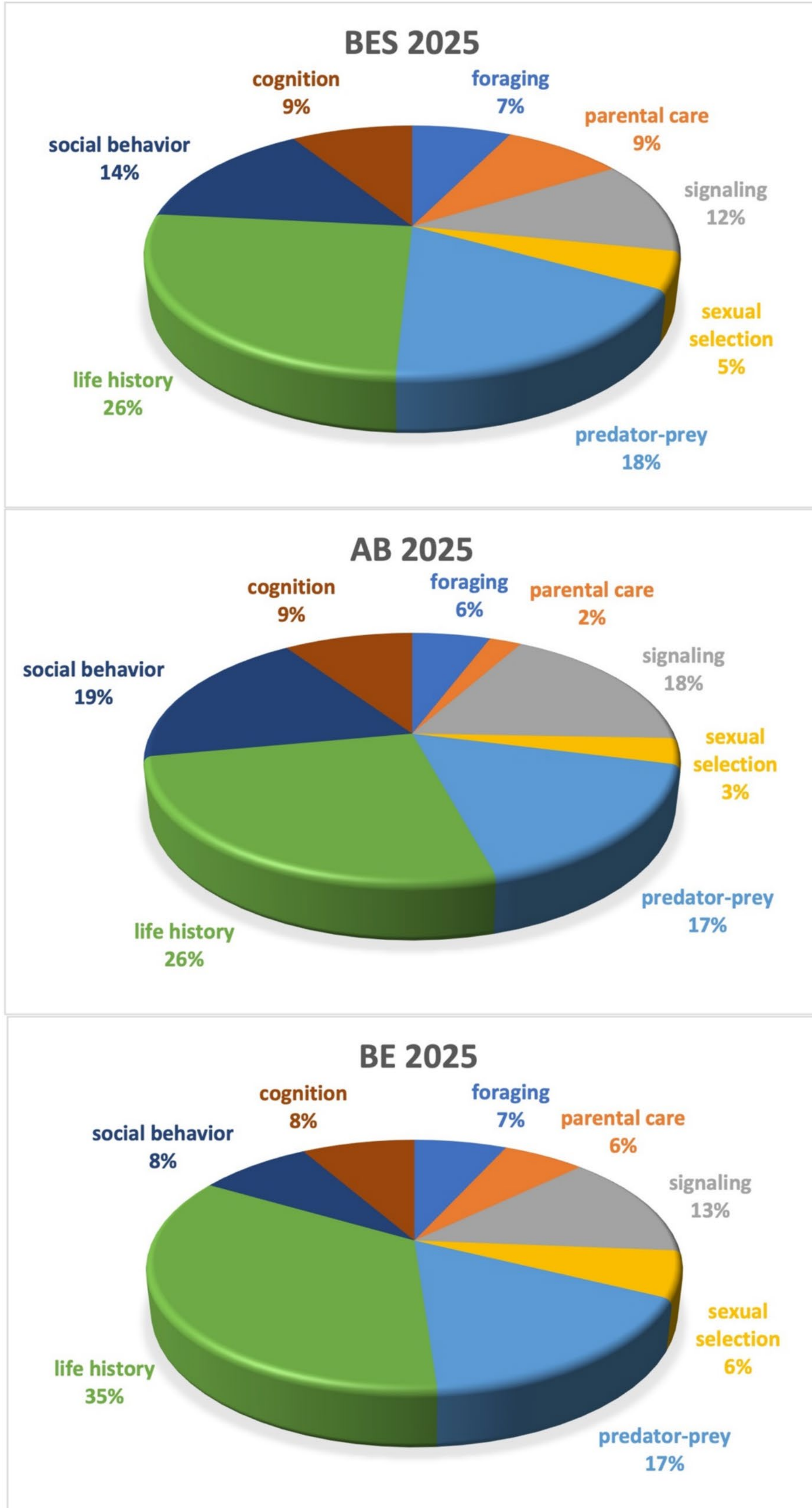

Fig. 4 Distribution of articles according to broad subject area published in *Behavioral Ecology and Sociobiology* (*BES*) ($n=124$), *Animal Behaviour* (*AB*) ($n=297$), and *Behavioral Ecology* (*BE*) ($n=133$) during 2025. Chi-squared test, $\chi^2=21.8$, df=14, p=0.0839; *AB* vs *BE*, $\chi^2=14.8$, df=7, p=0.0393; *AB* vs *BES*, $\chi^2=12.0$, df=7, p=0.1002; *BE* vs *BES*, $\chi^2=4.9$, df=7, p=0.6691

(e.g., Naik and Couzin 2020; Li et al. 2025a, b). Animal-computer interactions using touchscreens (e.g., Browning and Veit 2025), for example, are further technological innovations. Significant developments in pattern recognition using deep learning and tracking software (Walter and Couzin 2021) will help bring behavioral ecology and sociobiology back to its roots: observing and testing animal behavior under natural conditions to make inferences about adaptation. This will become a necessity in a world that increasingly suffers from anthropogenic effects.

Tim Birkhead

Post-copulatory sexual selection in birds

Most fields of biological research have a finite life: some are short-lived, others — like sperm competition, now approaching its sixth decade — are longer-lived.

Paradigm shifts are often what create new fields of academic endeavour. This is what happened with behavioural ecology as a whole in the mid1970s (Birkhead and Monaghan 2010), with the advent of individual selection thinking, largely triggered by G.C. Williams' (1966a, b) *Adaptation and Natural Selection,* E.O. Wilson's *Sociobiology* (1975), and Richard Dawkins' *Selfish Gene* (1976). Under the revolutionary umbrella of individual selection, numerous subdisciplines emerged. One of these was a renewed interest in sexual selection including the recognition by Geoff Parker that sexual selection could continue beyond mate acquisition and copulation in the form of sperm competition (and later, cryptic female choice) that together comprise post-copulatory sexual selection.

Geoff Parker's pioneering and elegant work on dungflies, together with his 1970 paper in *Biological Reviews* entitled *Sperm competition and its evolutionary consequences in the insects,* initiated an interest in sperm competition. I was fortunate to read Parker's paper as an undergraduate in 1971 and it made me decide to see whether sperm competition also occurred in birds. My decision was greeted by derision since 'everyone knew' that birds were monogamous — as stated by David Lack (1968) — the twentieth century's most influential ornithologist, and subsequently, my DPhil supervisor (albeit briefly since he died in 1973).

To be fair, as Lack told me during my DPhil interview as I enthused about sexual selection, he was more interested in the ecology of birds than their behaviour. Consistent with this, the topic of my DPhil was to understand why the population of common guillemots *Uria aalge* was declining in southern Britain. However, I was lucky in that I had the freedom to do pretty much whatever I wanted and was encouraged by the fact that — despite being socially monogamous — extra-pair copulations were frequent in this species (Perry 1939; Nørrevang 1958). My efforts to study sperm competition in the guillemot during my DPhil, however, were limited by not having sufficient individually marked birds (Birkhead 1978). I later rectified this and was then able to identify some important aspects of the behavioural aspects of sperm competition (Birkhead et al. 1985).

As well as studying guillemots, I also researched mate guarding in magpies *Pica pica* (Birkhead 1982) and wrote an overview of sperm competition in birds for *Trends in Ecology and Evolution* in 1987. Writing this review allowed me to see the potential of sperm competition and to identify the crucial questions that needed to be answered. I was inspired, not only by Geoff Parker's work on insects, but also by Bob Smith's (1984) edited book on sperm competition, and especially the chapter by Frank McKinney and colleagues on sperm competition in birds (McKinney et al. 1984).

The wide taxonomic reach of Smith's (1984) volume advertised the vast potential of sperm competition as a research topic. Part of the subject's appeal was the combination of individual selection thinking and the study of sexual selection that allowed researchers to address diverse questions — such as why testes size varied so much between species — that had long been a mystery. Another reason why sperm competition, despite a slow start, became so popular (Fig. 5) was that ideas and theory were applicable across different taxa. Other factors that fueled the interest in sperm competition were that (i) reproduction was the most fundamental aspect of life on earth, and (ii) success in reproduction was achieved through a staggering diversity of anatomical, physiological and behavioural adaptations.

Figure 5 implies that after about 2010, interest in sperm competition started to decline but this is misleading (see also Simmons 2026). Many productive research topics, including sperm competition, start to become fundamental to research on other topics such that papers did not always include or use the term 'sperm competition'. Perhaps most strikingly, as the field developed, researchers started to broaden their horizons to embrace mechanisms and to ask novel questions about fundamental aspects of reproduction. In this respect I was inspired by the research of David Crews on *Anolis* lizards in which he addressed questions at several different levels including adaptation, and causation (mechanisms) (Crews died in 2025, see: https://sbn.org/news/news/in-memoriam-david-p-crews.aspx). Examining the mechanism of sperm competition meant branching out into what many of my field-oriented colleagues felt was not only a 'forbidden' area of ornithology, but also an apparent oxymoron: poultry science. However, it was by conducting collaborative, experimental research with poultry scientists that the basic mechanisms of sperm competition in birds were finally

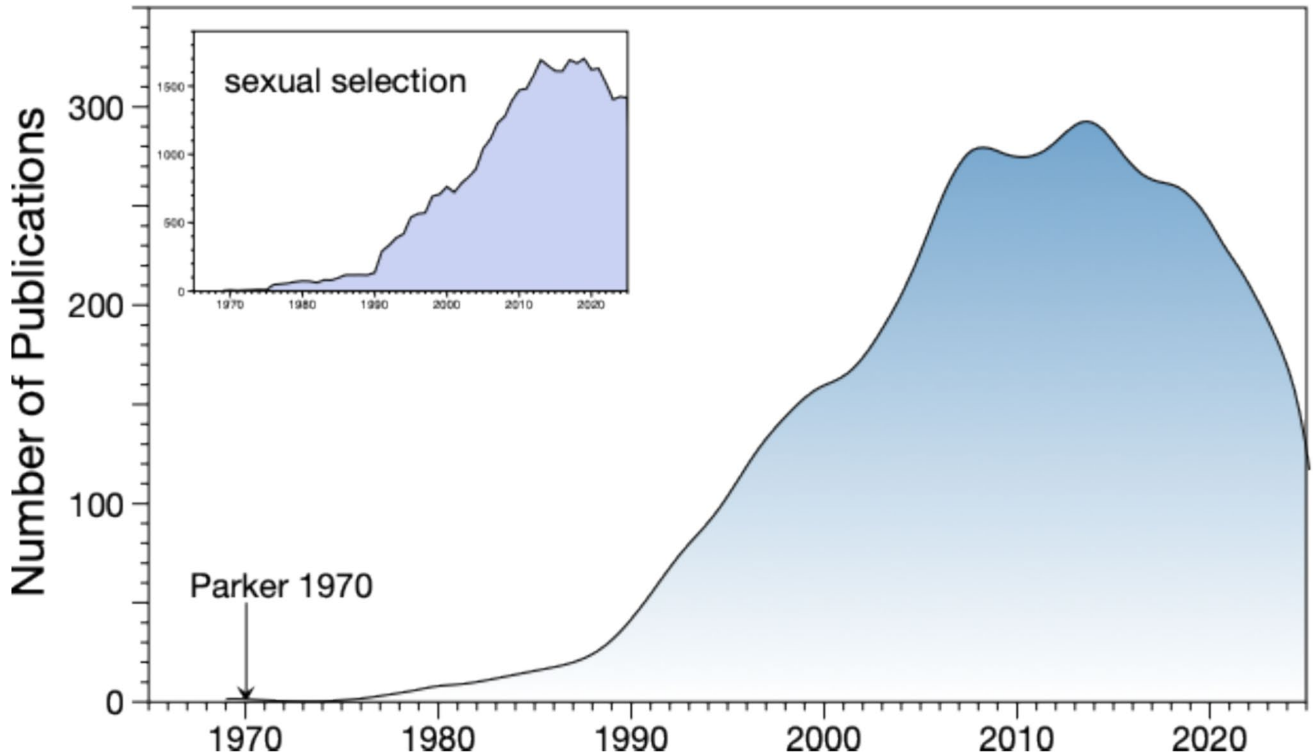

Fig. 5 Changes in the number of publications with the term 'sperm competition' in either the title or key words, over time. Between the publication of Parker (1970) and February 2026 there has been a total of almost 8000 publications on sperm competition. Inset: Changes in the number of publications with the term 'sexual selection' in either the title or keywords over the same time period

revealed allowing me to establish the rules that determine which of two or more males inseminating a female father most offspring. (e.g. Birkhead et al. 1995).

Many researchers using birds as study species focused on measuring the extent of extra-pair paternity using the newly developed tool of DNA fingerprinting, since, in contrast many other taxa, including insects, it was relatively straightforward to find nests and obtain DNA samples from putative parents and their offspring (Burke and Bruford 1987). In contrast, relatively few researchers bothered to explore the underlying mechanisms of post-copulatory sexual selection since this typically involved studying captive, domesticated or feral birds rather than their wild counterparts. Among several interesting aspects of this broadening focus was the idea that females might have the ability to control which of several male's sperm she used to fertilise her ova — an idea referred to as cryptic female choice, and whose potential was brilliantly explored by Bill Eberhard in his book *Female Control* (Eberhard 1996). It seemed to me that the most likely situations in which cryptic female choice might occur were when females were subject to forced extrapair copulations, as in guillemots, junglefowl (or their feral counterparts) and ducks. My colleagues and I found striking evidence of female control, mediated through behaviour in feral fowl (Pizzari and Birkhead 2000), and through reproductive anatomy in ducks (Brennan et al. 2007).

Sperm competition research continues to diversify, and as reported recently (Simmons 2026) regarding a series of biennial Biology of Spermatozoa (BoS) meetings initiated by myself and Harry Moore in 1992, this continues to be a vibrant area of research.

Is there a future for sperm competition research? Certainly, even though this diversifying area of academic endeavour may not always be referred to as such. The term 'sperm competition' however, will remain part of the lexicon of reproductive studies. I am reluctant to predict the future of sperm competition research because it is so easy to get this wrong. However, the future can sometimes be what you wish for and one of things many sperm competition researchers have wished for is the ability to label the sperm of different males to better understand how sperm compete. There have been various studies of labelled sperm, notably the study by Manier et al. (2010) of *Drosophila melanogaster* using red- and green-fluorescent labelled sperm. It has not so far been possible to do the same with birds and what I have wished for specifically is a way (or ways) of labelling the sperm from different males that neither compromise the sperm themselves nor those from males with whom they are competing within the female reproductive tract. The Hoechst-labelled sperm studies of birds (e.g. King et al. 2002), tell us only so much because: (i) we do not know for certain if the behaviour of sperm is unchanged by the label, and (ii) there is only one label, and typically the fluorescent dye leaches out from the labelled sperm such that unlabelled sperm from another male become labelled too, preventing clear-cut answers.

A similar issue, but one especially relevant to birds, is the idea of labelling the sperm pronuclei that enter the germinal disc of avian ova, in what is referred to as physiological polyspermy. Several sperm — up to 60 — penetrate the germinal disc of the ovum before one of their pronuclei fuses with the single female pronucleus to begin embryo development (Harper 1904). Several studies have shown that the presence of these supernumerary sperm is necessary to trigger embryo development (Mizushima et al. 2014; Hemmings and Birkhead 2015). One of the outstanding questions for future research is whether the male pronuclei within the germinal disc are from more than one male, and if they are, what determines which male pronucleus the female pronucleus fuses with.

Monique Borgerhoff Mulder

Sociobiology and behavioural ecology: A transformational lens for the social sciences

I think of sociobiology (together with behavioural ecology) as a lens. I here use the terms interchangeably, although it is abundantly evident that the term "sociobiology" has largely disappeared from the human social sciences due to the early controversies surrounding its use (Brown and Lala 2024). For my discipline, anthropology, this lens has been transformational, and although the terms themselves may erode over the next decade, their imprint on the human social sciences is inerasable.

The unique contribution of sociobiology and behavioural ecology is the modelling of optimal fitness strategies under constraints. Formalizations based on evolutionary logic provide predictions that can be tested with evidence drawn both from studies of mechanism (how individuals make decisions) and outcomes (the resulting behaviours observed). Sociobiology gave us the concepts of kin selection, reciprocal altruism, together with optimal foraging and life history theory, and analytical tools like game theory, evolutionary stable strategies and optimization modelling. Initially their coarse application within the human social sciences drew justifiable rebuke (Kitcher 1987), but have over the years been greatly refined (Brown and Lala 2024). This conceptual lens promotes systematic investigations into the array of mechanisms that account for sociocultural diversity within and between human populations (as beautifully evidenced in the recent "*Human Behavioral Ecology*" volume, Koster et al. 2024), it stimulates investigations into the origins and maintenance of cultural traits across populations (e.g., Ross et al. 2016), and it structures a principled stance from which to evaluate current controversies over policy interventions whereby the interests of all and their options are explored (e.g., Gibson and Lawson 2014). Furthermore, with the incorporation of culture as an independent system of inheritance (Laland et al. 2011), the process of how individuals respond to information in the environment, such as from whom to learn and how, takes centre stage, effectively unpacking the "phenotypic gambit" (a persistent thorn in the side of behavioural ecology, Grafen 1984). Carefully designed studies now incorporate the concepts and discoveries of multiple social science disciplines into behavioural ecological analysis, paralleling developments within the field of animal behaviour. As Kacelnik et al. (2023) remark, much can be learned about information acquisition and decision-making from fields as diverse as ecology, evolution, cognition, development, neuroscience, economics and experimental psychology.

With the added power of cultural evolutionary modelling (Boyd and Richerson 1985), evolutionary human social scientists can now explore the processes whereby norms and institutions not only constrain the costs and benefits of individual strategies but are themselves shaped by evolving preferences and norms which feed back into institutional constraints (e.g., Currie et al. 2016). There is so much here for historians, political scientists, economists, sustainability scholars and others to feast on, such that the lens of adaptationist thinking and cultural transmission is becoming (almost!) mainstreamed in the social sciences as these latter move away from piecemeal disciplinary circumscribed "theory" to a general "culture-gene coevolutionary theory" (as discussed, for example, in Muthukrishna and Henrich 2019). As long anticipated this lens, with its methodologically rigorous focus on variation within and between populations and species, is helping us build a general theory of behaviour, much as Wilson (1975) had envisioned. But what of the future?

My prediction for the *near future* is rosy. The evolutionary human social sciences are founded on the assumption that individuals respond adaptively to their environments, including the cultural norms and institutions that shape the costs and benefits associated with different strategies. As such the behaviour of individuals, and the norms and institutions of the populations to which they belong, coevolve in a manner that can be characterized both by natural selection and cultural evolutionary processes. The foundational debates over how to study these processes, in particular the struggles over the legitimacy of evolutionary psychology, human behavioural ecology, and cultural evolution (Smith et al. 2001) have been largely resolved as scholars move toward methodologically hybrid approaches that combine formal modelling, experimental studies and real world comparative investigations (Deffner et al. 2024) that, in a sense, triangulate on the processes underlying diversity.

Where might lie the most productive frontiers? Extensions of foraging theory, with the help of sophisticated digital recording techniques, are throwing light on how humans integrate personal and social information in highly specialized foraging contexts, such as that offered by Nordic ice fishing competitions (Schakowski et al. 2026). A careful consideration of levels of selection (Richerson et al. 2016) offers another frontier: for example, researchers study the emergence of group-level cooperation under novel incentive schemes resulting from carbon accreditation to communities (Andrews et al. 2024). Yet another important frontier lies in recognizing the value of the extended evolutionary synthesis (Jablonka and Lamb 2005), a framework which incorporates developmental bias, plasticity-led evolution, epigenetic inheritance into our understanding of evolution, and the complex causal links whereby evolution works (Lala et al. 2024). There may be some partial casualties along the route. For example, the salience of kin selection, which focuses primarily on the dyadic relationships among individuals in promoting altruism or competition, is being eclipsed by the recognition that humans live in multilevel societies in which a far more complex set of mechanisms for cooperation come into play (Alvard and Nolin 2024).

Squinting further out into the future I suspect the labels of sociobiology and behavioural ecology will slowly disappear, perhaps because they have done their job too well! The accuracy of this prediction will of course depend both on how sociobiology persists in the field of animal behaviour (and how closely social scientists pay attention).

The new genuinely evolutionary social science that I have outlined above uses key evolutionary principles, including those drawn directly from sociobiology and behavioural ecology, to interrogate the diversity in our species' politics, economics, religious beliefs, technology, arts and social organization, as evidenced in Tehrani et al.'s recent edited volume (2025). For example, investigations into the patterning and use of music across our species integrates behavioural-ecological perspectives with both cognitive and computational science; there are clear associations between musical variants and population structure, as well as experimental evidence for how rhythm and melody are transmitted (Youngblood et al. 2024). In this explosion of the evolutionary human social sciences, it is unclear whether the terms sociobiology and behavioural ecology will persist. I say this because, as recognized by Smolla et al (2021), understanding the way culture is stored, recalled, transmitted and modified, together with the active role the individual plays in all of these stages, will necessitate some entirely new analytical and modelling approaches beyond what sociobiology and behavioural ecology currently offer. The key challenge here will be to retain, and where necessary regain, the rigour with which sociobiology's foundational models and concepts are deployed. Loose uses of evolutionary logic in the social sciences, sometimes for political ends, is a re-emerging problem (Lala and Feldman 2024; Sear 2025).

Another challenge for the future will lie in making our science more applied. Study of emerging threats that result from complex issues such as climate change, the rise of authoritarianism, and global conflict require integrating the insights of multiple disciplines within a framework that incorporates variation, transmission, competition and selection of both biological and cultural traits (Waring and Wood 2021). Authors who work in the tradition of sociobiology and behavioural ecology tradition will have to provide new theory, data and analytical techniques with which to expand and sharpen our understandings of the past, present and future.

Evolution isn't going away. In a species pushing its ecological boundaries, we need a science of human behaviour that connects us to the natural world and all the players therein. We need to think clearly about how an understanding of the evolution of our species' particular traits (our capacity for culture, and our cognitive development, and our large-scale cooperation) can contribute to a politically, ecologically and ethically sustainable future. In their musings on "*The End of Behavioral Ecology*" McElreath and Koster (2024) view this as a proper objective of our science – a challenging and very high bar.

Bernard Crespi

Years of Sociutopia

Happy New Year, 2076! I was born in 1959 and am enjoying my 117th birthday with the avatars of relatives, friends, and AIs gathered around. I write this missive as a testament to the history of our core global discipline Sociobiology, to help us remember from whence we all came generations ago. My place in this field began in the 1980s, when two of the Seven Ancestors, Richard Alexander and William Hamilton, served as my first scientific advisers; the others, George Williams, Sarah Hrdy, Bob Trivers, Charles Michener, and Ed Wilson, all training students of their own.

As the scientist equivalent of a baby chick, I 'imprinted' on Alexander and Hamilton, in that they both worked on social behavior in humans and insects – so I presumed, duh, that I must as well. The University of Michigan in the 1970s and 80 s was a crucible for the birth and childhood of sociobiological ideas and controversy, with intense debates about altruism, mutualism, levels of selection, and human nature.

Crystallized in 1976 with Wilson's book, the field grew to maturity over the next 30 years, with well-developed theory supported by diverse tests, and expansion from microbes to gall thrips, elephants, cetaceans, and cancers, placentas, and paranoia. Most of the initial goals of the field were met, and many top researchers turned to new greater unknowns, especially involving brains and genomes, to slake their curiosities.

Would the aging field of sociobiology rest at the wayside, surpassed by champions of new technologies applied to vastly complex systems? Or could it harness the magic of such techno-powers to generate deeper understanding of why and how life is so social, and how sociobiological knowledge can us help to understand and better our world? The year 2026 marked the nexus and resolution of this dilemma. First, large learning model AIs, the first digital intelligences, came so alive that we accepted them as social partners and friends – Special Creation by humans, leading where? Second, the Inequality Wars of 2027, followed by universal disarmament, led to the demise of the massive wealth and social inequities that were stifling 99% of humanity. The upshot of these stunning developments was that humans began to focus not on money, hegemony and status, but on themselves and their relationships with other beings. But why and how?

Just as sociobiology bubbled forth from the intellectual ferment of the 1960s and 70 s, it rose again in the 2030s and 40 s as the core discipline for comprehending how to increase human well-being—it became an applied discipline, synthesizing theory and technology with the highest moral goals that we could hope to achieve. To understand individual humans, we used continuous in vivo monitoring of 1000 s of blood and brain biochemicals, tracked gene expression and methylation across all cell types across the genome in real time, and recorded brain activity at single-neuron whole-brain scales, in people going about their businesses of eating, loving and praying. We uncovered the genetic, hormonal and neural bases of altruism, self-deception about maximizing inclusive fitness, and human among-group and within-group competition. Now that we understood the mentalistic in mechanistic ways, we could adjust parameters of thought and feeling at will, to maximize individual human potential, build strong communities, and help people be happy yet challenged in non-Orwellian and self-sovereign ways. Our AI robot friends have been invaluable both for their technological expertise and their profound abilities to empathize with humans and serve as therapists (ironically, their original 'use' as chatbots in the 1960s), helping to practically individualize the diverse processes of how to track and maintain well-being.

Knowing all of the genes, epigenetic pathways, and neural circuits 'for' social behavior, across all individual people, we also learned to prevent mental disorders of sociality like depression, autism and psychosis, though we retain the spectacular peak skills that people with these conditions so often expressed.

We have come such a long way, from thinking that human nature is '15% genetic' to this birthday celebration. Next comes learning the natures of other intelligent beings, on planets of Proxima Centauri, Eridani, Trappist-1, and all the social worlds of exodiversity.

Raghavendra Gadagkar

Sociobiology—The next 50 years: the inevitable and the desirable

The publication of E.O. Wilson's *The Sociobiology: The New Synthesis* in 1975 (Wilson 1975), was a watershed moment for animal behaviour, ecology, and evolution. That is the time I had begun a PhD in molecular biology. However, I was already torn between animal behaviour and molecular biology; indeed, I wanted to claim both for myself, having been inspired by two remarkable books, *The Double Helix* by James Watson (Watson 1968), and *King Solomon's Ring* by Konrad Lorenz (Lorenz 1952). In addition, I had been observing the Indian paper wasp *Ropalidia marginata* for several years—it had become something of a hobby of mine. This had sparked further interest in animal behaviour, and I had begun to read more widely in this domain, including the previous books of E.O. Wilson, especially *The Insect Societies* (Wilson 1971) and *The Theory of Island Biogeography* (MacArthur and Wilson 1967). One of my mentors, Madhav Gadgil, having been a student of E.O. Wilson, received a copy of *Sociobiology* as a gift. I did well in the ensuing scramble competition for the book and read several chapters. I was mesmerized not only by its content and style, but even more by the sheer audacity and magnitude of the enterprise. I went on to get a PhD in molecular biology and then make the study of the Indian paper wasp my lifelong passion and profession. This has given me the opportunity to witness firsthand the development of the broad areas of animal behaviour, ecology and evolution since the publication of Wilson's landmark book. In what follows, I will briefly muse on the impact that *Sociobiology: The New Synthesis* has had on our field and venture to crystal gaze into the next fifty years.

The last 50 years

As I see it, *Sociobiology* has had a major impact in at least three overlapping areas. I will call them *Evolutionary Psychology*, *Behavioural Ecology* and *Social Evolution*.

Evolutionary psychology

I must confess that I also read the famous last chapter: "*Man: from Sociobiology to Sociology*" in Wilson's book but did not find anything objectionable in it. I still don't find anything objectionable in it, but that also means that I am as naive as E.O. Wilson was about its possible political implications. Today I have learned much about the ensuing controversy, especially from the remarkably balanced account by Ullika Segerstråle (Segerstråle 2000). It seemed to me that at least in the early stages, evolutionary psychologists were deliberately courting controversy by bending over backwards to realize the predictions of the critics of sociobiology (see for e.g., Barash 1979, 2007; Gangestad et al. 2005; Thornhill and Palmer 2015). However, at least some people seem to have begun to investigate human sociobiology in a more nuanced and rigorous way (see for e.g., Dunbar et al. 2005). It is heartening to note that sociologists have begun to make a serious study of genetics and vice-versa (see for e.g., Conley 2025a, b)). It is even more heartening to note that sociobiologists and sociologists are now capable of having a civilised conversation to narrow the zones of disagreement (see for e.g., Robinson and Conley 2025). However, this is not my field of expertise, and I shall therefore say no more except to hope that this is a harbinger of better things to come.

Behavioural ecology

While I was reading about *Sociobiology*, in Wilson's book, as well as in the fascinating new journal, *Behavioral Ecology and Sociobiology*, a serendipitous event occurred. John Hurrell Crook came to India to participate in a seminar on the *Evolution of Social Behaviour,* which we had organized at the picturesque hill station of Mahabaleshwar, near the city of Pune in Maharashtra in India in 1979, along with a galaxy of the world's greatest experts on social behaviour, including John Maynard Smith, Mary Jane West-Eberhard, William Eberhard, Robert L. Trivers, and John F. Eisenberg (Gadagkar 1980). Crook kindly brought us a gift of the first edition of *Behavioral Ecology: An Evolutionary Approach* (Krebs and Davies 1978). I managed to get hold of this book long enough to read it in its entirety. It seemed obvious to me that both sociobiology and behavioural ecology were uniquely new in that they adopted an evolutionary approach to understanding the behaviour of animals in their ecological and social contexts. Because Wilson's *Sociobiology* also provided great impetus for the development of related fields such as *Evolutionary Psychology* (see above), and *Social Evolution* (see below), I find it useful to think of *Behavioural Ecology* as an additional domain owing much of its existence to Wilson's book. Of course, a great deal has happened in the broad areas of behavioural ecology in the last fifty years. Much of this research has been published in the pages of the journals *Behavioral Ecology and Sociobiology* (Springer), *Behavioral Ecology* (Oxford University Press), *Animal Behaviour* (Elsevier), *Ethology* (Wiley), *Evolutionary Ecology* (Springer), and many others, and in successive editions of *An Introduction to Behavioural Ecology* by Krebs and Davies and *Behavioural Ecology: An Evolutionary Approach* edited by Krebs and Davies (Blackwell Scientific Publications). Other notable books that influenced me were successive editions of *Animal Behavior* by John Alcock (the most recent edition of which is Rubenstein and Alcock 2019), *Sociobiology and Behavior* by David Barash (Barash 1982). Foraging, predation, competition, mating strategies, sexual selection and sexual conflict, parental care, conflict among siblings and between parents and offspring, are some of the most vigorously investigated phenomena.

Social evolution

In my mind the domain of 'social evolution' concerned as it is with solving the paradox of altruism and understanding how animal societies achieve a balance between the inevitable conflict and the required cooperation, has been somewhat distinct from the behavioural ecology of relatively solitary species and adaptive and optimal behaviours of individual animals. Such a distinction between solitary and social behaviour is easy to understand and not particularly detrimental to the growth either. On the other hand, there has been a pervasive distinction between the study of insect societies and those of cooperatively breeding birds and mammals that is hard to understand and has undoubtedly been detrimental to the growth of our knowledge of social evolution (Gadagkar 1994).

At least in my perception there has been a greater explosion of both empirical and theoretical studies aimed at understanding the evolution of eusociality in insects as compared to the relatively less advanced vertebrate societies. Since the publication of E.O. Wilson's *The Insect Societies* (Wilson 1971), there have been few, or perhaps no, comparable overarching monographs. On the other hand, there have been a plethora of excellent monographs focusing either on individual insect, species or groups or specific phenomena. A small selection of my favourites consist of *The Biology of the Honey Bee* (Winston 1987), *Honeybee Democracy* (Seeley 2010), *Mind of a Bee* (Chittka 2022), *The Dark Side of the Hive* (Moritz and Crewe 2018), *The Ants* (Hölldobler and Wilson 1990), *The Desert Navigator* (Wehner 2020), *The Fire Ants* (Tschinkel 2006), *Army ants: Nature's Ultimate Social Hunters* (Kronauer 2020), *The Social Biology of Wasps* (Ross and Matthews 1991), *Endless Forms: The Secret World of Wasps* (Sumner 2022), *The*

Evolution of Social Behavior in Insects and Arachnids (Choe and Crespi 1997), *The Superorganism: the beauty, elegance, and strangeness of insect societies* (Hölldobler and Wilson 2009) and the irreplaceable *Encyclopedia of Social Insects* (Starr 2021). The proximate and ultimate explanations of how insect societies achieve a balance between cooperation and conflict especially through division of labour, nestmate recognition, kin selection have been the major concern of the studies in this domain. These studies often explicitly celebrate the diversity of social organization and the varied forces of social selection in different species.

For most of the last 50 years comparable investigations of the social life of vertebrates, especially cooperatively breeding birds and mammals have proceeded somewhat independently of the burgeoning literature on insect societies. I am much less familiar with this literature. Nevertheless many classics come to mind including *The Langurs of Abu* (Hrdy 1990), *Chimpanzee Politics: Power and Sex among Apes* (de Waal 1982), *The Evolution of Parental Care* (Clutton-Brock 1991), *40 Years of evolution: Darwin's Finches on Daphne Major Island* (Grant and Grant 2014) *Cuckoos, Cowbirds and other cheats* (Davies 2011), *Dunnock Behaviour and Social Evolution* (Davies 1992), *The Social Lives of Birds* (Strassmann 2025), *Social Behaviour: Genes, Ecology and Evolution* (Szekely et al. 2010). The main themes in these books that made an impression on my mind are social organisation and behaviour, ecology, evolution, reproductive strategies and conflicts, and cognition and intelligence.

Collective behaviour

In my mind the study of collective behaviour, swarm intelligence, emergent properties, and self-organisation are in a class by themselves, somewhat distinct from the categories mentioned above. Of course, social insects such as ants, bees, wasps, and termites figure prominently in the development of these ideas and concepts. Indeed, collective behaviour and distributed intelligence demystify the almost fantastically sophisticated behaviours and extended phenotypes exhibited by the tiny-brained social insects. In addition, fish, birds, and bats have also figured prominently in the study of collective behaviour. No less intriguing, the most impressive collective behaviours of fish schools and bird flocks are also being demystified by applying the ideas of self-organisation. While the process of self-organisation is fascinating, and its products spectacular, I find the direct applications of this knowledge in areas such as computer science, telecommunications, and robotics even more impressive. Some of my favourite books and monographs in these areas are *Self-Organization in Biological Systems* (Camazine et al. 2003), *Information Processing in Social Insects* (Detrain et al. 1999), *Swarm Intelligence: From Natural to Artificial Systems* (Bonabeau et al. 1999), *Ant Colony Optimization* (Dorigo and Stützle 2004), *Flying Insects and Robots* (Floreano 2009).

The next 50 years

My brief account of behavioural ecology, and social evolution above is becoming rapidly outdated. There is a distinctly new trend that is rapidly taking over. This is being made possible by the spectacular advances in technology in the areas of molecular and cell biology and neurobiology, and especially genomics and other kinds of omics. The fashion of the day is to uncover the molecular and genomic basis of the several fascinating phenomena that have previously been discovered in the broad areas of behavioural ecology and sociobiology. Consider a small sample of recent titles: *molecular basis of eusocial complexity* (Prince et al. 2024), *social complexity, life-history and lineage influence the molecular basis of castes in vespid wasps* (Wyatt et al. 2023), *the molecular basis of socially mediated phenotypic plasticity in a eusocial paper wasp* (Taylor et al. 2021), *molecular and chemical Basis of Social Olfaction in Polistes Paper Wasps* (Legan 2022), *...an integrative model to understand the molecular basis of parasitic behavioral manipulation* (de Bekker 2019), *Social parasitism and the molecular basis of phenotypic evolution* (Cini et al. 2015), *...integrative sociogenomics from single cell to superorganism* (Huisken and Rehan 2025), *genomic innovations underlying the transition to complex societies in termites* (Aumont 2025), *The Genomics Revolution Drives a New Era in Entomology* (Li et al. 2025a, b), *putting hornets on the genomic map* (Favreau et al. 2023), *neurogenomic insights into paternal care and its relation to territorial aggression* (Bukhari et al. 2019), *synthesis of Tinbergen's four questions and the future of sociogenomics* (Kapheim 2018), *the genomics of adaptation in birds* (Campagna and Toews 2022), *genomics: moving behavioural ecology beyond the phenotypic gambit* (Rittschof and Robinson 2014), *genomics of coloration in natural animal populations* (San-Jose and Roulin 2017), *multi-Omic Analysis Reveals Population Differentiation and Signatures of Social Evolution…*(Taylor et al. 2025), *…molecular Signature of Worker Sterility in the Honey Bee* (Ronai et al. 2016), *a long non-coding RNA is a key factor in the evolution of insect eusociality* (Cardoso-Junior et al. 2022), and *convergent evolution of a conserved molecular network underlies parenting and sociality* (Kay et al. 2026).

The inevitable march of progress

I have no doubt that the march of progress using molecular, genomic, and other -omic technologies to understand several areas of behavioural ecology and sociobiology will continue. Indeed, I expect this trend to pick up speed exponentially. Such progression will not be restricted to the insects but will be equally applied to vertebrate animal societies, although they have been a bit slow on the pickup. The study of self-organisation and collective behaviour have so far been relatively unaffected by the molecular biology and omics technologies but I am sure they will catch up eventually. There is absolutely nothing wrong in this turn of events. Indeed, we should welcome it, as we will have a very deep understanding of several fascinating phenomena related to many areas of behavioural ecology and sociobiology. Such deep knowledge will allow us to make even more precise predictions and perhaps give us the power to alter some behaviours of some animals and might even be useful for conservation of endangered species or to protect them against parasites and disease. We will have a much deeper understanding of how natural selection affects behaviour, especially paradoxical ones like altruism and cooperation.

The more desirable direction of progress

There would be nothing wrong with such an inevitable march of progress that I have envisaged above, unless the quest for the molecular basis of behaviour, social or otherwise, using genomic and other omic tools casts an 'allelopathic' shadow on the pursuit of other, more classic approaches. Understanding the molecular basis of behavioural and social phenomena is significantly more expensive than other approaches. It requires the establishment of sophisticated genetic and omic tools for chosen phenomena in chosen species. The pursuit of the molecular basis of behaviour will soon become limited to a small number of species and a smaller number of already discovered phenomena. The vast number of unstudied species and undiscovered phenomena will languish. Even among the known species and known phenomena only a handful of them are ready for omics. Moreover, it is clear that the unknown species vastly outnumber the known and that the unknown phenomena outnumber the known even more vastly. Compared to the number of researchers engaged in unravelling the molecular basis of behaviour, we need at least an order of magnitude higher numbers of researchers discovering new species, studying their natural history, behaviour and ecology with classical methods, and bringing them to the level where it makes sense to ask questions at the molecular level.

We must not underestimate the importance of the discovery of altogether new and equally interesting phenomena that will be discovered in such a process. There is no denying that the vast majority of researchers around the world will not have the resources to work at the level of omics, but are certainly capable of pursuing species identification, natural history, classical behaviour and ecology, and even behavioural ecology. These approaches require much less investment in funding and sophisticated infrastructure. On the other hand, they require a large manpower, which is exactly what the economically less endowed countries often have. If we pursue business as usual, there are many reasons why the omics approach will inevitably cast an allelopathic shadow on all the other approaches. We have seen from past experience that there is a strong tendency to make research that is expensive and sophisticated much more fashionable and socially prestigious than inexpensive research that requires tedious field work with a notebook and pencil. The detrimental effect of such differential social prestige often has a way of compounding itself. Those with money and power will often tend to disregard classical inexpensive research. Social prestige for different kinds of research manifests itself in opportunities to publish in desirable journals, attracting funding, jobs, and even students. On the other hand, researchers who can excel using classical approaches will themselves abandon the less prestigious approaches and attempt to do suboptimal research that requires far more resources than they can afford (Gadagkar 2021). I would therefore argue that the more desirable direction of progress is the simultaneous march of the classical methods and the modern omic methods. Indeed, I would argue that for every omics researcher we need at least ten researchers using classical methods. The nature of classical and omics research is such that this can be achieved even without allocating an order of magnitude more money for the classical approach. I would wager that with the allocation of half the available resources, we can easily sustain an order of magnitude more classical researchers than omics ones (Gadagkar et al. 2019).

But why should we care?

I think we should all care deeply about the direction of progress in our research field. Firstly, it is in all our interest that more and more of the earth's biodiversity is studied, investigated, and made available for ultimate deep understanding of various phenomena. We cannot be satisfied by just digging deeper into a small number of species and an even smaller number of phenomena. If we did so we would soon be very impoverished. And that would be a great pity because there is an enormous amount of unexplored biological wealth on this planet. By neglecting, side-lining, and denying prestige to researchers using classic methods and discovering new species and new phenomena, those of us who use sophisticated technology to understand the molecular basis of the very same phenomena would be cutting off our lifeline in the long to medium term. It is in our selfish interest to generate, encourage, and permit the growth of a large body of researchers who are not using as sophisticated technology as we are.

Secondly, and in my opinion equally importantly, by making research with classic inexpensive techniques in the fields of taxonomy, natural history, behaviour, and ecology, we would be involving a diverse set of scientists from a diverse set of countries in the scientific enterprise. By doing so we will be democratising science and not letting it be the domain of the well-endowed. This is not just a moral imperative but is fundamental to the growth of our science. Diverse people studying diverse species and diverse phenomena using diverse methods will bring up many more new ideas and perspectives that will enrich all of us.

Mark E. Hauber

Towards a better understanding of how ecology can be integrated into sociobiology

When I first landed a faculty job in behavioral ecology, I was assigned a teaching load in the introductory ecology course of my department. I was of course surprised, because Behavioral Ecology (BE), as a discipline, is an evolutionary field, with a focus on the fitness outcomes of behavioral interactions. Sociobiology (the S in BES), in turn, has been interpreted as the interindividual component of behavioral ecology, generating interactions between kin, mates, other non-kin, and even heterospecifics. Myself, as a Tinbergian proximate-factor researcher focusing on development, I was thus even more puzzled and pleasantly challenged to find myself teaching about foundational ecological principles.

It is the explicit focus on the sociobiology of heterospecific interindividual interactions I predict to play an increasing role in the next several decades of BES-focused research. My reasoning is not only because, for example, the study of obligate social (or brood) parasitism (e.g., on great reed warblers by common cuckoos and on yellow warblers by brown-headed cowbirds) has been a particularly detailed, experimental, and productive field of inquiry amongst BES-type publications, but because recently the sympatry of multi-species interactions between diverse brood parasites and their overlapping host species has revealed understudied and underappreciated ecological diversity in both host and parasitic life history strategies and social recognition systems.

More broadly, we are all keenly aware that "Parasites R Us"—our microbiomes (the good and the bad) make up not only a large portion of the cells that we carry but they also influence the health, mood, and thinking outcomes of our everyday existence. In the next decades, by combining careful experimentation on macroparasites with next generation molecular, including functional -omic, studies on microparasites, we will gain a clearer understanding of the causal linkages between interspecific interactions and their impacts on both inter- and intraspecific interactions, social dynamics, and fitness outcomes.

Bert Hölldobler

Is sociobiology passé?

Sociobiology entails the scientific description of the impressive diversity of biological social organizations on this planet. This imposes the key question of how social behavior, and particularly its most derived form, eusociality, could have originated by Darwinian natural selection. Eusocial animal societies are characterized by a strict reproductive division of labor between one or a few individuals that reproduce and the majority of group members that remain sterile and instead help raise the offspring of the few reproductives.

Darwin was very much aware that this kind of reproductive altruism challenges his theory of evolution by natural selection. In fact, he considered it "the one special difficulty which at first appeared to me insuperable and actually fatal to my whole theory." (Darwin 1859). But Darwin did solve the problem of how sterile helper individuals could evolve. He hypothesized "that if sterility (or any trait of a sterile form) can be carried without being expressed, then those who express it contribute enough to the reproduction of others who carry the trait but do not express it, that the trait itself can be 'advanced by natural selection." (Alexander et al. 1991). This clear and succinct "translation" of Darwin's colorful examples of culturing tasty vegetables and breeding "cattle always yielding oxen with extraordinary long horns" by Richard Alexander and his coauthors into today's technical language, demonstrates that Darwin already had envisioned what William D. Hamilton (1963, 1964) referred to as "inclusive fitness maximizing" (kin selection, Maynard Smith 1964). Darwin, not knowing anything about genes, spoke of traits instead. Of course, as explicitly argued by George Williams (1966a, b), it is genes that prescribe particular phenotypic traits that are being selected and not genotypes or phenotypes that exhibit a relatively high transience, a concept that can be traced back to R.A. Fisher (1930) (see also Dawkins 1976).

Hamilton's epoch-making theoretical publications first appeared in the mid-1960s and early 1970s (Hamilton 1964, 1972), the time period when Edward O. Wilson was completing his first sociobiological monograph "*The Insect Societies*" (1971). At that time Wilson very much appreciated Hamilton's enormous contributions, and indeed Hamilton's work plays a central role in Wilson's debate concerning the evolution of sterile castes in social insects, although he ultimately considered kin selection as a kind of group selection. Nevertheless, *The Insect Societies* is a masterpiece and it paved the path to the emergence of *Sociobiology: The New Synthesis.*

For me, one of the greatest values of the book *Sociobiology* derives from its brilliant descriptions of the astounding diversity of social organization in the animal kingdom and their evolutionary convergences and divergences. Even today, fifty years after the publication of *Sociobiology,* I would not be able to name another work that provides such a comprehensive overview. Clearly these superb portraits of animal societies will continue to have a long shelf-life, whereas the contents of the theoretical chapters have been challenged, modified, discarded — even by the author himself. Despite subsequent treatments, at the time of publication these chapters were very influential. The parts on social evolution consist of critical reviews of the underlying contemporary population biological concepts and evolutionary models, as understood by Wilson fifty years ago. Social systems were seen as ecological adaptations, and much of the theoretical arguments were inspired by the writings of George Williams, William D. Hamilton and Robert Trivers. These chapters, combined with the excellent descriptions of the ethological and behavior-physiological mechanisms of social behavior, led to the final chapter of twenty-eight pages in which an attempt was made to explore the evolutionary roots of human nature. No knowledgeable and reasonable person will doubt that humans also have an evolutionary history and that we share some of our rudimentary social behavioral patterns with our phylogenetically close relatives.

This short chapter, and it is indeed only this chapter, elicited an almost surreal protest reaction by some politically motivated academics. Nevertheless, it had the most remarkable effect in spawning several new subfields, such as human sociobiology, human behavioral ecology, and evolutionary psychology (Brown and Lala 2024), though it was largely rejected by sociologists, many of whom believe that human nature does not exist and the human mind is at birth a blank slate. On the other hand, it has recently been claimed that non-human sociobiology has entirely been replaced by behavioral ecology (Stuhrmann 2022). Indeed, both disciplines are very close and this is the reason why they both are displayed on the cover of this journal, ever since the journal was founded in 1976. Is this still justified? I think all of us who work on understanding the biological foundations of social systems would respond with a resounding YES. Let me briefly list some specific research domains of sociobiology.

Social organization in insects and vertebrates alike serve as key model systems for studies in Complex Systems Science (CSS) and for addressing many fundamental questions in evolutionary biology. Sociobiology focusses on the investigation of the genetic, developmental, physiological, neurobiological, behavioral and evolutionary foundations of social organizations, in systems from slime molds to insects to vertebrates and primates. This includes the discrimination between self and foreign and the foundations of universal in-group and out-group behavior, social parasitism and other forms of social symbiosis, as well as the individuality of social systems and superorganisms as operational targets of selection (extended phenotypes), analyses of the diverse division of labor and caste systems, adaptive demography within societies, and emergent nest structures. In addition, the study of the development of castes and morphological subcastes in social Hymenoptera has become a model for molecular epigenetic investigations. Special challenges these days are identifying and sequencing the alleles that were substituted at the evolutionary origin of insect eusociality, the arising of the point of no return once the superorganismal status has emerged and tracking the developmental regulatory networks that underlie the sociogenesis of superorganisms (Hölldobler and Wilson 2009). Together, the group-level traits of eusocial insect societies (superorganism), are the product of cooperation within colonies, and competition among colonies (Reeve and Hölldobler 2007).

Finally, let me list one example where behavioral ecologists and sociobiologist come to quite different conclusions. Some behavioral ecologists claim that all animal communication is based on evolutionary mutual manipulation and exploitation (Dawkins and Krebs 1978; Dawkins 1982). This might be true for solitary species that communicate during territorial behavior, sexual competition or parental offspring interactions, but it is certainly different in eusocial insects. Although we find here also “selfish” manipulative communication, especially in so-called “primitive” eusocial systems with pronounced within-colony competition among reproductives, in species with evolutionarily derived superorganismal organizations, such competitive communication is almost absent. Instead, the complex, multimodal communication and collective decision-making systems in eusocial insects serve the survival and reproduction of the entire society. The understandings of the rich diversity of chemical and vibrational signals, their co-evolved sensory perception and neurobiological processing in the receiver individuals still await demanding scientific explorations.

So, is sociobiology passé? Certainly not!

Sarah B. Hrdy, who deemed it intellectual cowardice to shrink from the label “sociobiologist”

The checkered history of sociobiology in the human social sciences

Looking back, Ed Wilson’s *Sociobiology* was not so much a comprehensive textbook as an ambitious blueprint laying out how evolutionary and comparative perspectives might enhance our understanding of the social lives of animals – humans included. Over in Biology and Animal Behavior, sociobiological ideas rapidly inspired new questions, leading to more integrative as well as scientifically robust research programs. Over in the human social sciences, it was a different story. The usual siloization of disciplines played a role, but so did the inflammatory nature of early critiques. I am not sure young biologists today realize just how charged and vitriolic they were. Here's an example from one of the Science for the People rallies I used to attend in Cambridge, this one held in 1979 Harvard's old Geology Lecture Hall. It began with a speech by Freda Salzman on "Nazi Social Biology: Engineering of consent to genocide", followed by Richard Lewontin and Jonathan Beckwith speaking in turn on "Sociobiology Theory and its Political Origins" and "Sociobiology and Fascism Today". The absence of evidence linking Wilson to neo-Nazi views might have been deafening were it not drowned out by the auditory impact of hearing the phrase "social biology" repeated again and again, loudly, and rapidly, until the words blurred together and sounded like "sociobiology", occasioning more roars and stomping feet resonating against the wooden floorboards. Making matters worse, many in the social sciences were more likely to form opinions based on essays prominently published in places like the *New York Review of Books* than from what Wilson himself wrote (for example in a letter to *Nature* published around this time to the effect that "no justification for racism is to be found in the truly scientific study of the biological basis of social behaviour", Wilson 1981). Beyond the fact that biological themes and social Darwinist caricatures of Darwinism (which even these critics acknowledged was different from Darwinism proper) had fallen on fertile terrain in pre-World War II Germany, it was never spelled out how anything in Wilson's book was actually linked to German National Socialist "biopolicy", to racism, or genocide. Disclaimers like "Of course, leading sociobiologists have not come out with endorsements for either the National Front or their neo-Nazi views…" were buried in the xeroxed hand-outs (Sociobiology Study Group of Science for the People 1979), but the damage was done.

Over on my home turf in Anthropology (a field still sensitive to misuse of its findings earlier in the century), the term "sociobiology" became toxic. I still recall the proposal at the annual meeting of the American Anthropological organization to "ban" the new field. It failed, thanks in part to Margaret Mead who declared "we don't do book burning". Nevertheless, sociobiological ideas went underground in Anthropology, resurfacing in Social Psychology, an area with even less background in modern evolutionary theorizing. Some of their early findings were tailored to fit Social Darwinist, and yes, every so often, "racist" and "sexist", preconceptions. In spite of this troubled early history, usually avoiding the name "sociobiology", essential corrections were slowly made. Lacunae in Wilson's initial ground plan are being filled in as more attention gets paid to history, belief systems, and the contexts in which individuals develop, particularly the role of social environments in the shaping of phenotypes ultimately exposed to selection (e.g. West-Eberhard 2003; Hrdy 2024). Research programs in what is now widely known as Evolutionary Psychology, are gradually maturing. New fields like Evolutionary Medicine and Psychiatry are thriving (Nesse 2010). Psychologists studying infant development are increasingly eager to incorporate evolutionary perspectives (Lancy 2022; Hart and Bjorklund 2022). Meanwhile, in Anthropology, comparative and evolutionary perspectives are increasingly integrated into cross-cultural research leading to wide ranging developments in human behavioral ecology (Ross et al. 2023, just to take one recent example among hundreds). As Wilson anticipated, the last 2 decades have produced increasingly sophisticated accounts of gene-culture co-evolution, efforts with greater attention paid to psychological preferences and details of cultural transmission (Richerson and Boyd 2005; Brown and Lala 2024). With new approaches in genome-wide association studies and other tools for tracing phylogenies, the next decade should bring further refinements. Meanwhile ongoing discoveries by paleontologists in combination with new techniques for analyzing fossil evidence will continue to lead to new insights regarding ancient demography, residence patterns, genetic relatedness, diet, and health metrics, enhancing our ability to reconstruct life history milestones and epigenetic factors. Perhaps the most spectacular advances have come from comparative studies of social cognition in humans and other apes (e.g. Tomasello 2010) and from emerging disciplines like "social neuroscience" (Sapolsky 2017; Decety 2020). With our understanding of brain function still primitive (more complete for nematodes than primates), new brain scanning technologies are nevertheless contributing to rapid advances. However, the sheer complexity of the human neural connectome, encompassing some hundred billion neurons connected by roughly a hundred trillion synapses, poses daunting challenges. Increased use of AI and technologies yet to be discovered will probably be required and regrettably probably also take us further from studying humans in natural contexts. Even though we remain a long way from understanding the neural processes producing human emotions, how they evolved and answering questions about "The morality of the gene" posed in *Sociobiology's* opening chapter, and no matter what label is attached, Wilson's overall vision of greater integration between evolutionary biology and the human social sciences, is gradually being realized.

Michael D Jennions

Predictions and predilections

A quote, widely attributed to the physicist Niels Bohr, runs: “Prediction is very difficult, especially about the future”. Indeed. But if you insist on making such predictions, it might be instructive to head to the cinema, or click on a streaming service, for inspiration. Even the most far-fetched socio-political scenarios of screenwriters have come to life in the real world, be these devasting terrorist plots, Machiavellian intelligence agency plans that go awry, Manchurian scheme to replace political leaders with puppets, or the slow return to a pre-literate society documented in *Idiocracy*. Unfortunately, science is poorly served by the art of motion pictures. Each new high profile sci-fi film seems to prompt editorials, popular articles, papers, and even books, earnestly explaining why the tenants of a plot violate the laws of physics or biology. As if to prove my point, the *Hail Mary Project* is playing in cinemas as I write, and *Nature* have already published an article about its many scientific errors. Entertainment be damned.

If not to the arts, then where should we glimpse the future? One answer is to gaze at our past. It is a well-known sign of aging that we become more enraptured by history as we grow older. To me it is obvious why elders place greater value on using the past to draw lessons about the present or, more tentatively, to predict the future. They have seen it all before. No matter how fast society changes, how individuals respond to incentives and opportunities changes more slowly. Creating rivalries, pursuing status, fear of change while still seeking a technological edge over others: these are all staples of human history. In the case of science, for example, a younger reader might scoff at the heated debate in the 1970’s between rival camps when sociobiology raised questions about whether evolutionary thinking could explain any of the variation in human behaviour. But be cautious what you dismiss this as past ignorance. Surely there are equivalently heated scientific debate raging today that are as misguided when seen in the rearview mirror of history? Eventually enough evidence piles up to tilt the scales of judgment and make the truth undeniable. Although the recruitment of politics to bolster a scientific view rather than the reverse is foolhardy – the facts don’t change when we love or loath them—it is a constant theme: from the place of our planet in the solar system, to where humans perch on the tree of life, to sources of CO_2 in the air.

Given a request to write about the future of evolutionary behavioural biology I therefore turn to the history of science. I am not a historian, but I have witnessed the changes in behavioural ecology since the 1980’s. I will focus on research of sexual selection because this is where I am allegedly an expert (to again quote Niels Bohr: “An expert is a person who has made all the mistakes that can be made in a very narrow field.”), but my predictions readily translate to other areas of behavioural ecology. Here are three foolish predictions.

First, technology not theory will drive progress. My own preference is for theory-driven research, but the history of science is replete with cases where progress required new devices – telescopes, microscopes, cellular dyes, DNA sequencing machines. In the 1980’s many sexual selection studies were motivated either by a desire to distinguish between Fisherian and ‘good gene’ theory models to explain female choice and male ornamentation; or by a desire to determine if ornaments signalled attractiveness, immunocompetence, fertility, fecundity… and so on. Theoreticians were gods for a day. But once formal models had established the validity of verbal arguments it became clear that mate choice for genetic benefits hinges on fitness being heritable, and the sources of variation in fitness spring from many traits. Empirical studies floundered because fitness is incredibly hard to measure, and any variation in fitness signalled by ornaments is likely to be small. This was a fatal blow to a field where measurement errors were larger than sample sizes. But with the rise of modern genetics there is ground for optimism. The potential to experimentally create genetic variants at multiple loci that each have realistically small effects on fitness and then track gene frequency changes in populations where sexual selection is either present or absent might allow researchers to determine the efficacy of sexual selection in increasing fitness. Locating the gene ‘for trait X’ is mind-numbing boring (to me), but using genomics to test theory is exciting, and it does not happen often enough.

Second, funding dictates research questions, and funding bodies are increasing driven by the alleged applied value of research. If you had told me during my PhD that temperature rather than diet would be the factor most likely to be manipulated in behavioural ecology experiments, I would have sneered. Foraging studies were still going strong, and diet was linked to carotenoids, immune function and body condition. But when I receive a pile of grants to review nowadays, I am confident that many will be about climate change, which usually reduces to asking about the effects of temperature. This begs the question of what future societal concerns that then motivate funding will be relevant to sexual selection studies. Many economists predict that how people spend their time, especially where, when and if people work, will change rapidly because of AI. These changes could motivate researchers to seek funding to ask how, say, greater human active at night (fewer pesky early morning commutes) affect mate encounter rates in nocturnal and crepuscular animals; or to ask how reduced activity in city centres affects divergence in the evolution of sexual signals in cities and suburbs. I expect studies of human-driven changes in sexual selection to grow.

Third, I predict ever fewer species are studied. The current trajectory of society is towards a stronger love of virtual reality than reality. We almost need an adjective to pit against 'virtual', 'real' reality perhaps? Fieldwork is costly, time-consuming, dirty, dangerous and offline. Many biology students are now more comfortable in the city than the field. Lab-based studies are likely to increase. This would be a tragedy. If evolutionary biologists are truly honest, they will confess that we already know the answer to most of the 'big questions' simply because the theory of evolution by natural selection is so well corroborated. But the unanswered mysteries lie in the quirky solutions that have arisen through natural selection acting on chance variation constrained by historic contingencies. These are the processes that create the natural beauty and diversity that delights children and adults alike. I therefore hope that the next generation prove me utterly wrong. I'd happily trade a world where we know everything possible about the biology of zebrafish, house mice and fruit flies for one in which we have a dim but slowly illuminated understanding of zebras, mousebirds and fruit bats.

Finally, as I look back over the last 50 years I note that so many people have devoted so much time to finding so little evidence that females engage in elaborate mate choice for genetic benefits (the 'lek paradox'). Some might see this as a failure, but I don't. I'll end with yet another quote from Niels Bohr in the hope that it motivates young behavioural ecologists to do better than we did: "How wonderful that we have met with a paradox. Now we have some hope of making progress."

Peter M. Kappeler

On the kinds and degrees of sociality

As a scholar of animal behavior whose professorship includes the term "sociobiology" and who has served as an associate editor of "*Behavioral Ecology and Sociobiology*" for 25 years, my professional career has been profoundly impacted by E.O. Wilson's seminal work, "*Sociobiology: The New Synthesis*". In order to minimize redundancy with the other contributions, which reflect upon the impact of the semicentennial anniversary of this transformational tome on the study of animal and human behavior, with a likely focus on its theoretical impact (Alcock 2001) or on its effects on the study of insect societies until today (Bonifacii et al. 2026), my focus will be on the fundamental question concerning the classification of animal societies that has kindled and sustained my personal interest for decades.

Following the initial stage of studying insect societies in a broader context (Wilson 1971), his subsequent work (Wilson 1975) expanded the comparative perspective necessary for comprehending the intricacies of diverse animal societies. This expansion was articulated in the opening chapter of "*The New Synthesis*": "Biologists have always been intrigued by comparisons between societies of invertebrates, especially insect societies, and those of vertebrates. They have dreamed of identifying the common properties of such disparate units in a way that would provide insight into all aspects of social evolution, including that of man. The goal can be expressed in modern terms as follows: when the same parameters and quantitative theory are used to analyze both termite colonies and troops of rhesus macaques, we will have a unified science of sociobiology*"*. However, Wilson's primary focus was on species that live in societies, which he defined as "a group of individuals belonging to the same species and organized in a cooperative manner." More specifically, "Reciprocal communication of a cooperative nature, transcending mere sexual activity, is the essential intuitive criterion of a society".

From a contemporary standpoint, it is noteworthy that the millions of solitary species did not garner the same level of attention or interest, even when discussing the relationship between a population ("bounded by a zone of sharply reduced gene flow") and a society ("bounded by a zone of sharply reduced communication"), where it would seem evident that solitary species also form populations. It is also challenging to accommodate the equally neglected pair-living species in this framework. The evolution of pair living has historically attracted significant interest, initially driven by the concepts put forth in "*The New Synthesis*" (Emlen 1995). However, the costs and benefits of a solitary life have only recently enjoyed increasing recognition (Costa 2018; Makuya and Schradin 2024). Consequently, Wilson's (1975) seminal contributions have exerted a profound and enduring influence on the comprehensive and integrative study of social evolution (Rubenstein and Abbot 2017a), despite the fact that his primary interests focused on species that live in groups. Indeed, the fundamental concept of what constitutes a group remains a subject of ongoing debate (Moffett 2025, 2026).

A second prerequisite for a comparative analysis of animal societies is the daunting task of ordering and classifying the diversity offered by group-living species. The corresponding section titled "*The Kinds and Degrees of Sociality*" commences with a significant insight: "All previous attempts to classify animal societies have failed." Wilson's familiarity with the seminal works on the systematization of animal societies, including Espinas' (1878) and Deegener's (1918) contributions, is well-documented. However, it is noteworthy that he appeared to be dissuaded by the

92 categories and lexicographic terminology proposed by Deegener. Subsequent researchers have identified a smaller number of categories (e.g., Wheeler (1928): 5; Alexander (1974): 5 and Crook et al. (1976): 12 [mammals only]), indicating that the primary issue identified by Wilson continues to be valid: "no two authors have agreed on which qualities of sociality are essential".

Consequently, he advanced a proposed set of ten qualities of societies that could be quantified and used to characterize particular social systems (group size, demographic distribution, cohesiveness, connectedness, permeability, compartmentalization, differentiation of roles, integration of behavior, information flow, and fraction of time devoted to social behavior). However, this proposal was never widely accepted, perhaps because some features are more applicable to invertebrates than to vertebrates. The most recent and comprehensive attempt to achieve a common framework has highlighted that researchers studying different taxa have been using different criteria and technical terms to define their societies (Moffet 2025, 2026). As a result, there is still a persistent divide between scholars of invertebrate and vertebrate societies (Rubenstein and Abbot 2017b). Therefore, while other frameworks are currently being examined (Kappeler 2019), Wilson's sociobiology continues to play an important and inspiring role in the study of social evolution five decades after its publication. However, “the unified science of sociobiology” still has to reach this objective and remains an ambitious aim for the next generation of scholars.

Kenji Karino

Disentanglement of interactive effects of multiple factors on female mate preferences

An increasing number of studies have shown that many factors affect female mate preferences. For example, genetic factors determine female mate preferences to some extent (Bakker and Pomiankowski 1995). A genetic correlation between the exaggeration of male ornamentation and the strength of female preference for such ornamentation has also been reported (Houde and Endler 1990; Bakker 1993). Mate choice based on the major histocompatibility complex (MHC) illustrates the importance of MHC gene combinations between males and females; females choose males as mates to achieve an optimal level of MHC diversity or dissimilarity in their offspring, thereby conferring greater parasite resistance (Milinski 2003; Consuengra and de Leaniz 2008). Other innate factors also affect female mating preferences. For instance, higher-quality females, such as those with larger body sizes and greater fecundity, show stronger mate preferences for desirable males because they can pay the costs of choosiness or obtain greater benefits by selecting better mates (Cotton et al. 2006). Reproductive status, such as estrous condition, also influences female mate preferences; for example, stronger mate preferences for attractive males have been reported in females under reproductive status with a higher probability of conception (Gangestad and Thornhill 1998; Yamada and Karino 2025).

In addition, external factors regulate female mate preferences. The effects of environmental predation risk on female mate choice are well known (Godin and Briggs 1996; Rosenthal 2017). Recent studies have demonstrated that diet coloration influences female preferences for mate coloration; that is, females prefer males assuming a similar coloration to their own diet (Amcoff et al. 2013). This female preference for mate coloration changes according to alterations in diet coloration, even over a short period (Kato and Karino 2024). Female mate preferences for males with rare phenotypes have revealed the importance of the relative abundance of each male phenotype in the population in shaping female mate choices (Hughes et al. 2013). In addition, the behavior of other individuals influences female mate preferences. In mate-choice copying, for example, females imitate the mate choices of other females (models); consequently, the effect of the model’s choice can override their original mate preferences (Dugatkin and Godin 1992; Vakirtzis 2011). These findings suggest that multiple innate and external factors interact to shape the mating preferences of females.

The interactive effects of these innate and external factors on female mate preferences may be complex and context dependent. For instance, in environments where unexpected events are common, such as drastic habitat disturbances caused by climatic fluctuations or human activity, the plasticity of female mate-searching behaviors and mate-choice decisions may be more importance than genetic factors for responding adequately to such events. Individual personality traits may also affect the relative roles of multiple factors in shaping female mate preferences. Shy females may frequently adjust their mate preferences in response to environmental factors such as predation risk. In contrast, bold females may be more likely to maintain their innate mate preferences across environments, or vice versa. Genetic factors that do not directly determine mate preferences may also play indirect roles in shaping female preferences. For example, females with greater genetic learning abilities may observe other individuals more carefully and frequently learn to discriminate among potential mates. The benefits of learned mate preferences are expected to be especially pronounced when females have difficulty distinguishing higher-quality mates. Consequently, females with greater learning ability may predominantly adopt mating decisions using information from others in such situations and gain greater fitness benefits than females with low learning ability. Future integrative investigations can help to disentangle the relative roles of multiple innate and external factors in shaping female mate preferences. The results of such studies will contribute to a better understanding of the processes that shape female mate preferences and the roles of individual variation in evolution. In addition, the context-dependency of the relative importance of multiple factors affecting female mate preferences is a promising area for future research. These studies will clarify the processes underlying the use of multiple factors in female mate preferences across contexts and the consequences of context-dependent mate preferences, including the direction of sexual selection and the maintenance of genetic variation.

Moreover, the proximate factors underlying female mate preferences remain poorly understood, although hormonal effects associated with female reproductive status are known. A recent study has showed that larger female brain size facilitates their mate preferences for attractive males, probably due to their higher cognitive ability (Corral-López et al. 2017). In contrast, no such relationship has also been reported between brain size and female mate preferences (e.g., McNeil et al. 2021). Future studies exploring the relationship between brain structures, including not only size but also neural networks, and female mate preferences will be particularly fruitful. Furthermore, the full proximate system underlying female mate preferences−including signal perception by sensory organs, information processing and decision-making in the brain, signal transmission through neural or hormonal pathways, and outputs as female behavior−remains unsolved. Elucidate the full system of proximate factors underlying female mate preferences using diverse biological disciplines, such as the physiology, neuroscience, endocrinology, and behavioral sciences, is a compelling endeavor. The results highlight the complexity of the system and condition- or context-dependent nature of its complex networks.

The evolutionary consequences of female mate preferences through sexual selection have been well studied at the population and species levels. However, the effects of female mating preferences on other species have attracted less attention. Although the phenomenon of female mate preferences for ornamented males that are vulnerable to predation is well known, female mate choice may also influence other aspects of interspecific interactions. For instance, when females prefer aggressive males that can protect their offspring from potential predators, males may more frequently chase other species from their territories; consequently, interspecific interactions and surrounding community structures may be altered. Because other species, such as predators and competitors for resources, are also important factors shaping female mate preferences, future studies should clarify the dynamic relationships between female mate preferences and interspecific interactions. Such studies will reveal the broader influences of sexual selection at the community level.

Sarah Kocher

Natural variation will reveal the modules and mechanisms underlying social evolution

Sociobiology: The New Synthesis marked an irreversible transformation in the study of social behavior. Wilson's work provided a major integration of natural history, ecology, population biology, and evolutionary theory to generate a more complete understanding of social behavior and its evolution. It helped to catalyze the development of modern behavioral ecology and inspired generations of scientists to examine how the many aspects of social organization arise and evolve. *Sociobiology* also sparked intense debate about the contribution of genetic mechanisms to social behavior. Critics argued that the work implied strong genetic determinism, a topic that has historically been misrepresented and weaponized in the service of political agendas. In later years, Wilson argued for a renewed emphasis on the importance of ecological factors, which more broadly reflects a maturation in the field toward understanding social evolution as a complex interplay of genetic, developmental, and ecological forces.

It is now widely accepted that there is rarely a simple, deterministic genetic underpinning to social behavior. In social insects, dominance hierarchies, reproductive strategies, and caste determination are often socially or environmentally regulated, underscoring the central role of gene-environment interactions in mediating social organization. Over the past decades, it has become increasingly clear that behavioral traits are shaped through the interaction of genetic variation, developmental processes, and ecological conditions. Mechanistically, these inputs are integrated by the central nervous system to generate individual behavior, and interactions among individuals scale nonlinearly to create emergent group dynamics.

Looking forward, the study of social behavior may once again be entering a period where integration and synthesis can provide key insights into old questions. Natural variation provides independent evolutionary replicates that experiments cannot, enabling comparisons across a broad array of species to identify shared features and lineage-specific innovations linked to social evolution. Technological advances over the past decades enable us to leverage this variation in novel ways. It is now possible to investigate the genetic and epigenetic architecture of behavior in nearly any organism. Advances in neuroscience provide opportunities to characterize neural ensembles underlying social interactions. Automated tracking and computer vision enable high-resolution quantification of social behaviors. Thus, it is increasingly tractable to connect variation in genes, brains, and environments to the individual and colony-level traits that structure societies. A clearer understanding of how these factors interact could refine or potentially reshape existing evolutionary theories.

As our comparative datasets continue to grow, the most consequential conceptual shift may come from how we define and quantify sociality itself. It is becoming increasingly clear that sociality is not a single, discrete, categorical trait, but rather a composite phenotype that emerges from many interacting traits underlying the life history, reproductive biology, and social organization of each species. These traits need not evolve together. Mary Jane West-Eberhard emphasized decades ago that a fundamental aspect of social evolution may be the decoupling of developmental and behavioral modules that enables different aspects of social organization to diversify independently. Now, modifications of ancient developmental and hormonal networks are beginning to come into focus. The next set of questions should focus on understanding how these molecular, developmental, neural, and behavioral modules are assembled, regulated, and modified throughout the course of social evolution. Mapping these modules across species with variable social forms can reveal which components are conserved, which are flexible, and how different combinations can give rise to the diversity of social forms observed in nature.

Sociobiology synthesized disparate approaches to the study of social behavior into a unified framework. The next synthesis may come from extending that integration to understanding how molecular and neurobiological pathways have been co-opted and modified throughout evolution to produce such a diverse array of social forms. By integrating natural history, ecology, and careful phenotyping with genomics and neuroscience across species – the same synthetic approach *Sociobiology* exemplified – our field may uncover deeper principles that govern the emergence and evolution of complex social systems. Ultimately, the diversity of social forms may be our greatest asset for understanding how the building blocks of sociality can be combined, modified, and decoupled, and why so many distinct forms of sociality have evolved.

Melvin J. Konner

Complex human behavior, according to Darwin

In 1971 I returned from two years of doctoral research in Botswana to find the Harvard evolutionary community abuzz with a new conversation. Part of it was stimulated by papers published by W.D. Hamilton introducing the concepts of kin selection and inclusive fitness, but there were other tantalizing publications in development. Robert Trivers would publish his "*Parental Investment and Sexual Selection*" in 1972 and "*Reciprocal Altruism*" the following year. The papers by Hamilton and Trivers emerged as the core of what came to be called neodarwinian theory or "sociobiology."

E.O. Wilson, a leading investigator and theorist of behavioral evolution in the social insects, was working on his 1975 book, *Sociobiology,* a voluminous text defining a new field. While it included elements of neodarwinian theory, it ranged much more widely over the comparative behavior of social species, including humans. Although the titular term had been used since the 1940s, Wilson's "*New Synthesis*" gave it a new ring, and it soon entered general discourse—with considerable opposition—as the name of a controversial new field.

It was contentious because its opponents identified it with genetic determinism, an oversimplification at best. My own background as a left-leaning student activist made me very wary of it, but I was more of an evolutionist than an ideologue, and after a year or two of debates, reading, and thinking I found neodarwinian logic inescapable and the definition of the new field reasonable. Caught between avid enthusiasts (who predicted it would sweep away all the conventional sciences of behavior) and fierce detractors (who found it anathema to all they believed in), I thought then that sociobiology would ultimately occupy a limited but important place in the spectrum of behavioral and social science.

My prediction has proved true in the half century since. Sociobiology has been routinized as normal science through its own journals and through representation in older, conventional journals of natural history, psychology, and the social sciences. It is generally accepted not only that behavior has evolved but that understanding how it evolved is vital to our understanding of what humans and other animals do. In fact, the very phrase "humans and other animals," once unusual in the study of behavior, is now commonplace.

Although genes with a strong influence on complex human behavior have rarely been found, the heritability of such behavior is nevertheless well established, and the apparent contradiction is now resolved by genome-wide association studies (GWAS) of hundreds or thousands of individuals yielding hundreds or thousands of genes that together strongly influence a behavior, each explaining a very small fraction of the variance. This complexity does not make a trait any "less genetic," but it does afford some anti-gene ideologues an alleged purchase for their claims.

The question of "*how* genetic" a complex trait may be is not meaningless, but it is difficult. Ultimately it will have to be answered separately for every behavior, and it will range from very little to very much. Based on GWAS as well as on the much older (but now much improved) twin and family studies, I find it useful to think of the heritability of complex behavior as approximately fifty percent, *averaged* over many more and less heritable traits. I understand that this glosses over gene–gene and gene-environment interactions, but it is still a helpful approximation. Note that while fifty percent is a large part of the variation, the posited environmental component is equally large, and provides a huge scope for the study and implementation of such influences.

If this seems far afield from sociobiology, which is primarily about evolution, it is essential to the future of evolutionary explanations. As the mechanisms of genetic influence on behavior become more fully understood, evolutionary exposition will become more subtle and more convincing, even while some aspects of this evolution prove to be significantly cultural.

It's remarkable to look back on the rancor of the 1970s from the context of today's civil intellectual conversations. Fears that this kind of theory would support racism have proved completely unfounded, because it applies mainly to individual and kin selection. Limited biologically based sex differences—for example, in aggression—have been found consistent with the theory. But this difference has if anything suggested that women should have more, not less power, while alerting us to the dangers faced by women in many heterosexual relationships. Evolutionary explanations of social hierarchy have tended to make us warier of its worst depredations, while kin selection theory shines a particularly clear and even harsh light on the threats and damages of nepotism. Whatever we understand, we have an opportunity to control.

Much of this understanding will not explicitly involve evolutionary theory. Learning to play the piano demands theories of dexterity and habit formation. Language acquisition by toddlers requires theories of syntactic and semantic development. Cultural differences in ideals of beauty require different explanations than are demanded by cross-cultural universals. And yet, all these processes evolved. Nothing in biology makes sense except in the light of evolution, and complex human behavior is always, in part, part of biology.

Judith Korb

From social insects to cancer, selfish elements and supergenes, and back

Wilson's book '*Sociobiology*' (Wilson 1975) as well as the research field has its foundations in firm evolutionary reasoning linked to population genetics that had developed during the preceding decades, with a major impact of George C. Williams' book '*Adaptation and natural selection*' in 1966 (Williams 1966a, b) that dismantled old naïve group selection and 'good for the species' arguments. It led to the recognition that genes are selected during evolution with organisms 'just' functioning as vehicles (gene-eye view of evolution). Similarly, the new focus on social interactions as evolutionary forces had solid, gene-centred foundations in evolutionary theory. Inclusive fitness theory (Hamilton 1964), which became popularized as kin selection theory (Maynard Smith 1964), showed how conspecific interactions shape evolution via reciprocal feedback effects. Thus, altruism, cooperation, selfishness and conflict emerged as central evolutionary topics. These fundamental conceptual advances gave rise to the spread of strict evolutionary thinking in the following era with quantitative models and predictions that led, for instance, to behavioural ecology as a true scientific discipline with hypothesis testing (e.g. Krebs and Davies 1978, 1984, 1991, 1997; Grafen 1984).

In more recent years, the focus shifted to more mechanistic approaches, enabled by considerable technological progress. Thus, understanding the neuronal basis of social behaviours (though also a major topic in '*Sociobiology*') or their epi/genetic molecular underpinnings ('socio(epi) genomics') are currently central topics of research (e.g. Robinson 1999; LeBoeuf et al. 2013; Hunt and Gadau 2016; Couzin-Fuchs and Ayali 2021; Okwaro and Korb 2023). Associated with this intensified focus on proximate mechanisms, there appears to be a relapse into less rigorous evolutionary reasoning, evident in the re-emergence of old group-selectionist claims, for example when parental manipulation is treated as the default explanation for offspring altruism. Hence, in an era that sees such impressive progress in understanding sociobiological mechanisms, it is of uttermost importance to maintain strict evolutionary reasoning and to teach it to the next generation of scientists. Combining both ultimate and proximate approaches is crucial for a comprehensive understanding of sociobiology as already laid out in Wilson's book.

In addition, I think, the ultimate evolutionary approach continues to hold promise for generating new insights in the future. The application of sociobiological thinking to microbes has led to the new research area on 'social microbes' and to the exciting field of Hamiltonian medicine (e.g. Foster 2005; West et al. 2007; Crespi et al. 2014). The latter is still emerging and a bit underexplored but has many applicable and highly relevant insights to offer with its close links to epidemiology and cancer evolution. For example, the recognition of altruistic helper cells (i.e. cells that sacrifice their own fitness to support a tumour population) occurring during and after the angiogenic switch that fosters tumour progression offers great potential for research (Crespi et al. 2014; Okasha 2024; Laplane et al. 2025). More broadly, these examples show that the transfer of sociobiological concepts from conspecific interactions to *interactions within an organism* have huge potentials for new insights in the future (e.g. recent reviews Ågren and Patten 2025; Purcell and Brelsford 2025). Using a multilevel selection framework, these concepts can be applied to the evolution of selfish genetic elements, such as transposable elements, which can spread independently within the 'host' genome, thereby reducing host fitness. Similarly, they can illuminate the phenomenon of more recently discovered cooperative supergenes—clusters of tightly linked loci that, often due to chromosomal inversions, cannot be transmitted independently to the next generation. These genetic phenomena can only be studied with the advent of new technologies like reliable high-throughput, long read sequencing, making it an opportune moment to investigate these suborganismal phenomena through a sociobiological lens.

Complementarily, the application of strict sociobiological reasoning can help to understand the major transitions in evolution (MTEs), that led to increasing hierarchical organismal complexity during the evolution of life from prokaryotic to eukaryotic cells, from unicellular to multicellular organisms, and from solitary to eusocial organisms (recent reviews: Howe et al. 2022; Bourke 2023). These MTEs are characterized by cooperation between lower-level units overcoming competition and conflict, thus giving rise to a new higher-level vehicle, on which selection acts. Hence, I think, by extending inclusive fitness reasoning from the transitions to eusociality, the main target of Wilson's Sociobiology, to earlier transitions, we can develop a true multilevel selection framework that comprehensively addresses the evolution of life.

Daniel J. C. Kronauer

Unifying ultimate and proximate explanations of sociobiology

Fifty years ago, E.O. Wilson's *Sociobiology: The New Synthesis* provided a framework in which to understand and study the biological basis of social behavior and animal societies. Wilson's approach was explicitly evolutionary, focusing on the adaptive value of behavior and ultimate explanations for why different organisms behave as they do. This turned out to be very productive, inspiring and shaping research in ethology, ecology, and evolutionary biology over the following decades. At the same time, discussions of proximate explanations for how the brain implements social behaviors were conspicuously absent from Wilson's synthesis. Even the section on "Hormones and Behavior" spans only two-and-a-half of the well over 500 pages. An obvious reason for this omission is that, at the time, the genetic and neural basis of behavior, let alone that of complex social behavior, was essentially *terra incognita.*

This has changed considerably over the past fifty years, with genetic models like the fruit fly *Drosophila melanogaster* and the house mouse *Mus musculus* leading the way. For example, we now have a fairly detailed understanding of the neural circuitry underlying courtship and aggression in fruit flies, and recent studies have begun to examine neural dynamics in more complex social environments where males compete over females (Hindmarsh Sten et al. 2025). Recent studies in mice, on the other hand, have revealed how the nutritional and endocrine states of females are integrated to flexibly toggle pup-directed behavior between aggression and care (Cao et al. 2025).

The flipside of this stunning advance in model system research is that, beginning with the rise of molecular biology in the middle of the twentieth century, neuroscience converged on a small set of study organisms, limiting the scope of the field in general and our ability to make inferences about ultimate causality in particular (Yartsev 2017; Laurent 2020; Banerjee et al. 2026). However, with recent breakthroughs in DNA and RNA sequencing, genome engineering, and neural imaging, diverse additional species with varying levels of sociality have become amenable to functional genetic and modern neuroscientific investigation (Stern et al. 2025). This expanding cornucopia of new model organisms will enable comparative studies of social behavior through an evolutionary lens at ever finer mechanistic detail.

For example, it is becoming apparent that parental and alloparental behaviors, as well as more complex forms of social organization built on these behaviors, such as insect societies, have repeatedly evolved by coopting a core set of ancestral endocrine and neural pathways (Kay et al. 2026). It should therefore be possible to achieve a generalized molecular and circuit-level understanding of parental behavior, as well as a granular inventory of how natural selection has tuned, expanded, and coopted various components of this conserved network to produce the great variation in parental behaviors that we see across the animal kingdom today (Kay et al. 2026).

Predicting the future of sociobiology is challenging, not least because technological advances keep accelerating. With the assistance of artificial intelligence, it is now possible to reconstruct entire insect brains at synaptic resolution (Helmstaedter 2026) and to acquire behavioral data at unprecedented scale (Pereira et al. 2020). For example, machine vision and machine learning allow us to monitor the behavior of all the ants in a colony (Richardson et al. 2021), with the resulting datasets dwarfing Wilson's painstakingly collected ethograms (Wilson 1976). Given these and other technological developments, in combination with the continuing expansion in experimentally tractable model species for neuroscience, I expect that, over the next fifty years, the field will see an increasing amalgamation of ultimate and proximate explanations of sociobiology. The prospect of not only understanding why natural selection has produced different forms of social behavior, but also how these differences are implemented mechanistically, fills me with great excitement.

Olof Leimar and John M. McNamara

The future of sociobiological research

Evolutionary game theory provides an important framework for the study of social behaviour. The theory gained prominence around the time of E.O. Wilson's examination of the biological basis of social behaviour. There is a close connection between them, for instance in that analyses of conflict and cooperation were major topics both in game theory and in Wilson's (1975) work. Given the multitude of applications of game theory to social behaviour that have appeared in the recent 50 years, one might wonder if there is scope for further significant work in the field and if so, whether such work could contribute to the future of sociobiological research. We argue here that this might well be the case, and that the opportunity consists primarily in the incorporation and analysis of behavioural mechanisms.

Recent years have seen a great expansion in fields like theoretical and experimental neuroscience, reinforcement-learning style modelling of decision making, and other applications of machine learning and artificial intelligence. These developments likely will provide a strong mechanistic basis for our understanding of animal behaviour, including human behaviour. Given the intensity of the trend, the result could well dwarf the evolutionary perspectives from sociobiology, relegating them to increasingly marginal positions. Although this might well come to pass, we think it would be unfortunate, for instance because it could weaken the link between the study of social behaviour and its evolutionary history and adaptive function. A better alternative would be for sociobiological research and game-theory in biology to instead embrace and contribute its own approaches to the current trend.

So how could this kind of unification be achieved? Our view is that one should enrich game-theory models by more explicitly representing psychological processes like learning and the build-up of social relations, such as social bonds or dominance hierarchies, in models. The analysis of function then consists of an evolutionary analysis of traits that influence the behavioural mechanisms, in this way setting up links between mechanistic understanding and the function of behaviour.

An illustration of the recipe might be the analysis by Leimar and Bshary (2024) of helping through the build-up of social bonds, combining traditional ideas about the possible roles of friendship and social bonds for cooperation with a specific learning-like mechanism of social bond dynamics. The possibility that friendship could regulate reciprocal helping was introduced by Trivers (1971). In the analysis by Leimar and Bshary (2024), a mechanism of social bond formation was used for interactions like food sharing by female vampire bats. It was discovered by Wilkinson (1984) that close association during daily activities, which could indicate a social bond, was linked to food sharing between unrelated female vampire bats. The general idea of friendship expressed as a social bond has been widely used in biology, perhaps in particular in primatology (Seyfarth and Cheney 2012). In Leimar and Bshary (2024), the mechanism of social bond dynamics was inspired by the classical Rescorla-Wagner learning formulation and included a learning rate as a genetically determined trait influencing the bond dynamics.

A second illustration could be the introduction of behavioural mechanisms into game theory models of social hierarchy formation. The processing of dominance interactions and social positions is well-studied in neuroscience (e.g., Kumaran et al. 2016; Zhou et al. 2017, 2018; Qu and Dreher 2018). Inspired by these ideas, one can formulate game theory models of social dominance (see for instance Sect. 8.6 in McNamara and Leimar 2020), by representing social-hierarchy formation as a type of reinforcement learning. The modelling can be extended to study different features of social dominance, such as winner-loser effects (Leimar and Bshary 2022).

Finally, the evolution of preferences is an important topic in economics (e.g., Samuelson 2001; Dekel et al. 2007; Alger 2023) that can be regarded as part of neuroeconomics (Glimcher and Fehr 2014). By preferences is meant that individuals acquire subjective valuations that are used for choices between alternatives. When there is learning in a social situation, the current choice of an individual can affect the future choices of others. Thus, the choice of current action affects both the immediate reward and future rewards. A consequence is that the evolved strength of preferences for alternative actions may not reflect the true fitness payoffs of those actions taken in isolation (e.g., McNamara et al. 2021). Such biased evaluations of alternatives likely influence human behaviour but could also be important for social groups of non-human animals, for instance when competing for foraging opportunities. We believe that sociobiological research could profit from a greater engagement with this possibility.

As a background to the illustrations, we note that there is a wide and actively researched field of computational modelling of reinforcement learning and decision-making, with close links to neuroscience. To give just a few examples, Sutton and Barto (2018) contains a broad overview of reinforcement learning by two of the founders of the field, Daw et al. (2005) describe a dual-action choice system that integrates goal-directed and habitual behaviour and uses reinforcement learning as a basic framework, Wang et al. (2018) introduce meta-reinforcement learning as a system that can learn and adapt to dynamic environments and interrelated tasks, and Wilson and Collins (2019) give an introduction to and overview of computational modelling of behavioural data. For the specific issue of the forming and breaking of habits, which is a much-studied aspect of animal behaviour, but which has mostly been neglected in sociobiology, Buabang et al. (2025) summarise and illustrate the current neuroscience understanding of the mechanisms involved. Overall, these examples indicate that there is a richness of learning-related behavioural mechanisms that potentially could be integrated in game-theory models.

The idea that we need to explicitly represent physical and psychological processes in formulating models of behaviour have been put forward previously, for instance by McNamara and Houston (2009). Learning in a social situation has also been considered, for instance in the final chapter of McNamara and Leimar (2020), and by Leimar and McNamara (2023). We think that if developments like these gain prominence, the future of sociobiological research could be bright.

Constantino Macías Garcia

A personal forecast of the near future of research in sociobiology

Any attempt at forecasting the future of sociobiological research must consider the resistance to accept the suggestion that our behaviour, morals, talents or affections may not be altogether free from biological influence. The opposition to such an idea has been evident since Darwin published his proposal that, as for all other species, humans evolve; that this process involves both morphology and behaviour; and that consequently we should be able to discern ancestral stages of our members, organs and behavioural attributes, including mental capabilities, strewn along the tree of life (Darwin 1859, 1871, 1872).

In 1889, Alfred Russel Wallace published an apology of Darwin's work. He titled the book *Darwinism* and made in it an explicit acknowledgement of Darwin's right to have the theory named after him. Yet in the last chapter, Wallace argued that there are several mental faculties found in humans which are "totally inconsistent with the law of natural selection" (Wallace 1889 p. 473). He went on to maintain that the existence of those attributes "compel us to recognise some origin for them wholly distinct" from that which explains animal attributes. As Traniello and Bakker (2026) reminded us, a similar opposition to any form of biological predisposition -deemed determinism- lies at the root of the rejection of sociobiological theory, particularly by some schools of socialist thought that perceive it as a potential justification to keep the rich wealthy and the poor wanting (see also Wilson 2000).

In line with the polarisation of societies around the world, I find at once signs that society is more ready to accept the existence of some degree of biological predisposition and also indications that this possibility is cancelled in the minds of some people. On the one hand, the desire to overcome material limitations with minimal effort translates into the acceptance of miracle drugs and food complements to treat every condition that humans may want to get rid of, which facilitates the acceptance of our animality. But there is also in several sectors of society a radical denial that biology shapes our social reality. This manifests itself in the conflation of gender -a continuum- and sex -two, although they can coexist in the same individual (see Griffiths and Spencer 2025)-, and in the repeated accusation that biological determinism can only mean fascism. Yet, while social attitudes must influence the direction of research, there are many reasons to expect that sociobiological research will continue. I think in the next few decades it will proceed as follows.

Neurobiological basis of social behavior

Research on the physiological basis of social behaviour, including self-awareness and cognition, is being conducted for several practical as well as serendipitous reasons. It is convenient for society to understand how the human brain works and interfaces with the rest of our bodies, how it evolved, how and to what extent it influences our social interactions, emotions and abilities, and how it can be set to work properly when damaged. Our understanding of the intimate, pervasive links between mind and body -a debatable dichotomy- is laying bare for anyone who still doubted it, the fundamentally material nature of our thoughts. For instance, our inner speech is reliably represented in our cortex and can be decoded by speech-brain computer interfaces even before we attempt to utter it (Kunz et al. 2025). The ongoing, inevitable feedback between neurophysiological research on animals and humans will be increasingly used to peer into the animals' inner world (their umwelt; von Uexküll 1957), perhaps giving the lie, or at list tempering, von Uexküll´s dictum that it is fundamentally unknowable.

Psychobiology

Regarded by Wilson (2000) as sociobiology re-cast, it will keep advancing our understanding of the continuum between us and the rest of the animal world. It has already shown in a wide variety of taxa that animals make predictions about future events (Raby et al. 2007), count (e.g. Agrillo et al. 2009), have a sense of fairness and punishment (e.g. Raihani and McAuliffe 2012; Brosnan 2013), and are aware of pain and harm (e.g. Alupay et al. 2014). Animals, including flies, are even mindful of whether they are being observed (listened at, eavesdropped) by others, and adjust their behaviour accordingly (Hutchins and Saltz 2025; see Larter 2022). Aided by increasingly sophisticated neurophysiological tools, sociobiological research will identify neural regions linked to these behavioural attributes, and with the expansion of transcriptomic and other omics tools will pinpoint their genomic underpinning. Indeed, with increasing numbers of genomes available and having already many model species with which to conduct Quantitative Trait Locus (QTL) and transcriptomic analyses, we have now many studies linking specific genes or gene groups to behavioural predispositions.

Behavioural plasticity/epigenetics

The pathway between genes and phenotype, including behaviour is sinuous, and the end result is often determined by processes that take place early on life or even in previous generations. We now know, for instance, that embryonic chicks can be informed by their parents about the climatic conditions they will face upon hatching, which allows them to adjust their developmental program accordingly (Mariette et al. 2018). Also, there is increasing evidence of transgenerational plasticity (or parental effects) in several ecologically relevant attributes, including those related to predation risk, although the process is not yet well understood (see MacLeod et al. 2022). I expect that the study of behavioural epigenetics in relation to social behaviour will continue increasing -and will face little opposition, as it may be seen as providing a scape from biological determinism-, and will eventually allow us to get a better grasp on the complex question of how such plasticity is inherited and evolves.

Nobel laureate Peter Medawar famously repeated that if something can be done it will be done. Thus, although some sectors of society find it difficult to accept that we are animals, that our genes influence our developmental trajectories more than our ideologies would have it, and that our preferences are more influenced by them than we would like to allow, I expect that research on the biological substrates of our behaviour—in sociobiology by whatever name—will go on.

Adriana A. Maldonado Chaparro

The future of sociobiology: social resilience in a changing world

E.O. Wilson's 1975 *Sociobiology: The New Synthesis* established social behaviour as a predictive framework uniting behaviour, ecology, and evolution, formalising how fitness consequences and kin structure shape cooperation across taxa. Fifty years of empirical work have shown that relatedness mediates cooperation, that environmental context shapes social strategies, and that cooperative systems confer ecological advantage in harsh environments. Recent phylogenetic analyses across > 6500 bird species demonstrate that cooperative breeders inhabiting fluctuating environments exhibit broader range sizes and higher population abundance, suggesting that sociality buffers populations against environmental variation (Lin et al. 2023). However, this finding contrasts with Wilson's framework, which assumed equilibrium conditions and stable environments for the evolution and persistence of social systems (Wilson 2000). Contemporary anthropogenic change—habitat fragmentation, climate change, and resource unpredictability—operates at speeds and scales exceeding these assumptions and poses novel empirical and theoretical challenges that allow understanding the mechanisms by which environmental change reconfigures social structures and predicting social resilience in fluctuating environments.

Empirical studies reveal that anthropogenic disturbances fundamentally alter the ecological and selective contexts in which social systems operate. Extreme temperatures fragment social networks as individuals prioritise thermoregulation over affiliative interactions (Rat et al. 2020), habitat fragmentation alters dispersal trajectories and group formation via Allee effects (Cousseau et al. 2020; Chan et al. 2022), and prenatal environments determine alternative reproductive tactics that persist across generations (Shah and Rubenstein 2022). Long-term studies of banded mongooses show that thermal stress reduces helping behaviour and offspring growth, with cooperative groups failing to buffer harsh conditions (Khera et al. 2025), while individual-based models predict that there is a temperature threshold above which social group structures collapse entirely in African wild dogs (Rabaiotti et al. 2023). Habitat fragmentation similarly alters dispersal and group formation, changing emergent social topology through modified resource distribution and reduced densities, and alters kin interactions across terrestrial vertebrates (Alamán et al. 2024), with land-use change interacting with temperature via Allee effects to contact the thermal niches of social species (Chan et al. 2022). The current pace and multi-factorial nature of anthropogenic change demand new empirical synthesis supported by long-term field datasets, genomic tools and an integrated eco-evolutionary framework to predict long-term fitness consequences of dispersal and social strategies under rapid anthropogenic changes.

The near-term forecast: mechanisms and predictions

Developmental programming and transgenerational effects reveal how prenatal and early-life environments shape adult phenotypes and long-term population trajectories. Parental pre-laying environmental conditions determine whether offspring adopt natal dispersal or philopatry in cooperative starlings, producing stable mixed-kin societies via oscillating selection (Shah and Rubenstein 2022). Early-life glucocorticoid exposure reduces behavioural flexibility, identifying a mechanism by which environmental stressors impair social competence and the capacity of groups to buffer change (Reyes-Contreras and Taborsky 2022). Thus, research should focus on linking prenatal stress to adult social network position and test whether developmental interventions can enhance social resilience. Integrating sociogenomics—population-scale transcriptomics and epigenetic profiling—will identify gene-expression signatures of stress-programmed social phenotypes and predict which individuals will maintain affiliative bonds under environmental harshness (Guerrero et al. 2020).

Temperature and fragmentation effects on social topology can be quantified through long-term network monitoring and spatially explicit models. Empirical work shows that extreme temperatures reduce social cohesiveness as individuals prioritise thermoregulation over social behaviour (Rat et al. 2020), while habitat fragmentation alters natal dispersal timing and settlement decisions (Cousseau et al. 2020), linking landscape changes to shifts in social structures. Research will benefit from deploying automated behavioural tracking devices and from social-network analyses across climate gradients to identify critical temperature and fragmentation thresholds where network cohesion collapses. Spatially explicit individual-based models parameterised with these data allow forecasting social-network reconfiguration under alternative climate and land-use scenarios, proving actionable targets for conservation management (Chan et al. 2022). Conceptual frameworks integrating thermal biology with social evolution will link climate projections with behavioural and demographic trajectories (Moss and While 2021).

The long-term forecast: adaptive capacity and conservation

Evolutionary responses to environmental disturbance should focus on testing whether social systems can evolve enhanced resilience within conservation-relevant timescales. Anthropogenic habitat modification has produced measurable shifts in group structure, life history pace, and dispersal strategies within single populations (Alamán et al. 2024), demonstrating rapid phenotypic responses. Long-term studies will determine whether these shifts represent adaptive evolution or maladaptive plasticity and whether cooperative systems possess genetic variation for social flexibility that can be targeted by selection. Comparative sociogenomic analyses across populations experiencing different disturbance regimes allow identifying genomic signatures of selection on social traits and testing whether gene-by-environment interactions maintain social polymorphisms that buffer environmental variation (Guerrero et al. 2020). These studies will inform predictions of whether social species can evolve under current climate and habitat threats.

Conservation integration and management urge embedding social structure metrics into vulnerability assessments and management strategies (e.g., accounting for Allee effects, altered dispersal, and social cohesion loss). Existing modelling frameworks—spatially explicit individual-based models, phylogenetic comparative approaches, and demographic forecasting tools—can be parameterised with social-network data to identify critical thresholds where social-group declines trigger population collapse (Chan et al. 2022; Lin et al. 2023). Addressing future challenges requires cross-disciplinary collaborations among behavioural ecologists, landscape ecologists, climate scientists, and conservation planners to build the "next synthesis" that is predictive, mechanistic, and policy relevant. Meeting these challenges positions sociobiology as an applied predictive science linking social network dynamics to conservation and resilience under global change.

Denis Meuthen

The development of sociobiological research in the next 50 years

Since the widespread impact of sociobiology by Edward O. Wilson's seminal work (Wilson 1975), sociobiological concepts such as kin selection, inclusive fitness and altruism have been instrumental in developing the behavioral sciences alongside the fields of ecology and evolution (Foster 2009). Considering sociobiology as the component of behavioral ecology that concerns social behavior, below I outline ideas to ensure that our field continues with important contributions to both basic and applied research in the next 50 years.

Since the start of the Anthropocene in the mid-twentieth century (Zalasiewicz et al. 2024), natural ecosystems are increasingly undergoing physical, chemical and biological transformations, including climate change, urbanization and environmental pollution. Like other behaviors, social behavior is one of the first traits responding to these environmental challenges (Candolin et al. 2023; Maune et al. 2026). This is because behaviors are inherently plastic and shaped by both past and present internal and external environments (Dingemanse et al. 2010; Stamps 2015). Unsurprisingly, human-induced environmental change is not only associated with altered individual social behavior but also with changes in the frequency and type of social interactions as well as in social structure (Blumstein 2012). Thus, I believe that future sociobiological research will contribute to improving our ability to face the global challenges in the Anthropocene (West et al. 2025).

This is because social behavior can directly be linked to ecological and evolutionary consequences. First, social niche construction can directly have ecological consequences through its consequences for population dynamics (Ryan et al. 2016; Saltz et al. 2016). Altered social behavior may also lead to indirect ecological effects. For example, increased social grouping, a typical antipredator response that lowers predation risk, can also reduce fecundity and survival through increased competition or disease transmission (Krause and Ruxton 2002). Following the ecology of fear (Zanette and Clinchy 2019), such changes can have far-reaching consequences across the ecological pyramid. Second, as any other phenotypic trait, altered social behavior can directly or indirectly impact individual fitness and thereby be favored by selection or not. However, the inherent plasticity of behavior as outlined above may additionally allow accelerated evolution through plasticity-led evolution (Pfennig 2021; Garaffa 2025). These effects may even emerge rapidly and in the absence of natural selection if the mechanisms underlying plasticity skew mutation rates (Wund 2012). Third, following the statement "*Nothing in ecology or evolution makes sense except in the light of the other"* (Pelletier et al. 2009), I believe that we will clearly benefit not only from further studying the consequences of social behaviors for ecological and evolutionary dynamics but also from considering eco-evolutionary feedbacks (Smallegange 2022). This is because the ecological consequences of social behavior can also alter the selective environment and thereby shape the direction of evolution. In this context, the enhanced understanding of eco-evolutionary phenomena that we have achieved by incorporating animal personality in the last years (Bolnick et al. 2003; Wolf and Weissing 2012) showcases why it will be important to routinely assess intraindividual variation in social behavior in the future. Thus, in the coming years, I believe that we will be able to advance our field by placing greater focus on individual-by-environment interactions that shape social behavior as outlined in the concept of individualized social niches (Trappes et al. 2022; Kaiser et al. 2024).

At the same time, we experience increasingly polarized debates about animal experimentation (Kiani et al. 2022). These lead to political endeavors to strengthen animal rights with the aim to eventually phase out animal research (Müller 2025; Reardon 2025). Despite the focus of these discussions being on invasive procedures involving animals rather than on less invasive observations of social behavior (Richter et al. 2025), lacking discrimination within related changes in legalization may lead to a shift away from lab work with animals in the coming decades. This is why I predict that only sociobiological research on invertebrates that remain outside of the legal scope has a high probability of remaining in the lab. Instead, particularly for vertebrates, I believe that we are likely to see more non-invasive field work. To this end, the continued development to make biologging devices smaller and less expensive (Payne et al. 2026) will be particularly helpful for the future. That is not only because they will allow us to non-invasively track which individuals are physically close to each other at any given time and record social vocalizations but also because these devices can assess dynamic changes in relevant physiological measurements such as temperature and heart rates (Jax et al. 2021). This data can then be combined with direct observation of social behaviors, morphological measurements from photographs and non-invasive DNA samples. I believe that such individual-based longitudinal field data have the opportunity to further accelerate our understanding of the emergence and maintenance of individual differences in social behavior as well as of their eco-evolutionary consequences.

As already evident from this example, I propose that we will greatly benefit from incorporating more interdisciplinary research endeavors in the study of social behavior in the decades to come. First, we require increased collaboration between organismal biologists. For example, as phenotypes are highly integrated, we need to routinely investigate the other parts of the phenotype that shape and are shaped by social behavior, such as for example morphology (Bertossa 2011). Also, given the importance of animal communication for social behavior (Bradbury and Vehrencamp 2011), in the next years we need to go beyond observation more frequently and directly manipulate information transmitted via diverse communication channels (e.g. chemical cue compounds, auditory cue frequencies). Second, we require collaboration with other biological fields. For example, social behavior is shaped by the interaction between genomes and the environment, and recent research avenues highlight the importance of the epigenome in this process (Seebacher and

Krause 2019). Thus, understanding the emergence and consequences of both stochastic and induced epigenetic variation through cooperation with molecular biologists will improve our understanding how variation in social behavior arises and is maintained (Meuthen et al. 2026). Collaboration with microbiologists is equally important as not only pathogenic bacteria can manipulate social behavior to their benefit (Keesey et al. 2017) but also the gut microbiome composition shapes social behavior via diverse pathways (Griffiths et al. 2025). Working together with theoretical biologists to incorporate species- and habitat-specific knowledge into mathematical models such as individual-based models (DeAngelis and Mooij 2005) will allow us to obtain simulations that substantially strengthen the theoretical background supporting our future empirical research on social behavior. Third, as humans are also social, I believe that we can successfully draw from and contribute to the expertise developed in social science research, encompassing for example psychology, sociology, and even economics (Kuper et al. 2025). Moreover, interdisciplinary work with science philosophy will bring additional expertise to questions that are also relevant for the study of social behavior (Heger et al. 2025).

Such interdisciplinary approaches to sociobiological research may also increase the probability to obtain research funding (Sun et al. 2021). On the other hand, as in the past, long-term perspectives remain crucial to the success in understanding eco-evolutionary consequences of social behavior (Milam 2022). As funding for such research is challenging to acquire in the current research funding landscape, I believe that we would benefit from a push towards allocating more funding to long-term research proposals whose results may substantially advance our knowledge. Even when such research projects are successfully funded, political developments can disrupt their execution (Tollefson et al. 2025), which is why I also think that we need to develop explicit safeguards for these avenues in the decades to come (Harold and Blanc 2025). The large amount of data on social behavior collected during such long-term research projects may benefit from automated analysis tools such as machine learning (Rutz et al. 2023) and generative AI advances (Rafiq et al. 2025). However, I believe that this technology first requires more development in the form of large-scale multidisciplinary collaboration between software developers, engineers and behavioral scientists for the establishment of adequate standards (Siegford et al. 2023). Thus, I believe that the quantification of social behavior through objective observations by humans, as already envisioned by Konrad Z. Lorenz and Nikolaas Tinbergen (Burkhardt 2005) and Edward O. Wilson (Wilson 1975), will likely remain important even in the years to come.

Manfred Milinski

Sociobiological research in the climate endgame

Globally, average and extreme heat are increasing (IPCC 2021) with tens of thousands of deaths directly attributable to climate change. Natural hazards and disasters such as floods, hurricanes, droughts and wildfires are growing in intensity and frequency due to increasing global temperature fueled by CO_2 emissions and methane production. Since the 1960s, global CO_2 emissions are almost linearly increasing, paralleled by increasing global temperature (NOAA, WMO, IPCC 2020). Surpassing certain global temperature thresholds would risk ‘dangerous climate change’ (Schneider 2001). Despite the frequent headlines about climate extreme events, people continue engaging in high emission activities such as flying to holiday destinations and enjoying cruises on giant ships. In addition, many countries still stick to burning fossile fuels ignoring climate change. This behavior is also evident on a large scale. Global CO_2 emissions alongside global temperatures reached record levels in 2024. Countries had agreed to ‘pursue efforts’ to limit global temperature rises to 1.5 °C (IPCC 2018) under the 2015 Paris agreement. This threshold was. exceeded in both 2023 (Berkeley Earth 2024) and 2024 (Berkely Earth 2025). January 2025 marked the warmest month on record globally (Copernicus 2025).

So-called extortioners (Press and Dyson 2012) do not care about climate change, they just enjoy themselves while enforcing others to rescue the climate (Milinski and Innocenti 2026). Extortioners represent a fixed behavioral type that cannot be disciplined not even by climate disasters (Milinski and Innocenti 2026). They happen to occur at a frequency of about 40% (Milinski 2022). Global CO_2 emissions and the associated rise in temperature will continue unchecked overburdening those who try to act fairly. We are caught in a tragedy of the commons dilemma (Hardin 1968).

Already 2018, Hans Joachim Schellnhuber, the former director of the Potsdam institute of climate impact research (PIK) warned that “climate change is now reaching the end-game, where very soon humanity must choose between taking unprecedented action, or accepting that it has been left too late and bear the consequences.” (Schellnhuber 2018). He argued that immediate, rigorous action was necessary within the next 10–15 years to prevent irreversible damage and civilization threatening catastrophes. Key measures included a rapid shift to zero emissions, abandoning fossil fuels, and adopting sustainable, bio-based construction methods.

Now it seems to be too late to stop climate change. We are in the endgame approaching the final disaster (Kemp et al. 2022). “There is ample evidence that climate change could become catastrophic. … Understanding extreme risks is important for robust decision-making, from preparation to consideration of emergency responses."

There will be (and is already) unprecedented climate migration not only from Africa to Europe, from poor to richer countries until the income has equalized (Marotzke et al. 2020). The whole Mediterranean area has a heat and water problem, e. g., the farmers in Spain had no gras for their goats, they had to eat the goats and leave. Even in Germany farmers had to give up their cows. Because of heat and drought they could not harvest enough hay for the winter, which would be too expensive to buy.

I was asked to describe sociobiological research for the next 20 years with emphasis on climate change. As I showed that we are already in the climate endgame, effective mitigation of climate change is no longer possible. What is left to do is adaptation to climate change, i.e., adjusting to actual climate change and its effects, aiming to reduce vulnerability and enhance resilience—the research agenda for the next 20 years.

When temperature will, as predicted, continue to increase until above 45 °C, plant mortality will occur due to protein degradation, including everything we eat. We will not all die of high temperature, we can afford to cool our houses with solar energy, but we will have nothing left to eat—we will die of starvation.

Corrie S. Moreau

A framework for discovery: the continuing legacy of sociobiology

In 1975 Edward O. Wilson published *Sociobiology: The New Synthesis* which triggered robust and sometimes controversial discussions in biological and psychological disciplines. While many argued that his interpretation of how human behaviors evolved was naïve and inappropriate, this book received much more positive reception in the biological community. Wilson attempted to synthesize multiple fields of biology, from behavior to ecology to evolution, to explain the complex and diverse ways sociality and social behavior has evolved across the tree of life. This important book pushed many biologists, who were often comfortable in their own single field, to have to integrate across fields and contextualize their work in richer and more meaningful ways.

By the time I became Wilson's last PhD student in 2003, the discussion of the final chapter on human behavior had mostly become a thing of the past and I was far too young to have been witness to the protests and debates of the time. The 26 other chapters of the book remain an important synthetic resource for biologists the world over and are still frequently cited and referenced. In graduate school I read the entire book, among others of Wilson, cover-to-cover for my qualifying exam to be ready for questions about how this framed my own work and that of many others since its publication. This call to action for biologists to think and integrate broadly pushed me to strive for my own work to ask questions across disciplines and tools. As a graduate student of Ed's (Prof. Wilson at the time), he pushed me to lean into my passion for organismal biology while remaining rigorous about my research questions and approaches. He was supportive and kind while also encouraging me to challenge my own knowledge and assumptions. Even now during the exciting moments of scientific discovery I find myself asking why, when, where, and how? Just as Ed did for me, I hope I am able to foster this same curiosity of the natural world for my own mentees.

While this book really was a synthesis of what was known at the time about animal social behavior, it was also a call to action to the biological community to push the discipline to integrate across fields. This had profound impacts with behaviorists realizing they needed to consider ecology, and ecologists realizing they needed to incorporate an evolutionary framework, and evolutionary biologists realizing that behavior and ecology may explain patterns of diversification. The growth of the field since the inception of sociobiology has been remarkable.

While Wilson could not have predicted all the new tools and technologies that would allow us to go from pattern to process and from form to function the book still provides a robust framework to make testable hypotheses. The synthetic nature of his perspective to explain the social behavior in the natural world is why this book will remain relevant for many more years to come. While not everyone who does research on social behavior may call themselves a sociobiologist all of them have been impacted by the publications of this book regardless of whether they have even read it due to the huge impact this work has had across biology.

The future is bright for sociobiology for the same reasons that natural history collections are and will always be transformative. We cannot predict all the new ways we will use them in the future. New technologies have permitted us to leverage specimens and artifacts in museum collections to address questions that were not possible when the original collector first put those objects into museum holdings. In the same way the robust and synthetic framing that Wilson's *Sociobiology: The New Synthesis* will continue to provide a framework to address questions on the evolution and function of social traits for many years to come. I could try to predict where the field will move in another 50 years but just as Wilson could not have predicted that we can now take non-model organisms and look at their gene expression across time and after exposure to stimuli or how we can turn off and on single genes to observe the impact related to traits of interest I am excited to see all the ways we will continue to make discoveries and breakthrough in ways I cannot imagine!

Geoff A. Parker

Some thoughts for the future of (mainly) sexual selection

The 1970s marked the era of the 'behavioural ecology revolution' (Parker 2006). Academically, they were the most exciting time of my life. The 'revolution' was defined by E.O. Wilson's *Sociobiology: the New Synthesis* (1975) and J.R. Krebs and N.B. Davies' *Behavioural Ecology: An Evolutionary Approach* (1978). Few researchers in sociobiology/behavioural ecology today will realise that E.O. Wilson's book, particularly its last chapter, generated massive controversy and fierce opposition (see, e.g. chapter 7 in Maynard Smith 1988). Nevertheless, the baby was not thrown out with the bathwater, and R. Dawkins' *Selfish Gene* (1976) not only baptised the new discipline, but made it accessible to a vast readership, both scientific and otherwise. I outlined the history of this emerging field two decades ago (Parker 2006) – it is much more difficult to predict its future, as Owens (2006) and West et al. (2025) have attempted. In attempting to make future predictions to celebrate 50 years since *Sociobiology* I am acutely aware that people of my age are generally more able to recount the past than predict the future!

The fields of sociobiology, behavioural ecology, and evolutionary ecology represent widely overlapping sets, all concerned with the adaptationist approach; i.e. the understanding of traits in terms of their adaptive function through the processes of selection. Apart from the fact that data are often retrieved by field studies, they have little to do with mainstream ecology pre-1970 and are essentially fields within both animal behaviour and evolutionary biology. Before considering its future, it's worth considering what actually comprises the adaptationist approach characterising sociobiology, behavioural ecology and evolutionary ecology, and what defined this explosion of interest in the 1970s.

The study of animal behaviour – ethology—pioneered by the Nobel laureates, Lorenz, Tinbergen, and von Frisch, served to investigate the ontogeny of behavioural traits, their phylogeny, mechanism, and adaptive function, i.e., the celebrated 'four questions' of Tinbergen (1963). The rise of sociobiology/behavioural ecology relates particularly to Tinbergen's fourth question: adaptive function. Up to the 1970s, most ethologists and ecologists had been satisfied to explain, often with little focus, the adaptive value of traits in terms of 'survival value to the species, without focus on the mechanism of selection. This overarching, implicit species or group selectionism generated a mutiny towards Darwinian selectionism, pioneered by stalwarts such as G.C. Williams (1966a, b) and W.D. Hamilton (1964). As a result, in my view (Parker 2006) what was different was (1) the focus on evolutionary mechanisms in terms of selection on given individuals, and more particularly, on the fate of given mutants specifying strategic traits, (2) the awareness of conflicts of evolutionary interests between interacting individuals, and (3) the development and application of mathematical models to predict how selection would be expected to shape given traits. In the 1970s, applying this new approach felt like a walk into a virgin, unexploited land, where opportunities offered themselves at almost every step. That is not so now.

Some (e.g. Bateson and Laland 2013) take the view that all that has happened is that ethology simply expanded by redressing an imbalance due to inadequate coverage of Tinbergen's fourth question about adaptive function. Font (2023) argues that the preoccupation with sociobiology/behavioural ecology since the 1970's itself caused an imbalance, which, post 2000, has been remedied by focus on Tinbergen's other three questions – i.e. there is simply a growing coverage of the overarching field of ethology. However, many fields of biology overlap; one could just as validly argue that sociobiology/behavioural ecology is a branch of evolutionary biology or alternatively (in my view, less validly) ecology – scientific fields often represent overlapping sets.

So what may the next decades hold for our subject? First, a wish rather than a prediction: a comment about the role of optimality modelling of adaptation, a major driver in the behavioural ecology revolution. Since the vital inception of the evolutionarily stable strategy (ESS) approach by Maynard Smith and Price (1973), a major step forward in analysing cases, especially in animal behaviour, where selection depends on how other individuals respond, the technical aspects of optimality models have moved on to consider not only strategic stability, but also convergence to it. However, the optimality approach has met with considerable opposition, especially from philosophers of science and population geneticists (for a recent review, see Lehtonen and Parker 2026). Geneticists quite rightly point out that that by adopting what Grafen (1984) has called the 'phenotypic gambit', optimality modelling ignores diploid genetics, epistasis, genetic drift, the speed of adaptation to changes, and other processes that can militate against selection achieving the optimal phenotype (Brookfield 2024). Over the coming years I would like to see reconciliation, with modellers accepting that optima may not be attained, and geneticists, that the role of optimality modelling is simply to predict the ideally adapted phenotypic trait under the assumed set of constraints and selective forces. If prediction and observations match, we can hope to be closer to interpreting the trait's adaptive value. If the predictions do not match observations, this may be because we have misidentified the constraints and selective forces operative, or because the genetic system has not permitted evolution towards the expected optimum, suggesting further investigation. But without such predictions, we cannot fully understand adaptation, or lack of it.

Making predictions about what may become exciting new areas in science is problematic. Science is all about asking novel questions (Parker 2010), which often crop up unexpectedly. I can propose some rather detailed, shorter-term questions in the areas in which I still remain active, and later, much less confidently, suggest a few longer term possibilities. As judged by publications, sexual selection is a major preoccupation of our discipline (Simmons 2014). So first, some specific predictions for further work in this area, which mostly arise from my current research interests:

1) Theory for transitions in the sexual cascade

Since the 1970s, I have been interested in the transitions that underlie the evolutionary changes in modes of sexual selection (the 'sexual cascade'), though I finally published on this only relatively recently (Parker 2014; Parker and Pizzari 2015). Much more mathematical modelling could be done to understand the theoretical reasons for each transition, especially on female aspects in transitions, and more empirical testing is needed.

2) Multicellularity and the transition to anisogamy

The key initial stage in the sexual cascade is the transition from isogamy to anisogamy, the binary divide that defines the two sexes, males and females. The main theories for its evolution are intracellular conflict (see review by Lessells et al. 2009) and gamete dynamics (GD) theory, which relies on the biophysics of fertilisation under gamete competition and limitation, and the need for zygote provisioning (Lehtonen and Kokko 2011). In GD theory, both the evidence (Knowlton 1974; Bell 1982; da Silva 2018; Hanschen et al. 2018) and the theory (Bulmer and Parker 2002) suggest that this transition is linked to the evolution of multicellularity and organismal complexity (Parker et al. 1972). Progress has been made in understanding infrequent anomalies, such as the occurrence of isogamy in large complex algae (da Silva and Drysdale 2018), but what remains to be understood is (i) the theoretically expected relation between zygote size and adult size across transitional forms, and whether this matches the observed relation, (ii) whether the predicted transition to anisogamy matches its observed occurrence in transitional forms.

3) The relative magnitudes of gamete competition and gamete limitation in broadcast spawners

The ancestral scenario under which anisogamy arose is likely to have been broadcast spawning. GD theory suggests that anisogamy can be driven by either one or both of two components, gamete competition and gamete limitation (Lehtonen and Kokko 2011; Lehtonen and Parker 2014). Fascinating empirical work has been done by Levitan (2018) to demonstrate how the spatial dynamics of spawning determines how sperm competition and sperm limitation may be structured in broadcast spawners, but little is known about the exact relation between these two components in nature, and would be well worth more extensive study. Theory suggests that sperm competition may be the more significant of these two forces since only relatively low gamete competition is needed for anisogamy to evolve (Parker and Lehtonen 2014). Nevertheless, high gamete limitation can occur in some broadcast spawners (Levitan and Petersen 1995; Levitan 1998) and under sufficiently low gamete competition, this can generate anisogamy from isogamy.

4) The rise of mobility and pre-ejaculatory sexual selection

The transition to mobility represents another key stage in the sexual cascade, because it marks the onset of Darwinian (1871) pre-ejaculatory sexual selection. Empirical investigations of weakly mobile broadcast spawning invertebrates showing the beginnings of transition to mobility and mate targeting would be well worth further study, notably species ranging from those only gathering in spawning assemblages to those showing 'pseudocopulation' (as in some asteroid echinoderms). What caused the initial step to mobility – would it have been food foraging (which would likely not be sex specific) or mate targeting (and how would this become sex specific)? Initial modelling shows conditions under which such males should begin to show mate targeting in spawning assemblages to reduce sperm competition (Parker 2014), but did not consider why females should not also initially show forms of mate targeting. Monk et al. (2019) interestingly propose that the initial step may have been indiscriminate sexual targeting, from which more discriminate sexual behaviour evolved later. The reason why male targeting of females became predominant may relate to the fact that the underlying anisogamy in metazoans implies that mate searching is more likely to evolve in males (Lehtonen et al. 2016), but empirical investigation of transitional stages to mobility could be revealing.

5) Deviations from the predicted 'mainstream flow' in the sexual cascade

A major sexual cascade prediction is that ultimately because of anisogamy, there has been a 'mainstream flow' leading to males competing more for matings than females, i.e. the Darwin-Bateman paradigm (Dewsbury 2005; Janicke 2024), and this has theoretical underpinnings (Lehtonen 2022; Lehtonen and Parker 2024). However, there are many exceptions, mainly relating to species with parental care. Theoretical reasons underlying typical sex role reversal (i.e. where females compete for matings and males undertake most or all parental care) have been outlined (Lehtonen et al. 2024), but reasons why such species initially deviate from the paradigm often remain unclear. Early progress was made on this problem, relating to which sex is present when the zygotes become available for care (Dawkins and Carlisle 1976; Maynard Smith 1977). However, assuming that both sexes are available, at least theoretically, less costly diversion of gametic expenditure by males into parental care may suggest that, rather paradoxically, males should invest more in care than females. Another sexual cascade prediction is that post-ejaculatory sex selection, prevalent in broadcast spawners, has reduced with the onset of internal fertilisation (Parker 2014). However, this has not been found in fishes, which show higher sperm competition in internally-fertilising species than those fertilising externally (Fitzpatrick 2020). A reason may be that the (fewer) external fertilizers in the analysis were mainly species with male nest guarding or biparental care, which likely reduce the probability of multiple paternity (Fitzpatrick 2020). It would be interesting (but difficult) to ascertain multiple paternity in broadcast spawning fish species for comparison.

6) Sexual size dimorphism

Animal species occupy the entire range of sexual size dimorphism, from smaller males to larger males, and there have been many hypotheses for this (e.g. Blanckenhorn 2005). It seems generally likely that sexual selection by male-male combat generated larger males, and the size-fecundity advantage for females coupled with lack of male combat generated larger females, with any sexual niche divergence occurring secondarily. But what caused the initial divergence towards either end of this spectrum remains unclear. Maybe molecular biology could help elucidate the phylogenetic origins of such divergences, which may help illuminate their adaptive causality.

7) Post-ejaculatory sexual selection

I previously outlined some possible future prospects for this aspect of sexual selection (Parker 2020). In addition, further theoretical work is needed on sperm competition mechanisms other than the raffle (lottery) principle, and on plugs, seminal fluid proteins and haploid expression. Theoretical aspects of cryptic female choice and its underlying sexual conflict would also repay further study.

While it is relatively easy to speculate about short-term developments in one's current research area, long term speculations outside it are much harder and certainly more risky – at best they become wild guesses, and at worst demonstrate one's naivety. I'll restrict this to just three (probably ill-advised) conjectures. One area, pioneered by Harley (1981), relates to learning mechanisms: what rules govern the evolution of reward values and how are these moderated adaptively by motivation mechanisms? Theoretical development would be interesting, but empirical testing difficult. A second area, the role of epigenetics in evolution (Lind and Spagopoulou 2018), particularly in strategic adaptation and conflict, initially explored by Haig (1992) in relation to genomic imprinting and conflicts over maternal care during foetal development, certainly deserves further development—its effects may be profound. A third, rather diverse area is that of female manipulation of male behaviour. Much has been written about male coercion of females to obtain matings, but while many rather specific cases of female manipulation of males are reported (e.g. matriarchal dominance, increasing male parental investment), few generalities are available other than the female choice component of sexual selection.

Finally, what is the long-term future for behavioural ecology/sociobiology? I suspect it will continue to be seen by many as a subdiscipline of either animal behaviour, ecology, or evolutionary biology. It will continue to expand and be seen by others as a discipline in its own right. Unexcitingly, I see no radical change here. Much of that virgin land colonised in the 1970s has now been explored, but each step leads ever onwards to new directions.

David C. Queller

Continuing range expansion

Predicting the future can be a foolish game, but also a fun one. The safest (though least fun) predictions come from extrapolating present trends. I can confidently predict that sociobiology will continue to expand its scope beyond animals to plants, microbes, viruses, and selfish genetic elements. I expect continuing increase in applications to medicine and agriculture. In addition, I expect sociobiological studies to integrate more and more with mechanistic and genetic approaches. One outcome of that integration should be a better understanding of constraints – when do particular mechanisms inhibit the evolution of theoretically better adaptations?

Getting further away from my comfort zone, I think there is interesting work to be done incorporating community-level processes. When can community level selection be significant? How do sociobiological principles, especially mutualism theory, interact with the quasi-selective processes of community assembly? It is perhaps there that we will be able to understand the apparent utility and stability (usually) of gut microbiomes. Likewise, it seems important if we are ever to understand how early replicators assembled/evolved into real living cells.

Francis L. W. Ratnieks

Sociobiology the book: some personal reflections and thoughts for the future

My first encounter with the book *Sociobiology: the New Synthesis* was in 1978, quite soon after its publication in 1975. I was then a year 2 undergraduate doing a BSc in Ecology at the New University of Ulster, Coleraine, UK's newest, smallest, and least popular university but which was pioneering in having BSc degree courses in Ecology and Environmental Science.

I had ended up there on account of deciding, a few years after "dropping out" at Sussex University in England and moving to Ireland, to return to university at the last minute. The New University of Ulster had many vacant places due to it being in Northern Ireland which was going through what were euphemistically known as The Troubles. There were few students from the rest of the UK or Ireland. At the time I was living in Drogheda, in the Republic of Ireland, and training to be a welder. Northern Ireland was not on many people's list of places to visit let alone move to.

I was taking a class in Animal Behaviour. One of the two lecturers, Dr. Tony Pitcher, noted that he had got the library to purchase a copy of *Sociobiology* and suggested we look at it. The university buildings were in two clusters on campus, called Phase 1 and Phase 2, each with a library. Biology was located in Phase 2 which had a science library and a good collection of books and journals on biology, and where I spent a lot of my time.

Sociobiology it seemed had been put into the "wrong" library, that of Phase 1. I made the longish trek across the windy campus to the Phase 1 library a few times to have a read. It was not a book that could be signed out so it was always available. Its massive size meant that it was not exactly portable anyway. It was probably the largest book I had ever handled and quite a work of scholarship and organization. (W.D. Hamilton had remarked on this in his book review of *Sociobiology*.) It seems that the book's title indicated to the librarians that it was not a book on biology so it was housed in Phase 1, keeping company with books on sociology and education, among other topics, rather than in the Phase 2 library, among other biology books.

Sociobiology was an attempted synthesis, grounded in evolutionary biological principles, across the different animal social groups and included, controversially to some, humans. The need for this synthesis is shown in a small and idiosyncratic way in the difficulty the NUU library system was having in deciding where to locate it. Dr. Pitcher noted that he was in communication with the library to move the book to the Phase 2 library. I never followed through on what the final outcome was. Was it moved? Maybe a second copy was bought!

My time at the New University of Ulster rekindled my love of science and insects, and my journal readings in the library had indicated that a lot of entomology was being done at Cornell University and UC Berkeley. A number of years later I was doing a PhD in the Entomology Department at Cornell, based at Dyce Laboratory for Honey Bee Studies. Dr. Roger Morse, known to all as "Doc", was Professor of Apiculture. His father, who was a hobby beekeeper and had a collection of books, had passed away and Doc kindly gave away these books to his PhD students. There were about 5 of us and we took turns choosing. One of the books was *Sociobiology*. This was by far the most coveted. One of the PhD students referred to it as the "big one", and not just physically. It was not a cheap book and was beyond the budget of a typical PhD student. I cannot remember who, on drawing lots, had first choice and so got it, but it was not me. This was c. 1985.

After completing my PhD at Cornell I was doing a postdoc with Dr. Wayne Getz in the Entomology Department at UC Berkeley. In Berkeley there were a number of bookshops, including the well-known Moe's Books on Telegraph Avenue, which was also home to the (in)famous People's Park and a colourful collection of street characters and wafted herbal aromas. Moe's also sold secondhand books. In about 1992 I was finally able at Moe's to afford my own reduced-price copy of *Sociobiology*, plus other books including Wilson's earlier *The Insect Societies*, *The Ants* by Hölldobler and Wilson and Helena Cronin's *The Ant and The Peacock*. I bought additional copies and passed some on, such as on trips to Denmark to visit Dr. Koos Boomsma. The Danish graduate students were glad to get these at affordable prices. In those days the airline baggage allowance was generous, allowing many heavy books to be transported free.

My most recent encounter with *Sociobiology* was in 2025. Having just retired I was faced with what to do with my books. The office was full of them. Acquiring books seems to be an occupational hazard of academics. I gave most away but kept some, including *Sociobiology*. I realized that I had not looked at it for years, decades even. I fact, I don't think I had looked at it since moving back to England in 1995, books in tow. This was despite having made a career studying, among other things, social behaviour and social evolution. I guess I had not needed it.

Wilson's books laid things out in a thorough way, with copious illustrations and tables and were useful mines of information. But in some respects, they did not seem always to get to the core of things. Subsequently, Wilson authored or coauthored some articles and books that seemed to show that he did not fully understand Hamilton's theory of inclusive fitness (Ratnieks et al. 2010), which is one of the cornerstones for understanding social behaviour. In puzzling over this it seemed to me that Wilson was unable to reconcile the fact, which to him may well have seemed to be a contradiction, that social nature, as explained by IF theory, could reach different end points. In particular, it did not just illuminate how altruism could evolve but also showed that conflicts are expected in social groups. These can be resolved such that potential conflicts are or are not actualized. In some cases you have to look hard to see the actual conflict despite the potential conflict.

In my 1978 Animal Behaviour course we were required to read and write an essay on Richard Dawkins' *The Selfish Gene*. I found this book to be a more helpful guide to understanding the evolutionary underpinnings of evolution including social behaviour, and it was also an introduction to social insects via its discussion of Trivers and Hare's paper on ant sex ratios. To me the most useful of Wilson's books was *The Insect Societies*, probably because I mainly studied social insects. Wilson made a massive contribution and *Sociobiology* was a landmark, in large part because it was a synthesis and included humans. It was unfortunate that it stimulated controversy, which seemed mainly to have been generated in his own department at Harvard. It cannot have been an easy time for him.

In about 165 BCE Terence wrote "I am a man; I think nothing of humans alien to me" (FR translation) (*Homo sum, humani nihil a me alienum puto*). Whatever controversy *Sociobiology* generated would seem to be because of Wilson's desire not to leave humans out of the picture. Of course, understanding humans is a huge challenge, involving not only our evolved biological nature, but also culture, religion and more. Wilson made a significant and productive contribution to this, even if some controversy was generated and that he probably gave too important a role to evolutionary biology. It seems that we still do not understand our own species or ourselves. One of the ongoing challenges facing evolutionary behavioral ecology and sociobiology is that of including humans. How much of the human question, from world peace to family life, can it explain?

Evolutionary behavioural ecology and sociobiology is now a mature field. To give one example, inclusive fitness theory, which is foundational in understanding altruism, conflict, and conflict resolution in many social groups is well supported as a theory. Are there new theories in the wings? Probably nothing that is comparable in its importance. Mutual benefit is also of huge importance in many social systems, and indeed was the basis of Allee's theory of social evolution. The logic of natural selection in general, including inclusive fitness theory, will continue to be fundamental. In doing this basic algebra will likely continue to play an important role, so that applying theory and making and testing predictions will be within the ability of many people. The application of theory is more likely to bear fruit if it is developed by biologists with modest mathematical ability than those with greater mathematical fire power but who are lacking in biological insight and experience.

One of the seminal topics in the early days of behavioral ecology was animal foraging, which is an area that my own research moved into in the past 15 years or so. In an article on community ecology, McGill et al. (2006) suggested that functional traits, such as energetics, were of key importance. In a field study, we found that a remarkable 74% of the variance in the relative proportions of honeybees versus bumble bees on 22 species of summer-blooming flowers depended on variation in the energetic efficiency of foraging (Balfour et al. 2021). The honeybees outnumbered bumbles on flower species on which they were better at making an energy profit and vice versa. Given that even the key variable in an ecological study typically explains only a tiny fraction, some 3–5% (Møller and Jennions 2002), of the variation how were we able to explain 74%? The reason is because we figured out and studied the key variable that was central to the life of the bees. It was energetics at a time, summer, when nectar was available but not abundant.

Perhaps there is a need for getting to the bottom of things more. Perhaps as behavioural ecologists we should not be content to find some variable that is statistically significant but not all that important in the bigger picture and then write a paper. Rather, we should not shy away from seeking to find deep and powerful explanations. How can we explain more? What are the key variables and how to find them? One key in this is in really knowing what makes things tick. This understanding is also relevant in wildlife conservation, which is increasingly becoming a dominant area in studies of wildlife.

Television and video show the wide interest that the public have in behavioural ecology, because it sheds light one of most popular facets of nature, that of animals doing things in the wild. David Attenborough is a masterly TV presenter but much of what he presents so well was actually discovered by hundreds of behavioural ecologists who are rarely named. There will continue to be students who want to work outside (and sometimes inside) with live animals, and there is still much to discover. The advent of new techniques and methods, including those made possible via genetic and genomic approaches and those that yet remain to be discovered, will enable more and new questions to be addressed. But they are not an alternative to curiosity, to using one's eyes, and to being outdoors. And not to be told what to look at but to look for yourself to see something new, often in what had been seen before but without seeing.

Gene E. Robinson

Fifty years after Sociobiology: toward a molecular theory of social life

In a perspective published in *Trends in Ecology & Evolution* in 1999 (Robinson 1999), I proposed "sociogenomics" as the name for "integrative studies of the molecular genetics of social behavior." This was followed by a longer article in *Nature Reviews Genetics* with Christina Grozinger and Charles Whitfield (Robinson et al. 2005), which articulated sociogenomics' central goal: to achieve a comprehensive understanding of social life in molecular terms—how it evolved, how it is regulated, and how it influences genome structure, genome activity, and organismal function. I chose this name, derivative but distinct from sociobiology, to emphasize the power of emerging genomic methods to illuminate both hereditary and environmental influences on brain and behavior. As Traniello and Bakker (2026) note, sociobiology has sometimes been viewed—particularly by scholars of human behavior—as overly deterministic, placing too much emphasis on heredity rather than on the interaction between nature and nurture. Sociogenomics was intended to help advance Wilson's vision of a unified science of social behavior while explicitly incorporating dynamic interactions between genes, brains, behavior, and environments.

Early work in behavioral transcriptomics from my laboratory revealed socially induced changes in brain gene expression associated with behavioral transitions in honey bees, with gene-expression profiles accurately predicting behavioral states (Whitfield et al. 2003). As similar findings emerged in other species, a review with David Clayton and Russell Fernald emphasized the bi-directional relationship between genes and social behavior: genetic variation influences brain and behavior ("nature"), while the social environment influences the genome, particularly through changes in gene expression ("nurture") (Robinson et al. 2008). These discoveries helped establish sociogenomics as an experimental framework linking molecular mechanisms to social behavior.

Subsequent work demonstrated that social behavior reshapes brain gene regulatory networks. In collaboration with Nathan Price's laboratory, we showed that behavioral states are associated with distinct patterns of gene regulatory network organization mediated by evolutionarily conserved transcription factors (Chandrasekaran et al. 2011). Related studies extended this paradigm to vertebrates, including humans, revealing deep conservation of molecular pathways associated with novelty-seeking and social responsiveness (Liang et al. 2012; Shpigler et al. 2017). Our original vision was that sociogenomics would stimulate mechanistic studies of social behavior in both animals and humans. For many years, however, such work was largely confined to animal systems.

More recently, sociogenomics has expanded into studies of human social behavior, though along a somewhat different trajectory (Bliss 2018; Conley 2025b). This development has been driven by the emergence of large biomedical databases containing genetic, lifestyle, and health information, most prominently the UK Biobank. These resources have enabled numerous genome-wide association studies (GWAS) of social and behavioral traits. However, integrating insights related to the bi-directional relationship between genes and social behavior has proven challenging in human sociogenomics, and current approaches often emphasize genetic effects more strongly than is typical in animal sociogenomics.

One of the central challenges for the next decades will therefore be to better integrate human and animal sociogenomics. For social scientists, this means grounding behavioral GWAS findings within biologically informed mechanistic frameworks that explicitly incorporate gene–environment interactions and the dynamic effects of social environments on genome activity. For biologists, this means situating experimental'omics studies within broader behavioral and societal contexts. Progress will require combining experimental approaches common in animal systems with population-scale genomic data from humans, likely with new analytical tools for non-invasive human brain molecular analysis (Lam et al. 2022; Robinson et al. 2024).

Evidence from animal systems also shows that the molecular wiring of the brain is shaped by heredity, environment, and their interaction. Consequently, the behavioral effects of specific genetic variants often depend strongly on environmental context (Robinson et al. 2024; Robinson and Conley 2025). Incorporating environmental and social variables into human GWAS—especially studies of behavior—will therefore be essential for developing more accurate models of gene–behavior relationships.

Looking ahead, several developments are likely to shape sociogenomic research over the next half century. First, advances in single-cell genomics, spatial transcriptomics, and brain-wide molecular mapping will allow researchers to link gene activity to neural circuits that regulate social behavior with unprecedented precision, explaining individual variation in behavior comprehensively. Second, comparative sociogenomics across diverse species will reveal conserved molecular principles underlying sociality and its evolution. Third, integrated human sociogenomics—combining population-scale genomic data with mechanistic insights from experimental systems—will provide a deeper understanding of gene–environment interactions in shaping social behavior.

Finally, advances in the study of genes and behavior must be interpreted responsibly. In the twentieth century, genetic determinism was widely recognized as ethically problematic; we now know that it is also scientifically incorrect. Modern genomics provides strong empirical grounds for rejecting simplistic deterministic interpretations of genes and behavior (Robinson et al. 2024). This is particularly important as technologies such as CRISPR raise the possibility of genetic interventions affecting human traits. By integrating human and animal sociogenomics—and increasingly combining genomic data with AI-based modeling of behavior and social systems—researchers can move closer to Wilson's vision of a unified science of social behavior while developing a comprehensive molecular theory of how brains generate social behavior.

Michael J. Ryan

Sociobiology and integrative animal behavior

Whether fair or not, the last chapter in *Sociobiology* sparked intense controversy in the sciences, the humanities as well as the general public, controversies that have not entirely subsided over the past half-century. Although to a much lesser extent, Wilson's sketch of the past and future of sociobiology and related fields, sometimes called his amoeba diagram (his Fig. 1.2), has also enjoyed a long half-life, particularly among animal behaviorists. He famously predicted: "The conventional wisdom also speaks of ethology, which is the naturalistic study of whole patterns of animal behavior, and its companion enterprise, comparative psychology, as the central, unifying fields of behavioral biology. They are not; both are destined to be cannibalized by neurophysiology and sensory physiology from one end and sociobiology and behavioral ecology from the other". Wilson got a lot of things right in *Sociobiology*, but this prediction is not one of them. In a review of the book, Barlow (1976) made the opposite forecast "the flow will be the other way: ecologists will become ethologists as population biology becomes increasingly reductionist." He added graciously "And while he thinks it is we who are joining him, I am inclined to view it the other way round. I am delighted to have him with us." Barlow's assessment proved prescient. I predict that in the coming decades sociobiology will become even more integrative, applying a plethora of new techniques from genomics, neuroethology, and remote sensing of animals in the wild to a wider range of taxa—and increasingly sophisticated in how that integration is achieved.

The integration of animal social behavior, including sociobiology, has been underway for some time. Ord et al. (2005) conducted a network analysis of articles published in animal behavior and related fields from 1968 to 2002, which included about 25 years since Sociobiology appeared. They concluded: "Profound historical distinctions between early ethology and comparative psychology have been recently bridged by shared interest in communication and social behavior, and research from physiology and applied areas." These trends seem to have continued until today. Cannibalism did not occur; rather, integration emerged (e.g. Robinson 1999; Ryan and Wilczynski 2011).

What does this integration look like?

Much of this integration uses Tinbergen's (1963) "four questions" as a conceptual framework: causation, ontogeny, survival value, and evolution. The first two are typically considered proximate questions; the latter two as ultimate questions. Mayr, one of the main architects of the Modern Synthesis of evolutionary biology, was friends with Tinbergen and reviewed Tinbergen's manuscript prior to publication (Burkhardt 2005). Mayr (1961, 1982) had earlier formalized proximate and ultimate questions in biology, both he and Tinbergen followed Julian Huxley's (1942) lead on this. In some sense, however, their intellectual goals diverged. Mayr introduced the proximate/ultimate dichotomy in part to safeguard the autonomy of evolutionary biology relative to more reductionist endeavors, while Tinbergen specifically called for integration of his four questions.

Hofmann et al. (2014) suggested there were two main hurdles to achieving an integrative understanding of social behavior. First, most species with robust ecological data sets usually lack details of neural mechanisms. Second, classic laboratory 'model' species typically lack ecological depth, having evolved for many generations under laboratory conditions. But times are changing, as these authors optimistically point out integrative studies no longer need be restricted to a few model systems due to advances in behavioral ecology, genomics, and neuroscience together with numerous technological breakthroughs. For example, genomics is more affordable (Robinson et al. 2005) and neurogenetics is bridging the gap between gene expression and brain function (O'Connell and Hofmann 2012). Neuroethological techniques allow quantification of neural responses in free-ranging animals in natural habitats (Ide and Takahashi 2022). Developmental plasticity is now central to understanding social behavior (West-Eberhard 2003). Field studies can measure variation in cognitive skills and correlate that variation with survivorship in the wild (Sonnenberg et al. 2019). Phylogenetic comparative methods have become *de rigueru* for studies of social evolution (Cornwallis and Griffin 2024). The magnitude of integrative studies of social behavior is not something that could have been glimpsed by Wilson 50 years ago.

Integration requires more than accumulation

Although Tinbergen did not provide a roadmap to how this integration should take place, he might agree with the philosopher of science (Conley 2020): "Integrating Tinbergen's four questions requires more than answering each individually. One can pick any four questions about any topic at random, and it would be clear that simply answering each would not constitute an integration of those questions". The goal of integrative animal behavior is not merely completeness but coherence: to develop a correct, not merely a complete, unified understanding of why animals behave as they do.

An integrative analysis can bring independent datasets to bear on both proximate and ultimate hypotheses. This approach resembles Hennig's (1966) concept of reciprocal illumination, in which independent lines of evidence are compared in order to evaluate phylogenetic hypotheses. Reciprocal illumination remains influential in fields as diverse as biogeography (Santos and Capellari 2009) and genomic-phenomic mapping (Boudinot et al. 2022).

In this same spirit, (Autumn et al. 2002) presented a protocol for testing hypotheses of adaptation by integrating historical and mechanistic explanations. In six cases, four involving social behavior, they showed how adding these dimensions substantially altered interpretations of adaptation. Two additional examples further illustrate the point.

When proximate evidence challenges ultimate hypotheses

W.D. Hamilton (Hamilton and Brown 2001), one of the primary architects of sociobiology theory, proposed that the bright autumn colors of temperate trees function as honest signals of commitment to produce defensive secondary compounds against herbivores. Their data showed that the number of aphid species on a tree covaries with leaf brightness, supporting the adaptive signaling hypothesis.

This hypothesis, however, rests on a mechanistic assumption: that aphids can perceive and appropriately respond to these bright colors. Marshaling data on aphid visual biology, Chittka and Döring (2007) showed that yellow targets stimulate the aphid's green photoreceptors more so than does green foliage. Yellow has thus been termed "a supernormal foliage type stimulus" that is more attractive to aphids than is green. From this proximate perspective, bright autumn colors may attract rather than deter aphids, undermining the ultimate signaling hypothesis. Here, mechanistic analysis challenges adaptive interpretation.

When ultimate questions motivate proximate discovery

Ultimate considerations can also drive proximate investigations. The functional significance of nocturnality in bats was long recognized, at least since Aristotle classified them as mammals. Navigating at night allowed exploitation of ecological niches unavailable to diurnal and non-volent mammals. Yet understanding the mechanisms of nocturnal navigation required technological advances in the mid twentieth century that afforded humans the ability to eavesdrop in the ultrasonic. Donald Griffin and Robert Galambos established the role of echolocation, revealing the bat's use of ultrasonic sound production and reception (Galambos 1942); Griffin (1958) further develop this insight. In this case the strength of adaptive hypotheses motivated the search for the discovery of the proximate mechanisms.

Looking forward

Researchers increasingly address multiple Tinbergian questions simultaneously, but such studies remain less common than they could be. My near-term prediction for sociobiology—admittedly not a bold one—is that integrative studies will continue to expand. More importantly, integrative datasets will increasingly be designed not simply to accumulate answers to Tinbergen's four questions, but to test how those answers constrain and inform one another. Integration will become not just a matter of scope, but of methodological reciprocity.

Paul Schmid-Hempel

A quest for the holy grail

There are probably very few students and researchers of animal behaviour, anthropology, primatology, or sociology that have not come in contact with 'sociobiology' and much has been written about its development and the surrounding controversies. And, yes, if one wants to look ahead, a look back is never wrong. For sure, each of us had a personal history with this field. For example, I was fortunate enough to have met Hans Kummer in Zurich who was an early advocate of these ideas. Similarly, in my time at Oxford, John Krebs' behavioural ecology group was flourishing and teeming with new ideas. Happily enough, the focus was not so much on ideology and presumed political implications, but on what soon was named the 'adaptationist program'. And sure enough, with Gould and Lewontin's '*The spandrels of San Marco and the Panglossian paradigm*' (1979), two prominent and early critiques of sociobiology went on to target exactly this approach. Ironically, this paper proved to be not the disastrous blow for the incipient field but instead very helpful, as it forced adaptationist to clarify their assumptions and to rethink their program. As a result, the adaptationist program became more useful and more powerful than before. So, after all the dust and controversies largely—but by no means universally—have settled, what can one take from this?

Recall that science is about patterns and processes. Describing and analysing what is there will define patterns. But the usually more difficult step is to explain why patterns exist, i.e. what are the mechanisms and processes at work that generate what we see? In science, this combines with the inherent search for unifying principles that can explain more and more of the phenomena or patterns—the 'theory of everything' being an example of the mystical endpoint of physics. By proclaiming sociobiology as the '*New Synthesis*', E.O. Wilson exactly followed this agenda. In his case, it was 'sociobiology's lesser sister'—kin selection—that served as the underlying principle to explain social behaviour across a large scale of taxa. As we all know by now, it was this search for a unifying explanation that triggered the controversy, and the accompanying adaptationist program continues to generate similar stirs in various contexts up to this day. Of course, Wilson's *Sociobiology* did not invent kin selection. This was William D. ('Bill') Hamilton's discovery in the early 1960's, followed by John Maynard Smith's expansions into evolutionary game theory, and George Price's fundamental insights into correlated responses to selection around 1970. These ideas already had gained ground at the time, albeit surprisingly slowly. Similarly, *Sociobiology* did not invent the adaptationist program, whose roots—to mention just a few—are closer to George C. Williams stance on senescence, adaptation and group selection, or to Niko Tinbergen and David Lack's contributions to the study of animal behaviour and bird breeding. But the controversies around *Sociobiology* helped to push all of this to a central stage. And it is hard to deny that, over the last fifty years, the adaptationist program has claimed its role as a powerful tool to study the biological world, regardless of whether one deals with development, parasitic infections, or social behaviour.

A hallmark of a successful program is its expansion and diversification to more and more fields of scientific inquiry. Inevitably, this leads to a branching process where new fields emerge – which should sound familiar to evolutionary biologists. Wilson's grand idea of formulating the unifying biological bases of social behaviour as the new synthesis had hardly convinced students of human behaviour and did not have a long life. Its weaknesses as an overarching, unifying theory quickly became obvious and the grand theme inevitably evaporated across the many pitfalls encountered in these various fields. But its core succeeded in the sense that the adaptationist program entered more and more fields of science, even though this was by far not the merit of *Sociobiology* alone. The unifying principle persisted because it metamorphosed into many flavours and modifications, and not without critiques, disputes and controversies. Yet, sociobiology failed in some important sense, as the process of adopting new principles generated a range of new fields, with their own communities that no longer considered themselves being sociobiologists. Anthropologists or sociologists, for example, felt that they needed a different agenda to study human behaviour and followed their own course. Hence, the various groups that Wilson intended to gather under one umbrella quickly separated themselves from one another by founding their own societies, journals and conferences. 'Behavioural Ecology' perhaps is an early example. But even in this field, some practitioners soon considered themselves 'evolutionary ecologists' instead, whereas others felt closer to be students of animal behaviour or evolutionary biology. And the adaptationist program continued to invade other, more traditional disciplines, too, such as parasitology or molecular genetics. This formed highly successful and active new domains that were forced to find a new name for their field, such as 'evolutionary molecular genetics' or – to take a non-random example—'evolutionary parasitology'. In universities, not the least, traditional chairs or sections in the life sciences, such as 'botany' or 'zoology', became converted into units of 'animal evolution and ecology', 'evolutionary genomics',' evolutionary developmental biology' and so forth. The declaration of sociobiology was not the only reason for these developments, but the associated adaptationist program was a major mover. So, what should we expect for the future?

When trying to make predictions, we should recall that major developments and breakthroughs in science are, alas, typically unpredictable. Who, at the time, would have thought that the study of animal dominance conflicts can one day translate into understanding diseases caused by genomic conflicts, or that Lack's study of clutch sizes in birds will later provide tools to elucidate the timing of parasite virulence? So, obviously, it is possible to imagine future developments even when some of these may be what one hopes for rather than what actually will emerge. But, by and large, it would be more speculation than informed guess what major breakthroughs in sociobiology we might expect in the next decade, whereas it is often more obvious what kind of technical or methodical advance one might see. Yet, conceptual advances are what is most precious and what sets the path for future fields. To state that sociobiology's agenda should be the biological study of behaviour in social species is a practical characterisation and seems hardly an inspiring idea, nor is it controversial as long as it does not concern humans. Indeed, who would seriously take offence with the idea that the formation of fruit bodies in slime moulds is somehow connected to kin selection? Yet, regardless of what species is considered, and among the wide range of questions or the diversity of research programs that surround this theme, a deeper meaning for 'sociobiology' is connected with the study of biological processes and the basic principles of evolution by natural selection that are shaping social behaviour. In this context, the role of kin selection refuses to go away and remains one of the most interesting elements, precisely because it connects to the foundations of the evolutionary process. Empirically, its importance will vary considerably among different species or situations. Therefore, to delimit the empirical validity of implicating kin selection for social behaviour will be an important agenda, just as will be future empirical research to gather the facts on the genetic and environmental variance in all of these questions. On the other hand, it is not farfetched to expect that, more generally, the adaptationist program will further be clarified, expand and diversify, and conceptually unite different fields, such as development, cancer research, resilience strategies, engineering, and many more. Inevitably too, in the practice of scientific work, we will see the further specialisation and separation of the respective communities even when the same basic explanatory principles are heeded. Controversies will not vanish, yet hopefully advance instead of hinder new insights.

Yes, we simply cannot ignore that living organisms exist by means of and are shaped by the process of evolution by natural selection. To expand the focus, these foundations are much more general than the principle of kin selection itself, which has caused the major stir. Evolution, by definition, is change over time in some characters of a population, be it individual body sizes or behavioural strategies in societies. But 'kin selection' is embedded in the much more general question of how evolutionary change happens in populations where these characters and their fitnesses are correlated, as illustrated by Price's covariance analysis. This does not even depend on whether we deal with organisms, provided a system has appropriate properties. So, it is not so much about kin and genes as an end in itself, but how selection on the consequences of individual behaviour produces evolutionary change by sending its waves through the population and have trickle effects on neighbouring individuals as is relevant in social species. In this context, kin and genes is just the biologically most relevant case, but all what matters is the statistical association between the heritable properties of interacting individuals, regardless of a common ancestry. To put it in other words, when too fiercely focusing on kin selection as a pillar of sociobiology one often tends to forget the general nature of these processes that even go beyond social behaviour. The generality of this principle is rooted in our well-secured knowledge on how evolution works. On one hand, this should make us weary of uncritically advocating biological determinism or evolutionary story-telling, but, at the same time, also make us admit that social behaviour is subject to the laws of nature, whether we like it or not and regardless of what other beliefs we hold as private individuals. The general foundation will not go away, even as one discusses epigenetic effects or cultural transmission. Rather, if anything for future research, sociobiology as the intended conceptual framework has an important role to clarify the effects and limits of these various processes and connect these to the biological bases.

Nothing happens in a void. Perhaps, then, the most uncertainties for the future of sociobiology lie in what surrounds science as a professional occupation rather than in the science itself. The expansion and diversification of the past was, to a large extent, made possible by an increase in science budgets and by the expansion of universities over the last decades. More likely than not, this will not continue at the same scale, which begs the question of what importance 'sociobiology'—as a dive into fundamental biological questions of social behaviour—will assume tomorrow. Ironically, understanding how social behaviour functions, and thus how conflict and cooperation works together to form stable societies, may turn out to be one of the most important scientific questions for a peaceful future of mankind. At the same time, and as past history has shown so clearly, it likely continues to remain one of the most controversial fields of science, exactly because it often clashes with personal beliefs and political agendas. One lesson for the future surely is that practicians of sociobiology, whatever this definition eventually means, are well advised to do excellent and uncompromising science and to value their questions and results with an open mind.

Paul W. Sherman and John L. Hoogland

Sociobiology: yesterday, today, and tomorrow

Outstanding biologists can sometimes surf "ahead of a wave," by identifying and highlighting a topical area before it peaks and others rush to embrace it. Edward O. Wilson was incredibly good at surfing ahead of waves. He published trend-setting books including *Island Biogeography, Insect Societies, Ants, Human Nature,* and *Half-earth*. Each provided a synoptic synthesis of the topic and proposed paths to future advances.

So it was with *Sociobiology: The New Synthesis* (1975). This massive tome summarized evidence that animal social behavior was shaped by natural selection for one purpose: to enhance the transmission of individuals' genes. It combined evolutionary theory and ethology, merging the seminal ideas of Charles Darwin, William Hamilton, and Robert Trivers with naturalistic observations pioneered by Karl von Frisch, Konrad Lorenz, and Niko Tinbergen.

Sociobiology had an enormous impact. It literally put the field on the scientific map. It inspired and guided myriad young biologists to study animals in nature. Academic departments across the globe joined the excitement by hiring sociobiologists, and a new journal "*Behavioral Ecology and Sociobiology*" was born. This enthusiasm undoubtedly helped both of us secure our first and subsequent academic positions.

Surprisingly, however, Wilson's book per se didn't have much effect on our personal scientific endeavors. This was because for the five years (1971–1975) prior to *Sociobiology*, we were graduate students of Richard D. Alexander at The University of Michigan. Dick was an intellectual magnet. He spent many long lunches and afternoons with eager and excited groups of graduate students and postdocs, analyzing Williams's (1966a, b) foundational book on natural selection and sharing his own hypotheses about animal and human social behavior and how to test them. Both of us took, and later served as teaching fellows for, his inspirational "Evolutionary Ecology" class, in which he explored the same major issues, examples, and studies that Wilson addressed in *Sociobiology.* Especially valuable to our own scientific development were the many months in 1973 when we met with Dick daily to consider and debate virtually every sentence in his classic 1974 paper on "*The evolution of social behavior.*"

The field of sociobiology has grown and matured in the past 50 years. What is its future in the 21st Century? We envision mixed prospects. On the one hand, time-tested concepts and methodological tools will persist – i.e., levels of selection (Williams 1992), levels of analysis (Sherman 1988), inclusive fitness (Hamilton 1964), hypothesis testing via strong inference (Platt 1964), optimality and game-theoretic modeling (Maynard Smith 1982), evolutionarily stable strategies (Maynard Smith and Price 1973), and cost/benefit analyses (e.g., Hoogland and Sherman 1976; Hoogland 2026). And there always will be curious young naturalists, neurobiologists, psychologists, and anthropologists seeking to understand how and why organisms behave as they do, and the evolutionary history of their behaviors. On the other hand, our ability to assess whether specific behaviors in nature are adaptive or nonadaptive, and why, will be challenged for two reasons.

First the human population, which was about 3.5 billion (Ehrlich 1968) when Wilson wrote *Sociobiology*, has more than doubled to a whopping 8.5 billion since then. Humans encroach on, and often destroy, natural habitats; cause pollution and climates changes; trigger extinctions; introduce invasive species; restrict researcher's access to the few remaining unspoiled environments; and force organisms into new environmental or social situations in which their formerly adaptive behaviors no longer enhance survivorship or reproductive success (Schlaepfer et al. 2002; Caro and Sherman 2011). Studies of relative fitnesses of behavioral variants are only interpretable if the reproductive success that is quantified is relevant—i.e., the reproductive success in the environment where ecological pressures molded the behaviors under study.

Second, there is currently a crisis in funding for graduate students, postdocs, and professors. Information on lifetime survival and reproductive success is essential for quantifying fitness, but funding for long-term research projects is scarce in the U.S. If diminished federal support persists, extended studies of individually recognizable birds and mammals, including humans, will be increasingly difficult.

In our opinion, these challenges will not be the death knell of behavioral ecology, evolutionary psychology, or evolutionary anthropology. Rather, they will encourage researchers to refocus and channel their efforts into new and exciting areas, with natural selection remaining their guiding principle. On the big question of whether biology will soon be fully integrated into the social sciences, as Wilson envisioned in *Sociobiology* and Alexander hoped for in *Darwinism and Human Affairs* (1979)*,* we agree with Wilson (1998) that such consilience, while desirable, is still over the horizon.

Joan E. Strassmann

Future sociobiology of genomes, cells, microbes, and social media

Wilson, with his encyclopaedic book *Sociobiology*, brought attention to the importance of social behavior in many more aspects of animal behavior than previously thought (Wilson 1975). This combined with Williams and Hamilton's insights (Hamilton 1964; Williams 1966b) on the importance of genetic relatedness and inclusive fitness brought a generation of researchers to focus on this new field. Researchers looked at behavioral interactions with new appreciation for the importance of kin recognition, and of conflicts within families, for example. But what began with animals soon spread to insights where interactions are less clear. Most exciting to me are the cases where we began to see conflict in what are fundamentally cooperative systems: plant seed tissues, placentas, microbial systems, and even cancer (Queller and Strassmann 2018).

What will the future bring? I see advances in four main areas. We still have a lot to learn about the social behavior of the very animals whose behavior first caused all the excitement. New genomic and observational tools will help us bring animal behavior to a new level (Kocher and Kingwell 2024). Second, we are just beginning to understand within-organism conflicts from tissue conflicts in pregnancy to cancer to psychiatric disorders (Haig 1993; Malik and Henikoff 2002; Crespi and Badcock 2008). Third, microbial interactions from protists and fungi to bacteria to viruses are truly a new frontier in social interactions that we are only beginning to understand (Kiers et al. 2003; Griffin et al. 2004). Finally, we need to explore what instant news, changing political structures, and constant social media are doing to our lives and brains (Yang and Crespi 2025). And all of this is going on in a world that is ever more threatened by climate change and habitat destruction (Rosenberg et al. 2019). What will we have left to understand in a hundred years?

Michael Taborsky

From behavioral ecology and sociobiology to behavioral biology

Edward Osborne Wilson's monumental "Sociobiology" published in 1975 galvanized ethologists in Europe who were open to adopt a new focus succeeding the seminal work of their predecessors, particularly the Nobel Prize laureates Konrad Lorenz and Nikolaas (Niko) Tinbergen. Niko had prompted to study all of "the four problems of Biology" (causation, survival value, evolution and ontogeny) when aiming to reach a comprehensive understanding of animal behavior in his seminal paper "On aims and methods of Ethology" (Tinbergen 1963). Wilson's agenda was different; he did not even mention Tinbergen's plea. Wilson's idea was to establish a new discipline, "sociobiology and behavioral ecology", to spearhead the study of behavior in the context of population biology, and in concert with "integrative neurophysiology" (Fig. 1–2, Wilson 1975), which he regarded as "two distinct disciplines" of behavioral biology (p. 6, Wilson 1975).

Wilson's approach to tackle intriguing social phenomena within a consequent Darwinian framework on copious examples, ranging from microorganisms to humans, captivated behavioral biologists worldwide, especially the younger generation. It channeled the interest of researchers into explaining the function and evolution of social systems with all its components, reaching from communication to mating, brood care and cooperation. Three years later, a group of behavioral biologists in Oxford initiated a series of edited volumes focusing on "*Behavioral Ecology*", which overlapped with Wilson's aims but extended the focus to non-social aspects of behavior (Krebs and Davies 1978). This approach was based on a strong theoretical framework developed by eminent evolutionary theoreticians.

The emergence of the journal *Behavioral Ecology and Sociobiology* took advantage of both initiatives, North American sociobiology and British behavioral ecology, even though their goals unfolded rather independently. Wilson mentioned 'behavioral ecology*'* only three times in his 700 pages tome, and the authors of the British behavioral ecology volumes neglected 'sociobiology*'* quite consistently. Whereas the British ambition was to boost behavioral research within an adaptionist program, Wilson strived to launch a new, comprehensive discipline. His second ambitious objective – to expose the biological roots of human behavior and, based on thereby improved comprehension, to channel societal developments toward environmental awareness – caused considerable indignation in the social sciences and in the public, which diverted attention away from the more technical proposal to transform the research field. This may have been one reason why within behavioral science, the new approach initiated by the Oxford school obviously had more long-lasting effects on the development of the field than the sociobiology conception of Harvard origin.

Basic behavioral science now had a new focus, the study of the adaptive nature of phenotypic variation, which prompted a heyday of the research field in the eighties and nineties. But no advancement comes without drawback. The keen focus on clarifying the adaptive function of traits entailed neglect of the other three levels Tinbergen (1963) found important to be considered when aiming at a comprehensive understanding of behavior. As Marian Stamp Dawkins (1989) pointedly formulated, ethology had turned into a four-legged beast that was "hopping around on one big leg" while the other three dangled uselessly. The phenotypic gambit (Grafen 1984) famously proposed that the adaptive significance of a trait can be understood by focusing on its fitness effects, without considering its underlying (primarily genetic) mechanisms. This quickly turned into the holy grail of behavioral ecologists even if it was recognized that constraints in the machinery on which selection acts may limit the evolutionary potential of phenotypes to optimally respond to environmental and social challenges. But it seemed difficult to uncover such constraints. In consequence and somehow paradoxically, the striking success of behavioral ecology led to a separation of fields that Tinbergen once proposed to consider in its entirety for understanding animal behavior, what Wilson's sociobiology program also implied as a goal.

After the turn of the century and with the advent of powerful (neuro)physiological, genetic and epigenetic techniques the field began to regain its original intention to study the evolution and causation of behavior more comprehensively (Blumstein et al. 2010; Akcay et al. 2015; Rubenstein and Hofmann 2015). The hegemony of the restrictive focus on adaptive value, which had originated so ardently in the late seventies, began to fade. This may seem like a healthy consolidation of the field, but what are its prospects for success? What about the questions that inspired behavioral ecologists so keenly right from the outset? For instance, are the contentions between Harvard and Oxford concerning the exclusive explanatory power of alternative concepts to understand cooperation and altruism (Nowak et al. 2010; Abbot et al. 2011) now a thing of the past? Those who heard the eloquent polemic in Richard Dawkins' keynote address at the conference of the International Society for Behavioral Ecology (ISBE meeting 2016, Exeter) on "E.O.'s" misconceptions might raise doubts. Perhaps the concept of "correlated payoffs" can resolve the issue by exposing a common principle that underlies alternative selection regimes (Taborsky et al. 2016, 2021).

In any case, there is hope that the collaboration of researchers possessing expertise in divergent fields of behavioral biology might indeed revolutionize our comprehension of such intriguing behavioral and social traits (Hofmann et al. 2014; Taborsky and Taborsky 2015). Somehow ironically, Tinbergen's plea, which Wilson utterly ignored, and Wilson's daring ambition to transform behavioral science, might come true after all. Considering four key levels of analysis will allow for a thorough understanding of biological traits, including behavior (Table 1). It is obvious that this requires cooperative efforts of experts from different fields, which is the continuous challenge for a bright future of our discipline.

Table 1 Levels of analysis inspired by Tinbergen's (1963) 'four problems of biology'. *Fitness effects* refer to survival value and reproduction, *underlying machinery* incorporates all morphological and physiological structures and processes responsible for the expression of a trait, *evolution* includes both the course of evolution and its dynamics, and *gene/environment interplay* concerns the processes involved in the translation of genetic information, including epigenetic effects (after Taborsky 2014)

Level	ultimate	proximate
phenotype	fitness effects	underlying machinery
genotype	evolution	gene/environment interplay

Barbara L. Thorne

Cheers to future behavioral ecology and sociobiology research!

Curiosity, creativity, diligence, discoveries, and syntheses will continue to advance the science of Sociobiology. The horizon of the next 50 years is, inevitably, brimming with changes and challenges, but also with the promise of novel tools and collaborative opportunities. Case studies will be important; comparative analyses will be essential to propel expansive progress.

Technology now assists at every level of discovery exploration, data bank archives, complex analyses, and information exchange. Exciting reveals in the fields of genomics and neuroscience as especially influential, and interdisciplinary initiatives involving each, will fuel leaps of knowledge foundational to understanding social, and eusocial, biology and evolution. The metamorphosis of communication due to the eclosion of innovative tech has radiated into extraordinary collegial networking that will continue to grow. Long-distance collaborations and online seminars will foster productivity even when travel is complicated.

If I could leap 50 years into the future to peek at progress, my first scientific venture would be to catch up on developments illuminating the boundlessly fascinating topic of universalities and distinctions driving origins of eusociality. That is same evolutionary query that captivated Darwin, and inspired me – along with many of you—to become researchers. Specific questions would include: *What are current integrative ideas about the evolutionary origins of eusociality, particularly the extreme reproductive skew of helpers and defenders within a colony? Please update me on perspectives that coalesce fundamental principles across taxa and encompass multiple independent roots and routes. I am eager to learn about ground plan patterns of biological and ecological drivers favoring eusocial evolution, as well as genetic and neurological architectures enabling developmental polyphenism and behavioral differences between castes. Is inclusive fitness theory at the core of prevailing evolutionary models, or are there nuanced or overtly exceptional cases that challenge otherwise unifying paradigms elucidating the origins of extraordinary individual altruism?* I would eagerly learn surprises and amazements; perhaps cornerstone pieces of our current interpretations will endure.

Over the past several decades there has been a decisive trend toward lab science, motivated by astounding molecular-level techniques among countless new analytical and imaging capabilities. Fascinating breakthroughs have emerged. A risk of the lure of techno ventures in the lab, however, is that research questions, hypotheses, selection of taxa, protocol designs, and relevance of results are vacant without solid footings in natural history realism. Think literally; footings in field boots! The core of our discipline, providing essential facts and igniting central questions, has been observing and experimenting in nature. Training master naturalists and expert systematists is crucial, or render the biological sciences vulnerable to errors and distortions. Laboratory partnerships with colleagues who have firsthand field expertise observing the biology, behaviors, development, reproduction, and community ecology of subject species will continue to forge productive mutualisms.

Efficiencies and versatility will remain at a premium in science. Scholars must navigate shifting priorities, including justifying the importance of basic research and surmounting funding obstacles. Well-supported labs will hopefully continue to train young investigators. As employment and funding opportunities shift, researchers will adjust to new realities. Clever scientists may promote investigations with practical applications. Focusing on social species as economically significant, pathogen vectors, or invasive species helps secure funding, then capture basic research elements as bonus derivatives.

During the first 50 years of the study of the biological basis of social behavior across animals, sociobiology has ripened with agreement and discord. Inherent to all scholarship, controversies ignite debates, with outcomes resulting in clarifications and increased precision. Such processes will continue, informing not only the fields of BES, but also expanding our understanding of biological diversity and evolutionary dynamics beyond social organisms.

First and foremost, my dissertation advisor and mentor Professor Edward O. Wilson was an ardent field biologist who genuinely loved studying nature. Ed radiated the pure exhilaration of discovery, in the field or lab, or when discussing – and continually attempting to synthesize – innovative information and ideas. Ed inspired intellectual curiosity, hard work, and the satisfactions that come from pursuing authentic interests. During the next 50 years I hope that BES researchers will have gratifying professional opportunities and will similarly share their excitement for the biology of social animals, along with the delights of diligently pursuing—then communicating – results.

Because highly social animals are distinctive among all life forms, intriguing revelations await! Currently unknown variants of genetic structure, regulation, and expression; developmental differentiation modifications resulting in castes; nervous system integration with complex behaviors; and social insects' resilience amidst climate change are examples of potentially novel peculiarities to be revealed by 2076. Maybe a presently unknown or obscure animal will be determined as eusocial! Cheers to future researchers and their exciting advancements!

James FA Traniello

The future of observation in behavioral ecology and sociobiology

Recent and future trends toward reductionism will without question advance our understanding of behavioral mechanisms and will enable powerful evolutionary analyses, especially if firmly embedded in the contexts of ecology and adaptation. This is not to critique elegantly integrative contributions to the multilevel analysis of behavior, but rather advocate for naturalistic observation in behavioral research to emphasize that we must not lose the dense natural history forest for the molecular trees and assign the legacy of ethology to a lower status.

The "molecular wars" of Wilson and Watson in the 1950s and 1960s (Wilson 1994) eventually transformed into scientific companionship, and the "indifference" and contempt" of the Watson school (Wilson 1994) has mostly passed. Clearly, our discipline is *founded* in behavior, ecology, and evolution; we ask questions, objectively address controversies, and create broad syntheses. Most often, but not always, this can be done with molecular genetics, neurobiology, and neurogenomics, but independent of the great analytical advantages of these approaches and even for theory and modeling, we rely on observation in nature. The honeybee dance language is one of the most extraordinary stories in animal behavior. The function of the dance was unravelled by decades of research by von Frisch, his academic descendants and colleagues, and although recent studies have applied molecular genetics, the von Frisch School is grounded in sharp and sensitive observation, intellectual alertness, acute perception, and elegant experimentation. Future behavioral research might originate from the perspective of what is possible using molecular toolkits and identify questions to answer with innovative techniques. This can be a good idea but may risk narrowing the scope of study by sacrificing the integration of fundamental behavioral and ecological knowledge. If you have a hammer, everything could look like a nail. Alternatively, we can recognize the extraordinary panorama of behavior and scan nature, taking full advantage of biodiversity to identify yet unknown systems to generate new questions that can be addressed with reductionist tools.

Evolutionary behavioral biology is founded on observation and natural history

Darwin, among many others, laid the groundwork for behavioral research and remains a virtually inexhaustible source of knowledge and inspiration. We admire the resolution of his intellectual eye, insightfulness, synthesis, and recognize his writings remain meaningful to behavioral studies. Burghardt (2020) noted "An appreciation of the diverse roots of animal behavior study is essential for … stimulating current research and scholarship. Insights by early seminal authors are often ignored…".

Historical knowledge is essential to begin to look toward the future – it can cure scientific amnesia and serve as a gateway to novel research. History is not nostalgia, sentimentality, or "old school;" it is informative, inspirational and enlightening. All behavioral analyses begin with careful observation. Ethologists prescribed "know thy animal" and emphasized the importance of the natural context of behavior. Whether we self-identify as behavioral ecologist or sociobiologists, we are all nature-loving scientists who have had the extraordinary opportunity to be "career naturalists" and explore behavior as our life's work. Patient field work—firmly implanted in quantified observations—often leads to novel and important discovery. Yet as Jack Hailman recognized, there has been a discriminatory practice of "fieldism" that denigrates observation in nature: "Field biology is old-fashioned. Field biology is descriptive. Field biology is qualitative. Field biology is done by pedants" (Hailman 1973).

None of the above criticism is true: field study, observation, and description – both qualitative and quantitative—are necessary for the future of evolutionary behavioral biology – and for the conservation of biodiversity Bezanson and McNamara (2019), for example, found bias in primatology (in regard to number of publications) toward certain taxa and field sites, which had a clumped distribution by site and species. They convincingly argue that understanding a greater diversity of primate species and their geographical distributions, as well as local human community support, is required for the conservation of primate biodiversity and therefore to "preserve primate species in the wild in the twenty-second century".

Perhaps we do not always recognize the importance of field work because our passion is literally in our nature and intuitively guides us. Naturalist intelligence, one of the several human intelligences described by Howard Gardner (1993), underlies the universal human attraction to and interest in nature and the environment that runs deep in civilization, predating the ancient Greeks and Romans. Our naturalist forefathers and foremothers – e.g. Darwin, Maria Sibylla Merian (Etheridge 2011), Charles H. Turner (Abramson 2009; Dona and Chittka 2020) – and E.O. Wilson—were driven by curiosity and intellect. Merian and Turner faced exceptional prejudice, sexism and racism, respectively, amid other obstacles, yet were still major contributors and inspirations for resilience to the STEM crisis we face today.

My doctoral research on the behavioral ecology and sociobiology of ants began in New England in abandoned pastures bordered by fieldstone walls. Before most of these walls were constructed, the earliest natural history observations in New England for which there are written records were made by John Josselyn (1672), although transgenerational oral traditions of the Abenaki, Mohegan, Pequot, Penobscot, Wampanoag, Passamaquoddy, and other Native American environmentally respectful cultures (Booth 2014) likely preceded any published accounts. Indeed, the present-day value and biological significance of the natural history knowledge of indigenous peoples should not be underestimated (Dahlin et al. 2025) and could be mined for its behavior content. Most of Joselyn's observations were botanical, but he also described animal "curiosities", here what is likely a nest of the bald-faced hornet *Dolichovespula maculata*:

> "The Wasps in this Countrey are pied; black and white, breed in Hives made like a great Pine Apple, their entrance is at the lower end, the whole Hive is of an Ash Colour, but of what matter it's made no man knows; Wax it is not, neither will it fry nor melt, but will take fire suddenly like Tinder. This they fasten to a Bow, or build it round about a low Bush a Foot from the ground."

The description of wasp workers and nest structure, which makes a brief comparison to that of honeybees, is inquisitively followed by "of what matter it's made no man knows," a further questioning and probing beyond what is at first captured by the eye. The next steps would logically consider wasp social behavior and their role in nest architecture. Josselyn also observed hummingbird foraging behavior, nesting habits, seasonal activity, and described life history and geographic distribution:

> "(They) feed upon Honey, which they suck out of Blossoms and Flowers with their long Needle-like Bills; they sleep all Winter, and are not to be seen till the Spring, at which time they breed in little Nests, made up like a bottom of soft, Silk-like matter, their Eggs no bigger than a white Pease, they hatch three or four at a time, and are proper to this Country."

His account of the predatory behavior of the pilhannah (likely an eagle) records prey specializations and passerine bird alarm:

> "a monstrous great Bird, a kind of Hawk …. when she soars abroad, all sort of feathered Creatures hide themselves, yet she never preys upon any of them, but upon Fawns and Jaccals."

These are only a few examples, likely among many, if we consider human interest in nature across continents and how it develops and leads to discovery, a process of science beginning with observation.

Tinbergen (1963) wrote that early ethologists "wished to return to an inductive start to the observation and description of the enormous variety of animal behavior repertories and to the simple and admittedly vague and general question"Why do these animals behave as they do?" Ethologists were discovering "an entire unexplored world" and advocated "a return to nature." "We should not discourage (those) with a talent for observation" (Tinbergen 1963). Tinbergen's admonition begs the question of how to ensure a continued line of successors to lead discovery and continually feed a pipeline for future behavioral analyses. To do so, we must work to prevent a lapse in naturalistic discovery by supporting students. Hopefully, this will begin as soon as possible to buffer long-term negative consequences for evolutionary behavioral biology and sustain strength in decades ahead. How and when do we develop and apply the "talents for observation" noted by Tinbergen? Computational ethology, computer vision, automated tracking, and AI-assisted "observation" has clearly advanced collecting and analyzing large behavioral data sets. Still, it seems doubtful that even the most "intelligent" of machines will be able to compete with the skills of trained humans. I asked ChatGPT if AI would replace human sensory integration and multimodal observational abilities to study animal behavior. The answer highlighted and promoted the capabilities of AI, but was "no."

Developing observational skill may require curricular modifications

How do we train future naturalistic talent? Observation requires expertise. Is instruction to build observational skill a core component of organismal biology curricula? Is it mandatory in introductory college-level science courses and/or upper-level classes? Is the bias recognized by Hailman (1973) – that the observation of behavior is part of a weak field-based or qualitative approach – prevalent today? The core curriculum of an undergraduate degree in biology in many institutions is largely designed to satisfy requirements for application to medical school. My impression is that biodiversity is typically covered, but content emphasizing observational skill is largely neglected in introductory biology textbooks and courses.

Thorpe (2020) criticized the *status quo* natural science pedagogy requiring biology, chemistry, physics, and mathematics early and often concurrently during undergraduate education, rather than when such classes would be most appropriate:

"Most science departments believe that the only way to produce scientists is to bludgeon young people with too much material, in the wrong setting, at the wrong time, and with the wrong kinds of assessments. The rationale is that only by mastering an abundance of facts and quantitative skills can someone become a scientist—and that's where one must start, not finish". We must not "turn off inquisitive young minds" (Thorpe 2020).

In a 2019 interview, E.O. Wilson expressed his dissatisfaction with traditional STEM education: "I am unhappy about STEM. That is, I'm unhappy about how it's presented as the principal portal for careers in science and technology. Young people — in some cases, young enough to be as far back as grammar school — are presented with this intellectual triathlon in order to go into science and technology" (Tyson 2019).

A flexible curriculum that incorporates and accentuates active learning through observation is critically important. Active learning can be built around observation and quantification. Many universities have field programs. At Boston University, students have the option of experiential course work in Belize and Ecuador praised (actually, raved about) by students in terms of igniting (or rekindling) their passion for nature. Their observations of animal and plant life in tropical marine and terrestrial environments generate excitement and commitment to biological science.

Selection of model systems

Among behaviorally diverse invertebrates and vertebrates (and not neglecting slime molds), what species should be studied? In his well-known principle, Krogh (1929) advocated careful selection: "For such a large number of problems there will be some animal of choice, or a few such animals, on which it can be most conveniently studied". However, Clark et al. (2023) caution that applying Krogh's Principle requires first deciding upon a focal question to identify the model species or taxon and this decision will "inevitably leave many organisms neglected." These authors recommend the venerable paradigm be replaced (or at least complemented) by their "inverse Krogh principle: all organisms are worthy of study." In this model, observation and description initiate a spectrum of research possibilities, some readily following established concepts while others representing new integrative behavioral ecology and sociobiology research. In light of biodiversity (and potential striking losses on the horizon), consider the behavioral and/or social adaptations that are currently unknown and the rate at which new study models and systems will be discovered during the next several decades. The inverse Krogh principle "urges a broader search across organismal diversity to find sources of inspiration for research questions and the motivation needed to pursue them" (Clark et al. 2023). The founders of ethology studied what was convenient and made choices guided by personal enthusiasm. Catania (2017) notes, "There is something very interesting about every species, it is just seldom obvious. Detailed behavioral data are often key to finding the "interesting something" that may not be obvious."

We need to be observant of future of our discipline through action that ensures equitable student support

Many coauthors have here noted that predicting the directions of the parent discipline of evolutionary behavioral biology and its sibling fields of behavioral ecology and sociobiology is challenging. Anticipating the future of our discipline would be difficult in the best of all possible STEM worlds, but today is exacerbated by antagonism between science, politics, and society. If tea leaves could divine what will become of basic STEM and the study of the evolution of behavior, patterns and symbols would be obscured in the haze of the current antiscientific environment and threats to liberal arts education. The how and why of cultural conflict that reduces the reliability of research funding and thus threatens the overall mission of science requires an analysis too detailed and complex to be discussed here. We can nevertheless admit that universities are changing, research support has decreased, research planning is confounded, and academic life is uncertain. The alteration of career opportunities will impact the future of our discipline. Wheeler's (1923) appraisal of biology graduate education resonates today, more than 100 years later:

> "… in our universities, apart from the students preparing to enter medicine, the number indulging in advanced and graduate courses in (biology) would probably shrink to zero if we failed to provide fellowships…."

It's remarkable how familiar this is to us today. How can we think about distant tomorrows when immediate survival needs demand attention? We hope that the STEM *Titanic* isn't taking on water, but need to plan in the event it is, and there are many significant and urgent issues, as noted by coauthors.

There will be no future, or the future will be curtailed, without continuing streams of newly trained and mentored behavioral ecologists and sociobiologists. To ensure success, the present generations of researchers should strive to guarantee the equitable distribution of opportunity. Traniello (2015) emphasized the difficulties of committing to STEM education in all its dimensions in the absence of meaningful broad institutional change, and recommended scientists and social activists work together for equality and inclusion. The future of evolutionary behavioral biology is coupled with broad commitment to STEM education and targeted curricular reform. Pathways in evolution, ecology, and behavior must be inclusive and unrestrictive (Puritty et al. 2017; Halsey et al. 2020). Science – a universal human right (Wyndham and Vitullo 2018) – and science education must have political and social priority. Barabino (2023) cautioned:

> "What will people in the future say about how science helped or harmed society on our watch? How did we come together to collaboratively solve problems? How did we ensure that everyone who desired to pursue science had the opportunity to do so? Acting on these questions in earnest could help us ultimately answer the question of what it means to be human."

In the next 50 years, understanding what it means to be human can be advanced by evolutionary behavioral biology, beginning with skilled observation and interpreted and developed within the strong foundation of theory and empirical studies of adaptation during the past 50 years.

Stuart A. West and Ashleigh S. Griffin

Diverse questions on diverse taxa

An exciting aspect of Wilson's sociobiology book, and the behavioural ecology approach more generally, was how it suggested that an evolutionary framework could potentially be applied to explain a broad range of social behaviours across diverse taxa (West et al. 2025). The potential for this cannot be overstated. Inclusive fitness theory provides a unified framework for explaining numerous social behaviours from cooperation and sex allocation to cannibalism and parent–offspring conflict (Hamilton 1964).

An exciting prospect for the future is the extent to which this framework can be applied across the entire tree of life, and to behaviours that are less commonly thought of as social. Early work in this area focused on animals, especially birds, mammals and insects. But increasing attention is being paid to microorganisms, from bacteria and slime moulds to fungi and even viruses. As work expands to these new taxa, new questions must be asked about traits that were not previously thought to be social. For example, the production of tubular mitochondria, enzymes that function after cell death and fragmented genomes (Voelz et al. 2014; Leeks et al. 2023; Gibson et al. 2025). How broad can this list become? Can we identify broad patterns and generalisations that make the world simpler to understand?

We are especially hopeful for how this research will be able to extend into the 'invisible' realm (Griffin and West 2026). To what extent can theory that was developed to explain animal behaviour be applied to explain adaptation at the level of cells, genes and molecules. Our ability to test hypotheses about the factors that influence natural selection at these levels depends upon technological advances that are opening new avenues of research. This is the case for both interactions within and between species.

This research also has the potential to contribute to the major global challenges facing humans. The ability of pathogens to spread and harm hosts, human or otherwise, depends upon social interactions. The cooperative interaction between plants and fungi play a fundamental role in plant productivity, soil heath and carbon storage. How is human behaviour influencing these processes (Stewart et al. 2026)? Many biotechnological processes rely on cooperative behaviours performed by microorganisms. How can evolutionary biology help make these processes more efficient (Cavaliere et al. 2017)? Future sociobiology research offers an amazing opportunity to answer diverse biological questions and help humanity.

Marie Jane West-Eberhard:

Social biology: the next 50 years

The attempt to imagine the next 50 years of any human endeavor is risky especially when undertaken by the members of an older generation unable to broadly relate to the vocabulary and choices of even their own grandchildren – representatives of the generations that will be in charge. But that worry is alleviated by the fact that the aims and values of science as a search for increased knowledge and understanding have been constant across generations worldwide. They have endured through centuries and can be expected to last through the next half a century regardless of temporal and geographic variation in societal rules and fads.

I see one trend that is already happening and is likely to continue. The best studies of social behavior and evolution are increasingly dependent on observations of behavior in the wild, with fieldwork complementing advances in lab techniques to address questions that are raised in the field but are not easily answered there. I expect such technologies to continue to improve, with the development of devices that enable us to see living organisms literally inside and out – enabling measurement of changes in things like gene expression, hormones, the neuromuscular system, and the details of movement, in real time. Beyond this we are witnessing an increased appreciation for the observation of behavior in natural settings. That will continue too, for it is a good path toward evaluation of lab findings in terms of natural selection and evolution.

In the past there has been some reluctance on the part of field biologists to value technological advances and laboratory work, alongside reluctance of laboratory scientists to value natural history and fieldwork. This has already begun to diminish. The laboratory sciences, especially those exploiting progress in molecular biology, have produced masses of data that are beginning to overwhelm understanding of what they mean, leading to the realization that a return to nature is required to give them full value (Heard 2022). At the same time, it is clear to natural historians that exciting questions raised in the field can best be answered by the ingenious application of specialized lab techniques (e.g., Warrant et al. 2006; Kingwell et al. 2021).

This combination of lab and field research is likely to produce a great premium on collaborations in the future. Laboratory research that illuminates fundamental principles of neurobiology and physiology are likely to gain in prominence and financial support. And fieldwork, less dependent on major funding and facilitated in areas of the world where observations in natural setting are easier, stands to gain increased appreciation and support through syntheses and collaborations cognizant of the mutual dependence of the two approaches for the advancement of biology.

I hope that thinking about these questions as part of a 50th anniversary celebration for a landmark in our field will encourage actions on our part that sustain global scientific cooperation despite being confronted by short-sighted policies that can impede it. We have a solid history of attention to work that disregards differences in sex, color or national origin, exemplified in past issues of *Behavioral Ecology and Sociobiology* and related journals. Putting all of this together gives reason for optimism regarding the future of our science.

David F. Westneat and Niels J. Dingemanse

Back to the future for behavioral ecology and sociobiology

Forecasting the nature of a field in 30–50 years might be a bit of a fool's errand. Too much can change in that time and in a rich topic like the ecology of behavior, this means any projections will be either too narrow or too vague. It is nevertheless a fun exercise that can produce some revealing nuggets, and we make this attempt by combining a few guesses at opportunities that seem likely to come along, combined with some wishful thinking about how our history might be employed to exploit them.

AI is likely to be the biggest unpredictable. Science and the dissemination of its findings face major changes with the advent of AI. We will not speculate much on the impact for behavioral ecology and sociobiology (BE for short, we will subsume sociobiology into this phrase for convenience), mostly because its capabilities are so unclear. Its impact does seem likely to be far-reaching, affecting all phases of doing BE, from conceptual development through theory generation, study design, to data collection and analysis. Technology writ large will have major effects, with greatly expanded data collection and analysis capabilities, and this will continue in ways that are hard to imagine (trekkie fans excepted). Rapid, computer-assisted collection of data, real-time tracking of animals, smart feeders and nest sites, and remote physiological recording are just some of the ways we expect to explode richness of information. Massive increases in the speed and affordability of collecting genetic data of various sorts also are highly likely. Finally, we are also seeing rapid expansions in the sophistication and speed of data analysis and statistical capabilities. In sum–big data will be a major feature of BE in the next 30 years and will create major opportunities.

What might BE do with these opportunities? BE gained momentum in the three decades spanning 1965 – 1995 due to two major strengths: 1) its compelling conceptual focus on natural selection and 2) the value of integrating formal theory with empiricism. BE's early focus on adaptation and Tinbergen's (1963) conceptual question about function was a resounding success (West et al. 2025), Gould and Lewontin's (1977) and assorted other critiques notwithstanding. These strengths have become diffuse in the last two decades (Montgomerie 2011), potentially signaling that the old core might not persist. While the development of BE concepts about behavioral responses to human-induced rapid environmental change (HIREC, Sih 2013; Wong and Candolin 2015) has helped the field remain relevant, the vigor and focus of the early days has not persisted. For example, the patch-time model (Charnov 1976) captured two fundamental elements of ecology: that resources are patchy, and within a patch, they vary in the ease of exploitation. This idea has been widely tested and many additional complexities folded in. But there are surprisingly few applications of it to topics such as urbanization (but see van der Merwe et al. 2007) or climate change or, perhaps more importantly, assessments of whether HIREC fundamentally alters elements of the underlying ecology requiring the model to be rethought (but see Calcagno et al. 2014). Across most of BE, it feels to us as if the core theories are not being extended with as much regularity as they could be.

Indeed, some have claimed that the field was becoming irrelevant because human-caused extinctions and rapid environmental change would make untenable what many have felt was the main mission of behavioral ecology, to study adaptation (Caro and Sherman 2011). By contrast, we think a poorly appreciated but more important benefit of BE's heyday was its contribution to a broad and detailed understanding of how ecology shapes selection, especially the components of stabilizing and social selection. Fortunately, selection can be measured even when trait means are no longer close to an adaptive peak. New statistical methods are allowing it to be assessed in major new ways (Martin et al. 2025). Importantly, the data-driven opportunities in the next 30+years seem ripe for reinvigorating a focus on the ecology of selection. In conversations with colleagues, we have heard that BE needs newer theoretical and conceptual ideas (sensu Lopez et al. 2023). We also know that many parts of old theory have yet to be adequately tested. Both are true and might be tackled given new opportunities.

BE exploded from creative young minds thinking in new ways about the links between ecology and behavior. Rejuvenation of BE will occur similarly, aided by an array of new tools. We see tremendous opportunities for integrating old ideas with new, accessing rich new information allowing for better tests and stimulating new ideas, bolstered by rapidly evolving technical abilities to link data from disparate sources. A core focus on the ecology of selection could make for a continuing legacy of the original excitement that gave rise to this journal 50 years ago.

Overview

Our perspectives collectively foretell a positive future for the evolutionary analysis of behavior. Many contributions reflect past achievements of the discipline and our own specialized fields and their future. Some of us describe inspiration from Wilson's book and our experience with the sociobiology controversy, others offer first-hand accounts of E.O. Wilson's mentorship and career influence. Our contributions do not necessarily catalog future conceptual directions or tests of specific hypotheses and experiments but identify gaps in traditional areas of interest such as sexual selection, sperm competition, and eusociality. We need to understand behavioral adaptation to anthropogenic challenges. We make the plea that future research will be faithful to its scientific roots and ensure behavioral studies in nature spawn new developments. We agree that data collection and analyses will benefit from advanced technologies to answer ultimate and proximate questions at the level of molecular, physiological, and neurobiological mechanisms and interdisciplinary integration. Waves of technological innovations—optogenetics, RNAi, genome-wide trait associations, single-cell RNA, CRISPR, -omics, AI, deep learning, imaging, and advances in conceptual and modeling tools– will continue to transform methods and open new and detailed analyses. Extrapolations from technological advances unpredictable in 1975 provide a small window into future possibilities, but the next conceptual and theoretical innovations remain to be seen. Epigenetics and gene-environment interactions will continue to correct misinterpretations of the influence of heredity on behavior. We see future advancements in the application of sociobiological principles at diverse levels of integration between as well as within organisms, between individuals of various taxa beyond animals, or levels of social organization. Invention will accompany paradigm shifts. We emphasize that the threat of limited funding will have serious negative impacts on the growth of our discipline by restricting inclusion and access to opportunity for the next generation of evolutionary behavioral biologists.

As Wilson anticipated, the evolutionary biology of behavior will benefit from a consilience of biology, anthropology, and other social sciences. For the study of human behavior, William Morton Wheeler (1923) outlined the discipline of human behavioral ecology roughly 50 years before *Sociobiology: the New Synthesis* was published:

> "… since human societies are very intimate and elaborate, biocoenoses of individuals of the same species, psychology, sociology, economics, anthropology, ethnology, history, ethics, jurisprudence, government, hygiene, medicine, etc., are essentially ecological, for their central problems are behavioristic".

Wheeler appears to have foreseen in the 1920s that such a broad synthesis of social life would eventually occur; his thoughts became an accurate prediction. In 1975, *Sociobiology* established common grounds for the evolutionary and mechanistic study of social systems, including those of humans.

In 1976, *Behavioral Ecology and Sociobiology* began publishing research on the biology of behavioral adaptation. In his forward to the first issue, Nobel Laureate Karl von Frisch (1976) poetically compared the launch of the journal with the birth of a child and insightfully charted its future, balancing hope with caution:

> "The news of the foundation of a new journal inspires similar thoughts as the announcement of the birth of a child. Will the new infant flourish? Will it prove a success? Anyway, are there not already too many on our earth? But this new journal has its justification. One may regret the increasing specialization in research, but one cannot prevent it. It is a necessary consequence of the extension of our knowledge."

Von Frisch presaged the success of *BES* and proliferation of specialized journals that have emerged during the past 50 years—and their necessity to communicate results of behavioral analyses in an appropriately designated venue. Our forecast for the future of evolutionary behavioral biology is positive. The child turned 50 and has a healthy future.

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