READINGS AND WRITINGS ON ANIMAL BAHEVIOUR

PROJECT REPORT (SUMMER 2021)

A report on the online reading project carried out under the guidance of Prof. Raghavendra Gadagkar (CES, IISc)

By,

Vasudha Kulkarni
Third Year BS-MS
Indian Institute of Science Education and Research, Pune
22nd September 2021

Email address: vasudha.kulkarni@students.iiserpune.ac.in

Table of Contents

The Beginning

On a mundane evening in April, I came across an article in *The Wire Science* about how insect societies, such as honeybees and ants, deal with infectious diseases. I was hooked right from the very beginning. These insect colonies have an immune system, just like us, called social immunity. It is a fascinating phenomenon – every individual in the colony collectively participates in certain protective behaviour that reduces the risk of infection and controls the spread of disease. I spent that night exploring the papers and studies linked in the article, learning more about social immunity.

At the time, I had been away from normalcy for over a year, and the pandemic showed no sign of abating. Since January, I had been writing to various ecologists and animal behaviourists across India, asking to work with them over the summer to explore the field through a short project. I had written to several scientists without any success. After reading the article on social immunity in Dr. Gadagkar's column (*More Fun Than Fun*), I wrote to him requesting an online summer internship. I was pleasantly shocked when I received a reply – a positive one at that!

In my first month at IISER Pune, Dr. Gadagkar had given a fascinating talk about his work on sociality and altruism in the Indian paper wasp at the institute colloquium. I was nervous and, at the same time, excited to meet him. My first meeting with an eminent scientist felt like a dream. I was eager to get started immediately instead of waiting for the summer break to begin. I began by reading books about topics of interest, and I met with Dr. Gadagkar every week to discuss what I had read.

After taking a break for my end-semester exams, we resumed with a greater focus on reading and writing — my goals to read more and write well aligned with what Dr. Gadagkar had in mind. Over the course of this project, I have read several books on animal behaviour and many papers on social immunity. I have written a book review and three essays based on the books I've read and prepared a report on the impact of a research article that draws analogies between individual and social immunity. But more importantly, over the course of the project, I have had the opportunity to interact with a great mentor and work with an invested editor, so I could focus on both the form and the content of scientific writing.

The following chapters in this report contain an introduction to the work and my writings in sequential order. I hope reading them will manage to convey, with ease and panache, what I've learned over the summer.

Chapter 1 – Introduction

In the *Origin of Species*, Charles Darwin expressed his amazement at the colourful diversity of life by describing it as 'endless forms most beautiful'. What I find more fascinating and vibrant than the diversity is how these diverse life forms *behave*. Mainly, I'm intrigued by animal behaviour because it comes in a multitude of forms, results in stunning displays, and tells a story – one of evolutionary history and everyday struggles.

I began this online reading project with two goals in mind. The first was to read and learn more about the field of animal behaviour so that I could advance from a novice to an amateur on the track of expertise. The second was to learn to write well, to convey what I mean clearly in a way that also keeps the reader engaged. I think I have made progress on both accounts by reading about animal behaviour and writing about what I have read.

My Readings

Reading books, instead of research papers as in a conventional reading project, allowed me to explore these topics in depth. I have read the following books throughout the summer as a part of this project.

Survival Strategies by Raghavendra Gadagkar

It was an interesting and enjoyable read. It is a very well-structured book that explores the basic concepts of animal behaviour – cooperation, selfishness, altruism and spite – with a focus on explaining eusociality, a paragon of altruism. Altruism is a paradox in evolutionary theory because it reduces the fitness of an individual. This paradox can be explained through the inclusive fitness theory. I enjoyed learning about these interactions through a multitude of examples across various taxa. The language is simple and engaging, so the concepts of the book are at the forefront. It does an excellent job of introducing these concepts and telling the reader about their significance. It'd be a fun read for students and laypeople who wish to dip their toe into animal behaviour. I learnt the concepts of spite, game theory, and levels of selection for the first time through this book. It introduces several ideas in animal behaviour that act as springboards from which you can jump and dive into a world of new ideas and theories.

The Blind Watchmaker by Richard Dawkins

The book starts out very well with the description of the problem – complex design – and its importance before it sets out to explore the solutions. Darwin and Wallace explained the patterns of diversity and complexity through their theory of natural selection. Dawkins sets out to defend the theory of evolution against common misconceptions and allegations. The first few chapters of the book examine the problem (how can evolution explain the vertebrate eye or echolocation in bats?) and the mechanism of natural selection which solves the problems. The following chapters discuss the possible origin of life, encoding information in DNA and evolutionary arms race. The following chapters made me ponder the speed of evolution - what controls it, what shapes it, and in turn, how it shapes diversity. There is also a chapter addressing Gould and Eldredge's theory of punctuated equilibrium, which makes it seem like it was a matter of misunderstanding and not a matter of serious contention. A minor disquietude with the book was Dawkins' caricature of an irrational, unreasonable theist who will never be convinced about evolution. In conclusion, the book is a helpful read if you want to understand how complexity can evolve, and it stocks the reader with sound arguments against common misconceptions about evolution.

Are We Smart Enough to Know How Smart Animals Are? by Frans de Waal

It's an absolutely brilliant book that explores various facets of animal cognition, trying to show that the difference between the human mind and the animal mind is one of degree and not of a kind. The book takes on the challenge of rooting for and defending animal cognition. Cognition is defined as the processing of sensory input into knowledge about the environment and using that knowledge flexibly to solve different kinds of problems. This book is the culmination of many years of study and change in the field through numerous experiments with primates, corvids and even molluscs! De Waal stresses on learning the *umwelt* and natural history of the animal before conducting experiments. The book delves into the field's history and different facets of cognition such as tool use, language, perception of conspecifics and time, imitation, social skills, etc. It's a fluid read which takes you on a pleasant journey that is peppered with charming anecdotes. I found the book somewhat lacking in its depth of exploring concepts, but it's not an issue since the book aims to introduce the idea of animal cognition. De Waal effortlessly makes a case for animal cognition while also including criticisms, making counterpoints, and acknowledging that their scepticism has helped drive the work and design better experiments. In conclusion, this book is a must-read for anyone interested in cognition or animal behaviour.

Design for a Life by Patrick Bateson and Paul Martin

Design for a Life is a book about the development of behaviour, with a focus on the development of humans through the Seven Ages. It delves into how individuals become who they are. In a single phrase, it occurs through the process of behavioural development. The book takes a developmentalist approach to evolution by natural selection. One of the things that makes this book stand out is its use of descriptions about life and behaviour as written by notable poets and authors in their classic works. The authors also use several insightful metaphors – cooking for development, a jukebox for developmental constraints and how the environment affects development, and another one to describe the resilience of the process. Throughout, the authors highlight certain design principles that characterise developmental processes – they prepare the individual for the future, are resilient, and have certain scaffolding structures that help individuals build complex skills. This book is a thought-provoking read, enjoyable once you get used to the unique meter and style of the book. The writing style is easy on the mind but the authors' nuanced arguments are challenging and bound to sharpen your reasoning skills.

The Woman that Never Evolved by Sarah Blaffer Hrdy

Sarah Blaffer Hrdy, a primatologist and anthropologist, demolishes the myth of the 'coy female' in her book *The Woman that Never Evolved*, which shines a much-needed evolutionary spotlight on females and their sexuality. In her book, Hrdy narrates the societal structures of various primates across the world. She discusses many topics that were left unexplored due to the inadvertent male bias that had affected how the sexual selection theory had been applied. The book explores diverse themes of social organisation in primates, female-female competition, female sexuality, and the evolutionary theory tying them all together. This book is one of the first intersections of feminism and sociobiology. The author leaves us with a poignant message worth reflecting on, *"The female with "equal rights" never evolved; she was invented, and fought for consciously with intelligence, stubbornness, and courage."* With the far-reaching vision of an evolutionary biologist and the skill of a storyteller, Hrdy effectively conveys the importance of this hard-won equality, opening our eyes to the frailty of its assurance.

Cuckoo: Cheating by Nature by Nick Davies

It is a wonderful book that describes the life of the cuckoos from all over the world and throughout evolutionary history. Davies focuses on the common cuckoos and reed warblers of Wicken Fen (near Cambridge), where he has worked every summer for the past 30 years with these 'harbingers of spring'. Cuckoos have long been admired for their unique song and denounced for their brood parasitic nature. In many works of literature, comparisons to cuckoo's uncaring nature and the cuckoo chick's greed are common. The book is very descriptive – it makes you feel as if the scene is unfolding in front of you. Davies gives an idea of the history of cuckoo study and includes his work in it beautifully. The book is as much about his adventures as it is about others in the field who have worked towards understanding the cuckoo and how it came to be. The book focuses on the evolutionary aspect of the cuckoo chick and bird's behaviour which have been untangled by various experiments and field studies. It's important to highlight and recognise that, while discussing the cuckoo's "despicable" actions, Davies never vilifies it - it's just on one side of the evolutionary tug of war. In fact, contrary to popular belief, he shows how hard it is to be a cuckoo! The last chapters of the book discuss the decline of cuckoo in recent years. After reading an entire book about this fascinating bird, it's heart-breaking to read about its decline and think about the biodiversity crisis that we're facing (and conveniently ignoring) today.

My Writings

Science is a collective and cumulative endeavour – this means that it largely rests on the exchange of ideas and knowledge, across space and through time. I have discovered that a large part of doing science is about reading and writing. Writing well has several benefits. To the reader, a well-written piece can be one of life's great pleasures. Concise and clear writing prevents misunderstanding and, in the long run, aids the progress of science. Writing well also benefits a scientific writer through the joy of sharing, with a broad audience, what they have discovered, invented or put together. It is also vital that scientists write about their work for a general audience. While talking to my uncle about scientific writing, he said something that stuck with me – if basic science becomes invisible or stays out of the public's grasp, then even natural phenomena will start seeming bizarre.

With these motivations in mind, I wanted to make an effort to write well. I wanted to focus on improving the form and content of my writings. This prompted me to read Steven Pinker's *Sense of Style*. As suggested by the book and Dr. Gadagkar, the main thing I did while writing was to always keep the intended audience in mind. The first three essays are meant for a scientific yet non-technical audience (such as college students studying STEM), the fourth essay (about cuckoos) is meant for a general, non-scientific audience, and the last chapter (the impact report) is meant for a technical audience. I have also attempted to write different kinds of pieces – Chapter 3 is a book review of *Design for a Life*, whereas Chapters 2, 4 and 5 are essays based on the other books I have read. The last chapter is a work of technical writing, with the same layout as that of a research article.

Dr. Gadagkar counselled me that one of the critical components of writing well is to spend time on the writing, experimenting with different combinations of words and sentences. Each of the following chapters has gone through multiple revisions after my weekly discussion and feedback session with Dr. Gadagkar, with many additions and edits from his end. These sessions have taught me to focus on every word and every sentence, keeping in mind what the reader would make of the phrasing. I have learnt a lot about writing well – way more than can be distilled in this introduction. You can hear more about it in Dr. Gadagkar's keynote address of a science communication workshop.

The final chapter is an impact report of a review article. The idea of the impact report is to discuss the impact of the paper on the field. The paper I have focused on is *Analogies in the Evolution of Individual and Social Immunity* (Cremer and Sixt 2009). In the focal paper, Sylvia Cremer and Michael Sixt draw parallels between the organisation, function and evolution of individual and social immunity. I have analysed the impact of the focal paper by going through all the papers that cite it. Once I collected the citations, I tried to analyse the context and theme of the citations. We can understand the impact and implications of this paper by considering the context in which it was cited (whether the paper mentions, supports or contests Cremer and Sixt 2009), what kind of papers it was cited by and how the concept has been advanced since it was published. Studying the implications of the concepts proposed by Cremer and Sixt 2009 would help us assess the progress made so far and pave the way for the road ahead.

This project report is a compilation of my work over the summer of 2021. It has been a wonderful learning experience and has given me an opportunity to write, something I wouldn't have done left to my own devices. I hope the following chapters make for an interesting and enjoyable read.

Chapter 2 – When You See an Ant...

Imagine yourself to be a tiny insect, almost identical in sight and smell to hundreds of your kin with whom you share your colony. Take another leap of imagination and a few moments to consider your life as an ant in an experiment: you live in a colony smaller than a shoe-box, going about your day - tending for the brood, feeding the larvae and the queen, or going out to an adjacent box to collect food - with a strip of paper glued to your back. Although the weight isn't an issue (you're used to carrying several times the weight of that QR tag), it's like a pesky outgrowth that can't be moved. A while later, you're plucked from the colony and dusted with spores of pathogenic fungi. As soon as you're back in the colony, you start cleaning your forelegs and antennae while your comrades get to work on your back. They agitatedly get rid of the spores by eating them, caring for you at the risk of getting infected themselves. You know well enough to stay away from the queen and the eggs - their protection is paramount. And so, it continues for a day till the end of the experiment, after which the experimenter freezes you to preserve the state of the infection.

This imaginary portrayal attempts to sketch the *umwelt* of an ant – *umwelt* is a description of the world as experienced by a particular organism, allowing us to appreciate animal perspectives fully. We generally assume that most species are visual beings, like us, but imagine how different the world must seem to bats that 'see' through echolocation or elephants, which rely on auditory and olfactory cues. While we are thoroughly amazed by the ingenuity of animal behaviour we encounter, we rarely pause to appreciate their *umwelten* or entertain the notion of animal intelligence, purpose or desire behind their behaviour.

I first learned about the concept of *umwelt* in the book *Are We Smart Enough to Know How Smart Animals Are?* by Frans de Waal. This book explores various facets of animal cognition through numerous examples and fascinating anecdotes across taxa. Through these stories and descriptions of well-designed experiments, de Waal sparks a sense of admiration and curiosity about how animals behave and the nature of their cognition. In the book, de Waal defines cognition as "processing sensory input into knowledge about the environment, and flexible use of this knowledge".

In the history of human culture, we can find a plethora of examples where animals have been ascribed with human attributes (in our context the attribute is, mainly, intelligence) – from fables and fairy tales with talking animals to characters in popular cartoon movies, even featuring in a charming song! But some scientists haven't been as welcoming to the idea of animal cognition. A century ago, the then-dominant school of thought, called Behaviourism, was based on the theory that all behaviours are acquired through conditioning. Behaviourists stressed only on the role of experience, discarding the notion of animal cognition, and even disregarding an animal's ecology and natural history. All animals were viewed as instinct-driven robots with conditioning (remember Pavlov's dog conditioned to expect food after the ring of a bell?) or interchangeable black boxes that merely responded to stimulus.

The other principal study of animal behaviour, Ethology, focused on the evolutionary/survival values of the behaviour and stressed the role of innate wiring in animal behaviour. However, ethologists too were uninterested in the role of consciousness, intention and mental experience in animal behaviour. While any animal's behaviour arises from its biology, cognition and learning, each affects behaviour in varying degrees. Perhaps one of the reasons why we refuse to acknowledge human-like traits in animals (and animal-like traits in humans) is that humans are perceived as entirely unique (and sometimes superior) from other animals. This perception stems from *scala naturae* - the Aristotelian idea of the ladder of life, with man at the top, animals below and plants in the lowest rung. It was replaced by the evolutionary tree of life, where humans are just another branch in the magnificent tree. Thus, it is essential to stress and acknowledge that there is no *scala naturae* when it comes to cognition. Each animal has evolved the cognition to adapt to its ecological requirements. Comparing the brains of animals is akin to comparing their arms – are the fins of a whale better than the wings of a bat?

In his book, de Waal methodically makes a case for 'evolutionary cognition', the budding field of study of cognition from an evolutionary standpoint, one that rests on a less anthropocentric bias. The new perspective that this brings is the culmination of many years of research and change in the field through numerous experiments involving primates, corvids, cetaceans, and even molluscs! There are several modules under the broad umbrella term of cognition, and these cognitive capacities can be individually (or collectively) observed in many animals.

Widely, these cognitive capacities are - theory of mind and perspective taking (capacity to grasp the mental state of others); tool use and language (which isn't endlessly flexible in animals); perception of conspecifics (for example, facial recognition) and time (such as episodic memory); imitation and social learning, and other such ideas. De Waal explores each of these ideas in his book with numerous examples – New Caledonian crows which can construct tools, and monkeys helping other monkeys who cannot reach their food are just a couple of examples. From elephants recognising the voices of tribesmen who hunt them to Alex the Parrot, who could do math and all the way to octopuses opening jars to get to the fish inside, the narration of these experiments is seamless and captivating, peppered with many anecdotes mostly involving primates.

I can imagine that many readers might feel disconcerted by the words 'animal intelligence' and the possibility of attributing human-like traits to animals (this is the book for you, dear sceptic). It may momentarily allay your qualms to read what Darwin had to say - *"The difference in mind between man and the higher animals, great as it is, certainly is one of degree and not of kind."*

Looking at cognition through the lens of Darwin's evolutionary theory allows us to appreciate the convergence in cognitive strategies that many animals use to solve similar problems. For example, the complex eyes of vertebrates and the compound eyes of arthropods (insects, crustaceans) evolved separately, but they both serve the function of vision. Facial recognition is a function that helps many animals distinguish friend from foe. Humans and other primates recognise other members of the species through holistic processing – by taking in the face as a whole rather than remembering the shape of a nose or a specific mark. Astonishingly, golden paper wasps can do the same! They recognise and remember many individual faces, which helps them keep track of nestmates and who's who in a complex pecking order. This evolutionary convergence to similar cognitive strategies among diverse taxa reinforces us to leave behind anthropocentric scales and weights while discussing cognition.

Donald Griffin, a cognitive ethologist who pioneered the studies on animal cognition, remarks in his book, Animal Minds (1992) that, "...the most basic and essential aspect of consciousness is thinking about objects and events... its[animal's] awareness probably includes memories of past perceptions or anticipations of future events." This is one of the simplest ideas of a conscious animal. The adaptability and versatility of animal behaviour compelled scientists to acknowledge that animals think. But as Griffin points out, "The taboo against considering subjective mental experiences of nonhuman animals has become a serious impediment to scientific investigation." After reading this essay, I hope your perspective on animal intelligence has been revised. The next time you encounter a line of ants in your kitchen or a crow on your roof (be nice to the crow – it can remember faces!), be sure to take a moment and appreciate their umwelten and intelligence that influences their behaviour.

Vasudha Kulkarni
Indian Institute of Science Education and Research, Pune
30th July 2021

Further Reading -

1. *What scientific concept would improve everybody's cognitive toolkit?* by David M. Eagleman
2. *How to Apply the Concept of Umwelt in the Evolutionary study of cognition* by Nereida Bueno-Guerra
3. *Like humans, wasps seem to recognize faces as more than the sum of their parts* by Cathleen O'Grady.
4. Biographical Memoirs: Donald R. Griffin by Charles G. Gross

Chapter 3 – Development: The Designer of Life

"Babies, as everyone who cares for them knows, come trailing with their own particular essence. There are grave, contemplative babies still patiently solving some equation of Euclidian geometry begun in another world, scrawny high-powered babies apparently shot into life without the slightest need to eat or sleep, and placid agricultural babies whose only concern is to thrive," describes the children's author, Eva Ibbotson in her book *A Company of Swans* (2007). Perhaps not as starkly as romanticised as Ibbotson's descriptions, each child is unique. And yet, we can undoubtedly observe some distinctive abilities are present in all children - they can recognise their mother's voice while still in the womb, sit up and enjoy playing peek-a-boo by their sixth month, stand up and take a few steps by their first year, and understand and repeat a few words by their second. By the time they're five, they become more independent, imitating their friends more than their parents. How does this pattern arise?

Design for a Life: How Behaviour Develops (2000) is a book by Patrick Bateson, a professor of ethology at Cambridge University, and Paul Martin, a lecturer and researcher on behavioural biology at Cambridge, that delves into how individuals become who they are. In a single phrase, it occurs through the process of behavioural development. Bateson and Martin use the metaphor (first of many) of cooking to elaborate their meaning – genetic and environmental influences (the ingredients) come together, and through biological and psychological development (the process of cooking), they give rise to unique individuals. The authors begin by placing a special vignette on the development of humans, especially children, as they go through the Seven Ages (as described in Shakespeare's well-known poem).

Compared to other mammals, humans have a relatively long childhood. In this period, children learn the skills and knowledge required to be well-functioning adults in society. In addition, they seek out and acquire experiences that will change their future behaviour. This active role in seeking new experiences is called play behaviour which similarly helps them hone their physical skills and simulate situations they may encounter as an adult. This is the first design principle of development that I have identified - some attributes of a developing organism are forward-looking, preparing the young one for life ahead.

The second design feature of development is the resilience of developmental processes. In the face of disruptions, the developmental processes are altered to ensure that the behavioural results are the same. A rhesus monkey with abnormal brain development behaved as if nothing had been disrupted. We can also see this in psychologically traumatised children who rebound from the trauma and in emaciated/starved children who quickly regain their weight. The authors use another metaphor (first used by C. H. Waddington) to explain this feature - 'development is represented as a ball rolling down a tilted plane which is increasingly furrowed by numerous diverging valleys. If it's not completely stopped, it overcomes obstacles and keeps rolling down.'

The third design principle I gleaned is that of scaffolding. Animals have a neural scaffolding that allows them to build complex, foundational skills such as language. We can observe this idea of scaffolding in the way in which infants and adults learn languages. If two languages are learnt at different ages, then the areas of the brain engaged while speaking them are also different. Conversely, if someone is speaking in languages that they had learned in infancy, the site of the brain engaged is the same. Play behaviour, as described above, can also be considered as developmental scaffolding, which is stripped away once the animal has gotten its use. Hence the tendency to play diminishes as we grow older.

The most prominent theme in the book is to maintain a balance between the two extremes, genetic determinism and the blank-slate argument, better known as the nature vs nurture argument. In every chapter of the book, the authors highlight how the interplay between genes and the environment gives rise to the animal's behaviour. As we saw earlier, the broad development patterns are the same in most children, yet every individual is unique. This can be better understood with another insightful metaphor - the Developmental Jukebox. As explained in the book, "Like a jukebox, the individual has the potential to play a number of different developmental tunes. But during the course of its life, it plays only one tune. The particular developmental tune it does play is selected by a feature of the environment in which the individual is growing up..." Along the same lines, each animal's behaviour is constrained by the number of available tracks, that is, its genes.

A unique feature that makes this book stand out is the use of descriptions about life and behaviour as written by well-known poets and authors in their classic works. There are extracts from All Said and Done by Simone de Beauvoir, Anna Karenina by Leo Tolstoy, Nineteen Eighty-Four by George Orwell, etc.

The authors focus on human behaviour development, so most hypotheses and studies they state are from human-centred studies in the last 100 years or so. They cite studies that show how birth orders affect adult characteristics, how young girls are more expressive and young boys more assertive, and how girls have been entering puberty earlier in the past century, and they hypothesise about these results. For example, their adaptive hypothesis for the early onset of menarche is that, in recent years, with better environmental conditions, women can take advantage of the bountiful resources and start having babies early to maximise their reproductive success. But according to a WHO article on maternal mortality, "Pregnancy-related complications are the number one cause of death among girls between 15 and 19 years of age. Because adolescent girls are still growing themselves, they are at greater risk of complications if they become pregnant." I wonder if this wouldn't work antagonistically to the proposed hypothesis.

Given that there are different facets to a phenomenon and low chances of reproducibility in some studies, especially when it comes to human behaviour, I would have expected an expository discussion on what other possibilities could explain the results or what other studies show additional support to the offered explanation.

Design for a Life: How Behaviour Develops is a thought-provoking read, enjoyable once you get used to the unique meter and style of the book. The authors have sprinkled numerous quotes (from various classics) and insightful metaphors throughout the book that is sure to keep the reader engaged. Although, if at first you feel lost or perplexed by the lack of coherence, read the final, summarising chapter first and then go back to where you left off. In conclusion, the writing style is easy on the mind but the authors' nuanced arguments are challenging and bound to sharpen your reasoning skills.

Vasudha Kulkarni
Indian Institute of Science Education and Research, Pune
30th July 2021

Chapter 4 – The Lesser Equal

In 1793, Olympe de Gouges, a French playwright and feminist, wrote a document titled *Declaration of the Rights of Woman and of the Female Citizen* in response to the civil rights document of the French revolution which promised 'the natural and imprescriptible rights of man'. She criticised the revolution for failing to recognise gender equality. For this and her other political writings, Olympe was accused of treason and beheaded.

Sadly, this is not unusual – women have struggled for equality and against oppression for centuries. In patriarchal societies, this suppression has taken on some extreme forms for women – denial of equal opportunities to literacy and education, curbing the freedom of choice, restrictions on movement and attire, sequestration, and in worst cases, female infanticide, female genital mutilation, and widow immolation. Things have been getting somewhat better with the advent of education and universal suffrage, but even in the 21st century, gender disparity is apparent in the gender wage gap, the representation in governing bodies, the gender ratio in the workforce, and especially in the division of labour at home.

Such a state of affairs has long been justified by claims about childbirth and child-rearing being the 'natural' purpose of women. Nature has served as the primary argument for anyone justifying male domination, despite the glaring naturalistic fallacy ("if something is natural, it must be good") and the fact that women have repeatedly proved themselves equal in intelligence, initiative, and administrative and political capabilities in spite of the barriers imposed on them. At the far end of this 'natural order' argument, all women were reduced to their childbearing and nurturing functions, considered incapable of controlling their emotions and thus unfit to work or lead in the world of men.

These biases and misconceptions were carried over to the interpretation of Darwinism as well. The Darwinian idea of sexual interaction has two scenarios - females choose the most desirable male, or a dominant male excludes other males, so all females have to mate with him. For a long time, the prominent narrative was that these different goals for men (to maximise the number of offspring) and women (to choose the best male to sire her offspring) demand for males to be 'ardent' and females to be 'coy'. In simpler words, men seek sex more than women.

With the above reasoning and the evidence from some experiments now under scrutiny, some scientists concluded that females are sexually passive. It was supposedly a given that sexual selection had acted on women to be 'naturally' coy, monandrous, and modest. Although, it's important to note that a woman's sexual desire is considered eager enough that most of the world's cultures have made some effort to control it. Among many of our closest relatives – primates such as macaques, chimpanzees and langurs – we observe that females make brazen solicitations to several males around them. In some species, females are sexually receptive throughout the oestrous cycle (not just when they're 'in heat'), and female apes have enlarged, innervated clitoris and a capacity for sexual pleasure. Sarah Blaffer Hrdy, a primatologist and anthropologist, demolishes the myth of the 'coy female' in her book *The Woman that Never Evolved,* which shines a much-needed evolutionary spotlight on females and their sexuality.

In her book, Hrdy narrates societal structures of various primates across the world. There are several monogamous monkeys where both males and females look morphologically similar and defend their territory together. In these societies, males show gallant deference to females, and there is a considerable paternal investment in caring for the offspring. On the other end of the spectrum are polygynous, socially stratified primate societies where one dominant male, sometimes twice the size of the female, defends a harem of females from other males. All his energy goes into defending the harem, and there is little to no paternal investment. The behavioural descriptions of these eclectic primates distributed all the way from dense tropical forests to bare demanding savannahs, are captivating and offer insights into the behaviour of humans.

In this short essay, I would like to focus on the following set of behaviours called 'concealed ovulation'. In many species, females do not advertise their ovulation by sexual swellings around their genitals. They are continuously receptive to sexual encounters and mate with multiple males. In some species, females continue to exhibit oestrous-like or "pseudo-oestrous" behaviour for several cycles even after conception. This set of behaviours allows the female to plant a seed of doubt in her consorts about the paternity of her child. Since males are selected not to harm their own children, these behaviours help the female ensure the survival of her offspring by making her consorts suspect that her infant might be theirs. This strategy became evident when it was discovered that nearly half of the infants (in polygynous societies) were likely to be killed by another male.

Such infanticide is seen in many animal species, including *"lions, hippos, bears, wolves, wild dogs, hyenas, rats, rabbits, lemmings, herring gulls, storks, European blackbirds, eagles, and more than fifteen types of primates-or sixteen, counting man*." Infanticide is a strategy employed by the males to ensure that the female comes to oestrous and becomes sexually receptive sooner than she would if she was nursing her infant. The claim is not that the males do this consciously, but that any heritable tendency to do so would be favoured by natural selection. The genes of the infanticidal male would spread more rapidly than those of non-infanticidal males who wait for the female to wean her offspring before coming to oestrous.

As we saw, female primates use concealed ovulation to elicit help from multiple males to protect and care for her offspring — natural selection selected for such wily, competitive and sexually active females. When the ball was in the males' court, those males who could discriminate the oestrous status of the females were selected. Or, as in the case of humans, Hrdy hypothesizes that those males who could control the sexuality of a woman and thus ensure their paternity were selected. Through culture and other infrastructure (such as maintaining guarded harems, removing a woman's clitoris to reduce sexual impulses, or physically preventing intercourse using a chastity belt), societies have constrained women's sexuality to ensure that the male who invests in the offspring is certain of his paternity. The sequestration of women becomes even more pronounced in a patrilineal and patrilocal society where the property and the 'territory' is inherited by the natural heirs of the dominant male.

It is important to note that it's not only men but also several women who suppress other women. Many mothers and mothers-in-law have played a part in keeping the patriarchal culture alive. As Hrdy narrates, *"…the court ladies of ancient China, the* nu shih *whose job it was to supervise the wives and concubines of the emperor. As have mothers, fathers, in-laws of both sexes, neighbours, and nosy parkers through the ages, these women busied themselves with the sexual status and conduct of women…"* According to Hrdy's hypothesis, these human practices served to cloister women and control their fecundity.

The ideals of the French revolution and men's rights were only (relatively) recently expanded to include women and other minorities. In *The Woman that Never Evolved*, Hrdy discusses many topics that were left unexplored due to the inadvertent male-bias that had affected how the sexual selection theory had been applied. This essay is about a small section of the book which explores diverse themes of social organisation in primates, female-female competition, female sexuality, and the evolutionary theory tying them all together. The author leaves us with a poignant message worth reflecting on, *"The female with "equal rights" never evolved; she was invented, and fought for consciously with intelligence, stubbornness, and courage."* With the far-reaching vision of an evolutionary biologist and the skill of a storyteller, Hrdy effectively conveys the importance of this hard-won equality, opening our eyes to the frailty of its assurance.

Vasudha Kulkarni
Indian Institute of Science Education and Research, Pune
30th July 2021

Further reading –

1. Natural gender order and the nature of women
3. The brilliant woman for whom the word "scientist" was coined
4. Challenging a Classic experiment (Bateson's experiment demonstrating promiscuous males and choosy females)
5. All female mammals have a clitoris
6. Infanticide is common in many mammals
7. An Interview with Sarah Blaffer Hrdy

Acknowledgement

I have borrowed the title for this article from the title of a talk series hosted by the Literary Club (IISER Pune) in November 2019. The talk series was organised to commemorate the centennial of the women's suffrage movement.

Chapter 5 – Life is Hard for the Cuckoo too

On a cold morning in April, I was suddenly woken up at 4 in the morning by the call of a koel sitting on the neem tree right outside my window. *Koo-Ooo Koo-Ooo*. It was all I could do to ignore the calls. I wanted to shake the branch and chase away the bird. At that moment, I had no inkling of the fascinating explanations behind the koel's call, egg-laying habit and other behaviours. The koel (*Eudynamys scolopaceous*) is a member of the cuckoo order of birds *(Cuculiformes*). Male cuckoos are known for their distinctive calls and female cuckoos for laying their eggs in other birds' nests. While other birds mate, build nests, lay eggs, incubate them and feed the chicks till they're old enough, cuckoos don't exhibit any parental behaviour and instead trick other birds into taking care of their eggs.

Over a hundred species of birds lay their eggs in some other birds' nests. Such birds are called brood parasites and the birds that are thus parasitized are referred to as the hosts. In *The Avian Brood Parasites* (1997)*,* Paul A. Johnsgard, an eminent ornithologist, gives a comprehensive overview of brood parasitism, including detailed descriptions of all known brood parasitic bird species. In this book, Pied Cuckoo, Large Hawk Cuckoo, Indian cuckoo and Asian koel are said to be predominantly distributed across India. In my essay, when I use the word 'cuckoo', it is a placeholder for any of our brood parasitic songbirds, though I have chosen to use the specific example of koels to emphasise my points.

Several cultures worldwide have portrayed the characteristic calls and behaviours of the cuckoos in stories and songs and myths. In fact, in many languages, the bird's name sounds like its call (for instance, it's called coucou in French and kuckuck in German). The cuckoo's arrival announces the arrival of spring, and in India, the arrival of cuckoos is also associated with the joy of blooming of mango trees. The other dominant perception related to the cuckoos is that of laziness brought by its habit of laying its eggs in another bird's nest. Although considered lazy and vain for abandoning its parental duties, we shall see that the cuckoo has a hard life.

My grandfather, who is 89 years old and has lived in nine cities over 40 years of service in the Indian Postal Service, tells me that his most notable impression of the cuckoo is that, come spring, it sits on a mango tree and sings in the 'most beautiful voice among birds'. "And if you call out – *koo kooo* – the bird will 'reply' in a louder voice," he added. Like many migratory birds, cuckoos travel long distances in the spring to reach their destination, where they mate and breed. Usually, the males arrive first, establish their territories and start singing to attract females. It is only the males that sing the tune that is so familiar to everyone. When a male hears another voice singing in its territory – even a human trying to imitate it – it assumes that there is a competitor. It then replies and tries to chase away the intruder.

Once the females have mated, the hard part of the breeding season begins for them – sneaking their eggs into host birds' nests. It is common knowledge that cuckoos lay their eggs in the nests of crows. While it is true that the house crow (*Corvus splendens*) is the primary host of the Asian koel, other species of cuckoos in India and around the world target birds that are quite different from themselves – the incidental similarity of the adult koels or their chicks to crows appears not a necessary condition for successful parasitization.

When I spoke about my interest in cuckoos and koels to my uncle who is a scholar of ancient Indian texts, he told me about the 4th-century playwright and poet Kalidasa. In Kalidasa's renowned play, *Shakuntala*, the amnesiac king, Dushyanta, who has forgotten his tryst with

Shakuntala, refuses to accept her unborn child, suggesting that she is trying to pass off another man's seed as his own. Dushyanta says,

"The female's untaught cunning may be seen/ In beasts, far more in women selfish-wise;/ The cuckoo's eggs are left to hatch and rear/ By foster-parents, and away she flies".

The cuckoo has captured the popular imagination for centuries, inspiring poets with its song and storytellers with its unusual behaviour.

At the onset of summer, many birds mate and build nests to lay their eggs. Some of these birds are parasitised and raise the chicks of cuckoos instead of their own. The crow serves as one such host bird for the Asian koel. B.S. Lamba, of the Zoological Survey of India, studied crows' nest-building habits and parental behaviour over four years (1953-57) in Pune, Vellore and Akividu. He found that for 14 weeks in the summer, male and female crows form close bonds with each other and build a nest together. The pair go in search of dry sticks and twigs. Lamba also observed that the male crow doesn't let the female out of sight during this period. Although the male crow helps in collecting twigs, it is only the female that arranges the twigs and builds the nest. Once the nest's outer cup is secure, the crows line the inside of the nest with grass, coconut fibre, horsehair, feathers and the like. The nest is thus built in about four to seven days. Once the nest is ready, the female lays 3-6 eggs, one on each consecutive day.

After putting in all this effort, imagine that an intruder flies in, lays her own egg within a few seconds and flies away, tricking the crows into bringing up a foreign chick while their own starve to death. But this is exactly what happens to the crows on many occasions. Arne Moksnes, a professor at Norwegian University of Science and Technology, and his colleagues studied the interactions between Asian koel and its host species in the campus of Jahangirnagar University in Bangladesh. They found that the rates of parasitization ranged from 11% for crows, 31% for common myna and 35% for long-tailed shrikes. Understandably, many would find such trickery 'lazy' on the cuckoo's part. But we will see how the cuckoo does a lot of gruelling reconnaissance before it can complete its mission and that it does not always succeed.

When I asked an old schoolmate if she had ever seen a cuckoo, she said, "No, I've never seen one, but I've heard its song several times". The cuckoo is more often heard than seen and with good reason. The female cuckoo perches behind dense foliage and closely surveils potential host nests in her vicinity because she has to pick the nest very carefully.

Douglas Dewar, a British colonial officer at the turn of the 20th century, studied the parasitic habits of koels in Lahore in the summer of 1906. He reported that koel eggs always hatched before the crow chicks. For each bird species, the eggs need to be incubated for a particular number of days before they are ready to hatch. Crow eggs hatch after 16-20 days of incubation, compared to koel eggs which hatch after only 13-17 days. If a koel lays her egg in a nest where there are no eggs, the host bird is likely to realize that the koel egg is not her own and if the koel waits too long after the crow has laid its own eggs, the crow chicks will likely hatch first and the koel chick will have to compete with the crows. The best strategy for the koel is therefore to lay her egg after the crow has started but not finished laying her own eggs. That is the reason why the koels has to so carefully select her intended host nest.

While other birds generally take about 30 minutes to lay an egg, the cuckoo can do it in seconds. How does she manage this? In his book, *Cuckoo: Cheating by Nature* (2015), Nicholas Davies, a Professor of behavioural ecology at Cambridge University, UK describes this unusual egg-laying mechanism (and much more!). While the female cuckoo is picking out the nest, she sits still and lets the egg descend the oviduct. She can hold it there and has immense control over the timing of the final release of the egg. She can therefore wait for an opportune moment when the host from a suitable nest is away and quickly swoops in to deposit her egg and flies away, all within seconds! Sometimes, even if the host nest is occupied, she braves their attacks while laying her egg. And she has to repeat the whole process in two days when she lays another egg in another nest. Lamba found that, in koels, the male helps his mate by distracting the crows by drawing their attention. The crows get agitated and give chase to the male while the female koel swoops down on the nest and relieves herself of her egg. In the process, the male koel may suffer significant injury or even death.

On an evolutionary timescale, one of the problems the cuckoos have had to overcome is host defence in the form of egg discrimination. The host birds are not passive to the cuckoo's intrusion. In *Cuckoo: Cheating by Nature,* Nick Davies describes this battle between reed warblers (a small songbird) and cuckoos in a nature reserve near Cambridge. If the reed warblers detect that a foreign egg has been added or substituted in the place of their own, they eject the foreign egg from the nest. If they can't distinguish the egg but know that their nest has been tampered with, they abandon it and build a new nest elsewhere. In response to such defence, the cuckoos have evolved egg mimicry – the cuckoo eggs closely resemble that of the host species, down to the background colour, the colour and distribution of their spots. Arne Moksnes and his group found that, despite the koel's efforts, the proportion of parasitised nests that produced at least one koel fledgling was 25% for crows, 33% for common myna and 46% for long-tailed shrikes.

If the koel's forgery goes unnoticed, the crows accept the koel egg and wind up becoming its foster parents. Now, the koel chick's struggle begins. Publishing in the Bombay Natural History Society journal, both Dewar (in 1906) and Lamba (in 1963) described the interaction of crows and koels. The following description is based on their work. The koel egg hatches after 13-17 days of incubation (male and female crows take turns, even in feeding), three days before the crow chicks hatch. The koel chick takes advantage of being the lone mouth and continuously begs for food, fattening up and growing in the first few days before it gets competitors in the form of new hatchlings of the host.

Dewar showed that unlike chicks of other cuckoo species (which push the host eggs and chicks out of the nest even while the foster parents watch), the koel chick tolerates the crow chicks. When the foster parents arrive with a beak full of food, they are confronted by a number of gaping mouths as the nestlings raise their necks to beg for food. The younger chicks are not fed until the older ones have had enough. Because the koel chick has already grown and fattened up before the crow chicks hatch, it competes successfully for food by begging incessantly. When the weakest chicks, which usually happen to be the hosts chicks, don't get enough food, they starve and die and are thrown out of the nest by their own parents. Lamba found that if a koel chick is present in the nest, two out of five crow chicks will die of starvation, and if there are two koel chicks in a nest, it is unlikely that any of the crow chicks will survive.

Davies also describes other strategies that cuckoo chicks use. In some species of cuckoos, the chick rolls the host eggs out of the nest and even evicts the host chicks. Once the cuckoo chick gets older, its begging calls become louder and more frequent. This tricks the foster parents further because it sounds to them as if several chicks are begging for food. In the Horsfield's hawk-cuckoo, the chick has yellow patches under its wings which is the same shade as its open gape. When the chick is quite hungry, it spreads its wings and calls loudly, so it seems like three chicks are begging for food. Since the cuckoo chicks call loudly for food, they attract predators in many instances. So, the parasite chicks also exhibit some defensive behaviour to stave off threats – if you put your hand towards them, they erect their head feathers and open their orange gape and suddenly snap it close. If touched, the cuckoo chicks also release their foul-smelling brown liquid faeces.

Once the chick is fledged and capable of finding its own food, the juvenile cuckoo leaves the host nest, only to return next summer as an adult to parasitise another host nest and never build its own. Many people only know about the cuckoo's melodious voice and its habit of laying eggs in another's nest. This incomplete picture of the cuckoo's life creates a misconception in people's minds that it leads a carefree, lazy life, singing its days away. But we saw that it's only the males that sing while the female struggles to lay her eggs. And we also saw that, in reality, the cuckoo leads a tough life – from the time it's born, it has to compete for food in the nest, beg incessantly to be fed enough food, and ward off possible predators. Once it's an adult, it spends its days surveilling potential host nests and risks its life to lay eggs. Life is hard for the cuckoo too.

Vasudha Kulkarni
22nd September 2021
Indian Institute of Science Education and Research, Pune

References and further reading –

1. Cuckoo: Cheating by Nature by Nick Davies and James McCallum (illustrator)
2. The Avian Brood Parasites: Deception at the Nest by Paul A Johnsgard
3. The nidification of some common Indian birds by B.S. Lamba
4. An enquiry into the parasitic habits of the Indian koel by D. Dewar
5. Interactions between the Asian Koel (Eudynamys scolopaceous) and its hosts by Moksnes et al. 2011
6. Kalidasa's quote was extracted from Arthur Ryder's translation of Shakuntala
7. eBird – visit this website for more information about birds

Acknowledgements

I spoke to several family members, neighbours and friends to get an idea of how the cuckoo is popularly perceived. I'm grateful to them for their patience and indulgence.

Chapter 6 – Parallels between Individual and Social Immunity

By Vasudha Kulkarni
22nd August, 2021

Abstract

Social immunity is the collection of colony-level anti-parasitic protection that depends on the cooperation of social group members resulting in avoidance, control or elimination of parasitic infections. Individual immunity is the organism-level anti-parasitic protection that depends on its behavioural and physiological immune system. In this report, I assess the impact of the paper – *Analogies in the Evolution of Individual and Social Immune System* (Cremer and Sixt 2009) – that draws analogies between the strategies of the individual and the social immune system in terms of border, soma and germline defence. There are behavioural, genetic, physiological, spatial and morphological modes of defence. I assess the impact of this paper – and the concepts it introduces – on the field of social immunity and how it has influenced other disciplines. I have done this by going through the research papers and review articles that cite this focal paper, and analysing the context and themes of the citation. Most of the citations mention the focal paper, and a few advance the concepts introduced in it. They do so by expanding on the evolutionary aspect, reporting behaviours that act as examples to strengthen the analogy and contest some definitions by pointing out their limitations. Cremer and Sixt 2009 has also been cited by papers in the field of robotics, philosophy of immunology, medicine, anthropology, and eco-immunology. This impact report assesses the impact of the focal paper and, through that, explores a part of the expanding field of social immunity.

Introduction

Sociality is the tendency of organisms to come together and associate in groups. Some insects are eusocial - they exhibit strong division of reproductive labour, overlapping adult generations and cooperative care of the young. In many eusocial insects, such as bees, wasps, ants and termites, there is a reproductive caste (queen and males/possibly king) and a sterile (worker) caste. Such a system can be compared to the structure of germline cells and somatic cells in an individual organism. By extending this comparison, the eusocial insect colonies can be viewed as a single unit, and these colonies are often referred to as a "Superorganism" (**Wheeler 1911**).

Just as every organism has defences against parasites, the superorganism too has defences called Social Immunity. Since individuals in social insect colonies are closely related and live in densely packed conditions, insect colonies are susceptible to infections. Social Immunity is maintained by all the group members collectively avoiding, controlling or eliminating parasitic infections. A monograph by Paul Schmid-Hempel titled *'Parasites in Social Insects'* first discussed the parasites of social insects, their ecology and their selection pressure on social insect evolution (**Schmid-Hempel 1998**).

A decade later, in a landmark paper (**Cremer et al. 2007**), Sylvia Cremer, Sophie Armitage and Paul Schmid-Hempel introduced the concept of social immunity. This colony-level anti-parasitic protection is achieved by hygienic behaviour, physiological defences and a third major component: spatial organization and contact frequency regulation. Social immune responses can be prophylactic or activated and employ either a behavioural (hygienic behaviour), genetic (variation reduces susceptibility), physiological (such as social fever), spatial (spatial structure of the colony and its members) or morphological defence mode.

This report aims to assess the impact of a particular paper – *'Analogies in the evolution of Individual and Social Immunity'* (Cremer, Sylvia, and Michael Sixt. "Analogies in the Evolution of Individual and Social Immunity." *Philosophical Transactions of the Royal Society B: Biological Sciences* 364, no. 1513 (January 12, 2009): 129–42. https://doi.org/10.1098/rstb.2008.0166). I have done this by going through the research papers and review articles that cite this focal paper and analysing the context and themes of the citations. In the focal paper, Sylvia Cremer and Michael Sixt draw parallels between the organisation, function and evolution of individual and social immunity. We can understand the impact and implications of this paper by considering the context in which it was cited, what kind of papers it was cited by and how the concept has been advanced since it was published. Studying the implications of the concepts advanced by Cremer and Sixt 2009 would help us assess the progress that has been made so far and pave the way for the road ahead.

As we have seen before, the basis of this comparison is based on the fact that the life history of a colony is remarkably similar to that of a multicellular organism. There's a growth phase of the colony, which it has to cross to enter the reproductive phase. The authors show remarkable similarities between the strategies of individual and social immune systems. There are three layers of host defence against parasites, in both, individual and social immune system. They are - (i) **Border defence** to avoid parasite intake (ii) **Soma defence** for opposing establishment and multiplication of the parasite. (iii) **Germline defence** to prevent an infection of reproductive individuals and protect the daughter generation.

Individual border defence includes disease avoidance, hygienic behaviour, the presence of a thick cuticle, mucus lined epithelium and epithelia rich in antimicrobial secretions and mucosal immunoglobulins. Social border defence is maintained by the structure of the colony - only a few older individuals leave the nest to forage and are hence more susceptible to exposure. When a parasite actively tries to enter the nest, the workers try to block the nest entrance, similar to a clot. Honey bees have 'bouncer individuals', which guard the entrance and bar entry to infected individuals.

Individual soma defence needs to be activated. Some mechanisms involved in the process are – immune cells that phagocytose the parasite or kill it by secreting toxic substances, creating an unfavourable environment for the parasite by depleting iron or increasing body temperature (fever), and programmed cell death. If the parasite can't be removed from the body, it is encapsulated in a granuloma to isolate it from the tissue. Examples of social soma defence include encapsulation of parasites (honey bees isolate the parasite by a layer of propolis or surrounding it by a 'ball' of worker bees), 'natural killer insect workers' in termites which imprison infected termites behind a wall of antimicrobial faeces, and social fever, i.e., raising the temperature of the colony by several worker bees fanning their wings simultaneously. The modular organization of social insects favours the sacrifice of infected individuals for the benefit of the colony.

Germline defence in individuals manifests as a blood-ovary/testes barrier and a high number of immune cells around the gonads. In social insects, germline defence means the defence of reproductive individuals. The queen is usually cared for by young individuals (nurses) who have never left the nest and, hence, are less likely to be infected. In addition, contact rates are adjusted in case of an infection, and the social network is modified to minimise the infection risk of the queen. The offspring are also protected against infection. For example, in fire ants, the infected brood is sprayed with an antimicrobial venom to prevent further spread of disease.

Table 1 – Analogies between individual and social immune systems
(The examples in second and third column are not necessarily direct analogies)

Layer of defence	Individual Immunity	Social Immunity
Border defence	Thick Cuticle Mucus lined epithelium Mucosal immunoglobulins	Structure of the colony Guard honeybee workers Blocking nest entrance
Soma defence	Phagocytic immune cells Fever, depleting iron content Programmed cell death	Propolis in honeybee Social fever Social exclusion of infected worker
Germline defence	Blood-ovary/testes barriers Increased number of immune cells near gonads	Selective workers caring for the queen Social network plasticity

Another important aspect of immunity is self/non-self discrimination. It is crucial for the individual immune system to differentiate between self-structures (failing which leads to autoimmunity) and harmful non-self structures. Along with pattern recognition receptors and the ability to detect tissue damage (components of innate immunity), the acquired immune system of vertebrates also plays an important role. T-cells are cued to only react to antigen presented by dendritic cells, retain the memory, and get activated upon encountering the antigen again. In social insects, colony odour aids in discriminating between self and non-self individuals. Cuticular hydrocarbons are the major cues for nest-mate recognition in social insects and show colony-specific patterns.

This discrimination is also vital in maintaining individual/colony integrity. Allo-reactivity (rejection of transplants) and tumour suppression is a method of maintaining individual integrity. In ants, social immunity has to deal with individuals outside the colony who can enter and replace the queen. In honey bees, some workers lay haploid eggs to increase their own reproductive fitness. As such behaviour is 'antisocial' and reduces colony efficiency and the fitness of the other colony members, those cheating individuals are punished (worker policing).

The workers in an insect colony regulate the social immune system. They regularly patrol the nest, just like immune cells do in an individual. The decision of whether or not to care for or kill a specific individual may depend not only on its infection load but also on its future value for the colony. Workers grooming infected individuals are inoculated against the infection, which can be thought of as social vaccination.

When considering social and individual immunity in a colony, several findings indicate that a robust social defence may replace to a certain extent the need for a sophisticated individual immune system. This means that in insect colonies, selection not only acts at the level of the colony but concurrently at the level of the colony's individuals. Social immunity can thus only evolve if overall it enhances colony reproductive output, even if some individual interests are violated, as we saw in some examples earlier.

Through this impact report, I aim to assess the impact of this paper – and the concepts it introduces – on the field of social immunity and understand how it has influenced other disciplines. I have done this by going through the research papers and review articles that cite this focal paper, and analysing the context and themes of the citation as elaborated in the 'Methods' section.

Methods

Collecting papers that cite Cremer and Sixt (2009)

I searched the focal paper on Google Scholar using the following words – "Analogies in the Evolution of Individual and Social Immunity." – on 29th June, 2021. I got 165 citation results, as can be seen in the screenshot below.

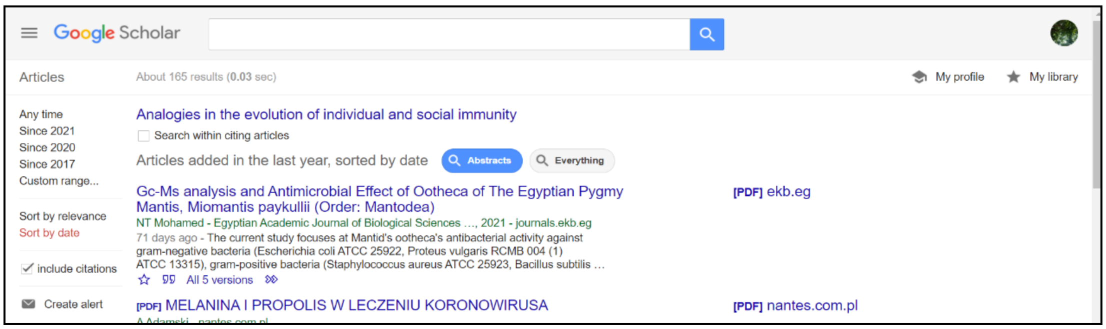

Fig 1 – Results of citations in Google Scholar

Out of 165 results, I was able to access and collate 107 papers that cite Cremer and Sixt 2009, which I have listed in the 'Appendix' section. Among the Google Scholar results, 21 citations were in a different language, 13 citations were citations in books, 5 results were repeated, and 16 papers were behind paywalls that I couldn't access through institutional access.

Then I searched the paper using the same keywords in a website called Scite, a tool to check how a scientific article has been cited and easily locate the sentence in which the focal paper was cited. I used this website to cross-check my findings and access the citation sentences of 3 papers I couldn't through institutional access.

ConnectedPapers is another useful website to discover the most relevant prior and derivative works. I entered the same keywords and created a graph using the website, which can be accessed at the following link. I used the graph to identify some important papers related to the focal paper.

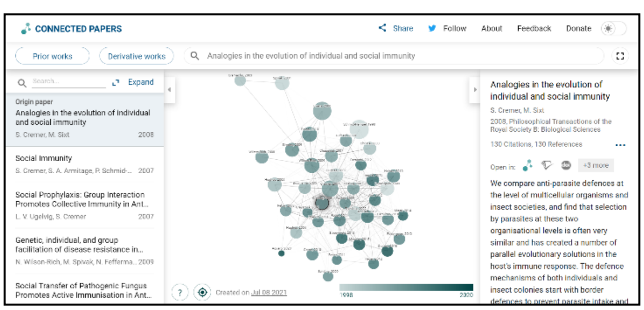

Fig 2 – Results from Connected Papers

Assigning the context and theme to the citations

Having collected all the papers that cite Cremer and Sixt 2009 and the sentences in which they cite it, I read the titles, abstracts and the relevant paragraphs to get an idea of the paper and the context.

The following are the conventions I have used while classifying citations based on the context of citation –

[M] Mentioning – where the paper cites Cremer and Sixt 2009 paper to mention the idea of social immunity or the analogy between individual and social immunity
[S] Supporting – where the paper cites Cremer and Sixt 2009 paper to advance the concepts introduced in the paper or supports the paper in strong/distinct terms.
[C] Contrasting – where the paper cites Cremer and Sixt 2009 paper to criticize or disagree with something in the paper.
[T] Take-forward – where the paper cites Cremer and Sixt 2009 and advances the ideas of comparison between individual and social immunity, or reports an example supporting the analogy
[U] Unexpected – where the paper citing Cremer and Sixt 2009 is from an unexpected field or context such as robotics or medicine

After going through the citations, I noted the keywords that stood out or seemed to occur multiple times in the papers. To assign themes to the papers, I searched those keywords in the results I had collected and tagged the papers based on the presence of those keywords in the title or the body. I crosschecked this by searching those keywords in my Zotero collection and adding any papers I missed. For example, 35 studies on ants cite the Cremer and Sixt (2009) paper, and those studies have been tagged with [Ants].

After annotating the citations with context and thematic tags, I counted the frequency of each tag. The tables are listed in the 'Results' section below.

To calculate the number of papers published in a certain year, I searched the years – such as "2010" – in the list I had created and noted down the number of papers (that cite Cremer and Sixt 2009) published every year from 2009 to 2021. I visualized the data using the matplotlib library in Python.

Results

The following tables and graphs contain the number of papers that cite the Cremer and Sixt 2009 paper in different contexts, themes and years.

Table 2 – Breakdown by the context of citation

Code	Category	Number of papers
M	Mentioning	85
S	Supporting	19
C	Contrasting	03
T	Take-forward	07
U	Unexpected	11

Table 3 – Type of literature citing Cremer and Sixt 2009

Type of Literature	Number of works
Research articles	66
Reviews	26
PhD dissertations	12
Books	3

Fig 3 - Number of citations each year since 2009

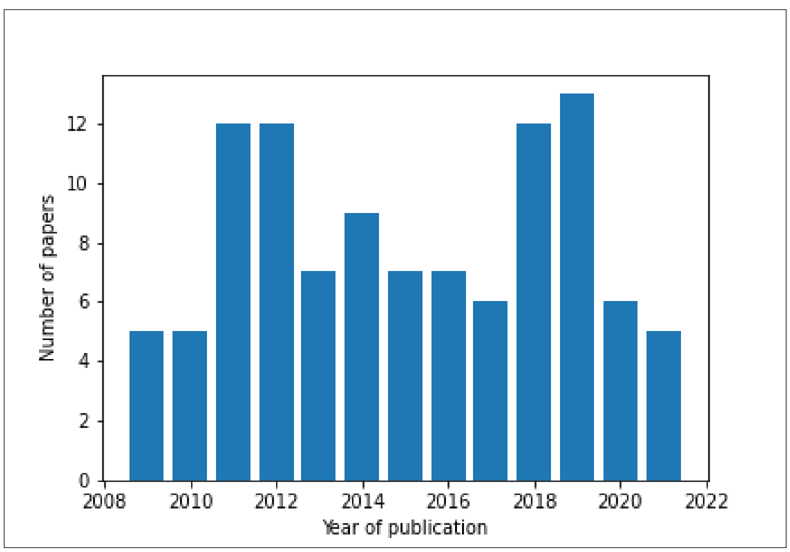

Table 4 - Thematic categorization of the papers citing Cremer and Sixt (2009) –

Keywords	Number of papers
Ants	35
Bees	32
Evolution	20
Fungi	15
Microbiome	9
Individuality vs Sociality	8
Sensory Perception	8
Termites	7
Genetics	6
Medicine	4
Bacteria	3
Cognition/Learning	2
Beetle	2
Robotics	1

Discussion

Social immunity is the collection of colony-level anti-parasitic protection that is achieved by the participation of all individuals in the colony. Just as organisms are protected from parasites by individual immunity, colonies of social organisms are protected by social immunity. Considering the colony as a superorganism, we can understand social immunity better by comparing and contrasting it with individual immunity. Cremer and Sixt 2009 is the earliest paper to draw analogies between individual and social immunity. They provide a new framework in which different physiological, morphological and behavioural characteristics of social insects can be better understood by situating their role in social immunity. Studying social immunity and comparing its features across different species could help us understand the evolution of sociality itself.

Studying the implications of the concepts advanced by Cremer and Sixt 2009 would help us assess the progress that has been made so far and pave the way for the road ahead. We can understand the impact and implications of this paper by considering the context in which it was cited, what kind of papers it was cited by and how the concept has been advanced since it was published.

A good majority of the papers citing Cremer and Sixt 2009 mention it and move on to discuss other topics. The number of publications with the keywords 'social immunity' has increased steadily since the conception of the idea in the eponymous landmark paper, **Cremer et al. 2007**. Although social immunity has been gaining traction, there is no apparent trend in the number of times Cremer and Sixt 2009 paper has been cited annually. Many articles cite the focal paper to introduce social immunity or mention the similarities between individual and social immunity and move on to discuss other points.

Several papers and reviews support the focal paper by adding to the list of analogies through newly discovered behaviour, advancing the concept of analogies, or supporting the focal paper and highlighting its importance in strong terms. Many of the supporting papers are also tagged

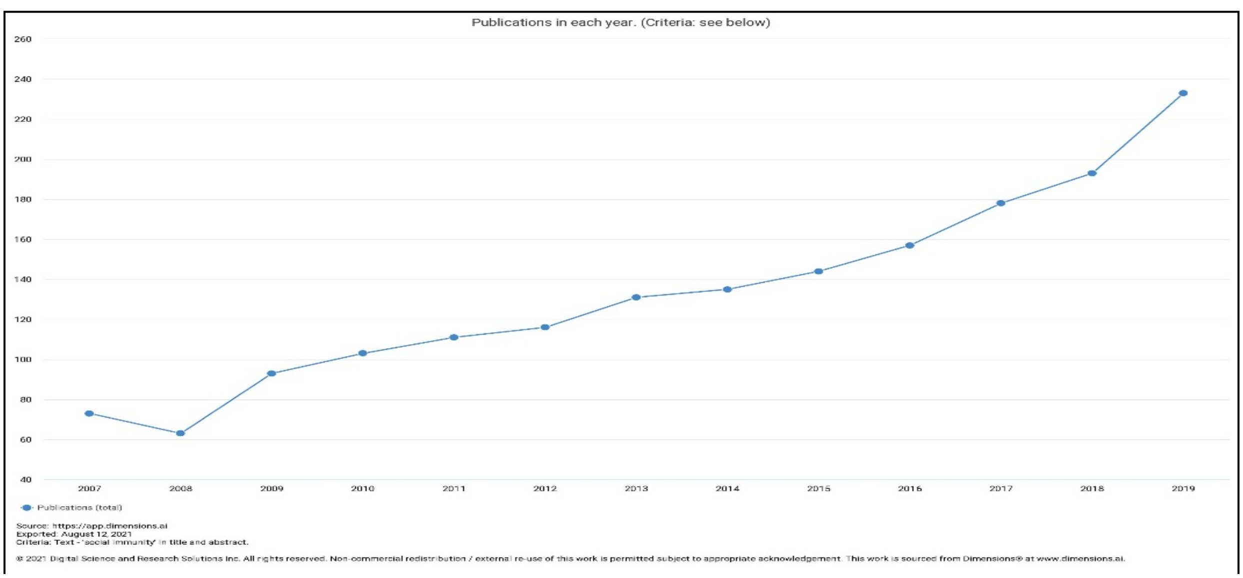

Fig. 4 – Plot of number of publications (with 'social immunity' in title or abstract) annually from 2007 (~80) to 2019 (~240)

with the *'Take-forward'* tag since they advance our understanding of the concepts in Cremer and Sixt 2009.

Pull and McMahon 2020 is one such paper that discusses the convergent properties of organismal and superorganismal immune systems, especially in the context of major evolutionary transitions. They list several examples of how organisms and superorganisms use comparative mechanisms for immune policing, immunological memory, immune privilege (some organs are prioritised over others), and apoptosis. They also discuss the immune system's role as a pivotal factor in the transition to superorganismality at the stages of group formation, group maintenance, and transformation into a biological individual.

One of the prominent themes in the papers citing Cremer and Sixt 2009 is Individuality vs Sociality. These papers consider the similarities and differences between individuality and sociality, focusing on immunity as a fundamental factor. Thomas Pradeu, a philosopher of science, writes that the immune system plays a key role in surveilling every part of the organism, maintaining connections within, making each individual unique and constantly re-establishing the boundaries between the organism and its environment (**Pradeu 2012**). In **Pradeu 2013**, he argues that the social immune system could have been instrumental in the evolution of superorganismality, just as immunity is thought to have been essential for the evolution of multicellularity. Along similar lines, **Cotter and Kilner 2010** examine the trade-offs between costs of investing in personal and social immunity for a sterile individual living in a colony. They suggest that further studies should be conducted to determine how cooperation and conflict influence an individual's contribution to social immunity. Exploring this idea, **López-Uribe et al. 2016** showed that social insects living in large societies have evolved behavioural immune defences that lower disease risk within the group, resulting in lower investment in immunity at the individual level.

Some other papers that advance the concepts proposed in Cremer and Sixt 2009 are – **Kennedy et al. 2017** discuss many aspects of studying social insects, including our understanding of disease defence. The authors suggest that different complexity levels of different social insects can be useful in addressing various questions about epidemiology and disease dynamics. Meanwhile, the analogies between individual and social immunity could provide insight into the evolution of immune defences across domains. **Rueppell et al. 2010** and **Pull et al. 2018** provide new examples of social behaviour in honey bees (altruistic self-removal, which is similar to apoptosis) and ants (poison-spraying infected brood, which is similar to the action of Natural Killer immune cells), respectively, that add to the list of analogies between immune defences of individuals and superorganisms.

Concepts can be advanced not only by supporting evidence but also by pointing out their shortcomings so that they can be resolved, failing which a new theory can be adopted. Only three papers out of 107 contrast the ideas presented in the focal paper. **Cotter and Kilner 2010** were the first to suggest the limitations of the framework proposed in Cremer et al. 2007 – that it was too restrictive and only applicable to eusocial insects. Instead, they proposed that the immune system that arises from collective action should be called "collective immunity", a subset under the broader term 'social immunity'. **Van Meyel et al. 2018** and Dr Körner, in his PhD thesis (2019), extended this argument and pointed out the limitations of Cremer et al.'s 'eusocial framework'. They posit the 'group-living framework', which considers social immunity as an ancestral phenomenon present in many forms of group-living. The argument against the restrictive definition of the eusocial framework is that it can create misconceptions about social immunity and sociality. It suggests that social immunity can only evolve when the unit of selection shifts from the individual organism to the superorganism. They propose that a broader definition of social immunity 'would provide novel major insights into our understanding'.

The social insects frequently chosen to study social immunity are ants and bees, as indicated by the popularity of the keywords. Most of the work in social immunity has been carried out on social insects such as honey bees, bumblebees, leafcutter ants, garden ants, and termites. But based on the citations, it seems like wasps (the third group of social hymenopterans) and other social insects and mammals are underrepresented in these studies. The current situation may be driven by the commercial value of understanding social immunity in honey bees and relatively easy maintenance of ant colonies. A prominent counterexample: **Nuotclà et al. 2019** have conducted a study on Ambrosia beetles to show that pathogen defence is a potential driver of social evolution. **Van Meyel et al. 2018** suggest that it is crucial to expand primary studies to other taxonomical groups to understand whether social immunity evolved in social insects as a response to high risk of infections or whether it stayed the same in group-living and eusocial insects. It could also help us answer if, as **Biedermann and Rohlfs 2017** suggest, the general risk of pathogen exposure for a solitary individual could have been selected for the emergence of group living in order to obtain an additional line of defence such as social immunity.

While honeybees and ants are popular host species to be studied, fungal pathogens are the most popular social parasites to be explored. Most of the studies focus on how ants, bees and termites deal with fungal pathogens. Perhaps this is because fungal spores are easier to manage in an experimental setup, and they are an abundant natural pathogen of these insects in tropical forests (**Evans 1982**). A good number of studies on leafcutter ants focus on their ability to cultivate fungi and study how they deal with unwanted, potentially pathogenic strains of fungi (**Heine et al. 2018, Fernández-Marín et al. 2015, Yek et al. 2013**). Two studies (**Vang et al. 2020 and Vang et al. 2018**) report on controlling the sacbrood virus infection in honey bees. In comparison, social immunity studies with bacterial pathogens have not come up in this list of citations. But there are several studies on symbiotic bacteria that protect the insects and aid in resisting diseases (**Lanan et al. 2016, Kaltenpoth and Engl 2014, Woodhams and Brucker 2013**).

A more direct (but less metric) way of assessing the impact of the paper is to follow up on the further questions suggested in it. Cremer and Sixt 2009 mainly highlight three things. The first one is to explore in detail some features of the individual immune system that haven't been discovered in the social immune system yet. An example mentioned was to check for the analogue of activation and regulation of immune effector cells (T and B cells) by antigen-presenting cells. They mention that it wasn't known whether social insect workers actively recruit and guide others to the site of infection or whether each individual performing hygienic behaviours acts autonomously. After some digging, the only relevant literature I could find was a study (**Esparza-Mora et al. 2020**) that examined the inhibition of Gram-negative Bacteria Binding protein 2 (GNBP-2) in termites. GNBP-2 is an immune effector molecule and an entomopathogen degrading enzyme. Esparza-Mora et al. had hypothesized that GNBP-2 might play a role in recruiting more workers to the site of infection, but they reported that it doesn't play a major role in recruiting workers.

The next suggestion by Cremer and Sixt 2009 is to pinpoint the differences between individual and social immunity. It may highlight evolutionary or organisational constraints, differences in selection pressures or simply alternative routes to the same problems. There are some examples of differences – there is no 'vomiting response' strategy in social insects, i.e., the flushing out of pathogen after intake. Along the same lines, there are no germ-line parasites in most animals, while in ants, there are slave-making species whose queen enters the host colony, replaces the host queen and starts laying eggs in her place. Such 'germline slavery' is not observed in vertebrates – they face no threat to their individuality. I couldn't find any article that has explored this interesting question so far. Along these lines, it might also be insightful to compare social immunity with individual plant immunity – one of the greatest similarities between them is the modular nature of the superorganism and the plant where individuals (in a colony) and leaves (in a plant) are dispensable and replaceable. . It would be interesting to see if further comparisons would reveal some insights.

The third major suggestion is to use social insect colonies as epidemiological models to study disease dynamics in livestock and human societies. Most epidemiological models are based on data collected after an outbreak. But Sylvia Cremer (**Cremer 2019**) opines that, "...research on insect societies, however, allows for prospective experimental studies with full surveillance of the social interactions and their effect on pathogen spread. This even allows us to test how manipulation of the network properties, or the individual behaviours, affect disease outbreaks". Once again, I couldn't find relevant literature that has reported on this aspect. **Milutinovic et al. 2020** might be indirectly relevant – they examine the role of social immunity in modulating competition between coinfecting pathogens. They found that 'host social interactions can hence modulate infection dynamics in coinfected group members, thereby altering pathogen communities at the host level and population level'. They make a concluding remark that in any group-living organism, the role of social interactions should be considered while making epidemiological models.

In the last section, I would like to present some unexpected citations I came across in my literature review. Alan Millard, a computer science graduate student (at the University of York), cited Cremer and Sixt 2009 in his PhD thesis on detecting faults in swarm robotics. He designed a system to detect faults in individual robots based on an artificial immune system. The system programs each robot to compare the 'behaviour' of each robot with the expected behaviour, and if there is a great discrepancy, eliminate the disparate individual. Brianna Beechler and her group (**Beechler et al. 2012**) studied the innate immunity of wild, free-ranging buffalos in South Africa. They cited Cremer and Sixt 2009 in the context of how the concepts of social immunity can be applied to group-living mammals. Bruce E. Wampold (**Wampold 2021**) recently examined healing in a social context and the role of the patient-clinician relationship in healing. Social healing is present in eusocial animals and appears to be well-developed in humans. Wampold theorizes the possible mechanisms for how the patient-clinician relationship can be therapeutic. Niccolo Caldararo cites Cremer and Sixt 2009 in his PhD thesis (with the Dept of Anthropology, SFSU) on the role of disease in the evolution of complex human society. Through the specific case study of the Black Plague in the 13th century in Europe and the AIDS epidemic in the US, he examines how humans' response to diseases and epidemics impacts the complex social structure. He also discusses how human behavioural changes, such as disease avoidance and hygienic behaviour, have influenced the course of the disease.

Social immunity provides an extra layer of protection that has likely furthered the evolution of group living and sociality in animals. It is an idea that compels us to see that we are all more similar to other animals than we are different. Similar to the shared genetic code at the molecular level and the concepts of population genetics, the comparison of organismal and superorganismal immunity at the physiological and behavioural level could act as a unifying concept that allows us to answer interesting questions in both individual and social domains, using our understanding in one to explore the implications of what we find in the other.

References

Listed in order of appearance in the report –

1) Wheeler, W.M. (1911), The ant-colony as an organism. J. Morphol., 22: 307-325. https://doi.org/10.1002/jmor.1050220206
2) Schmid-Hempel, Paul. *Parasites in Social Insects*. Princeton University Press, 1998.
3) Cremer, Sylvia, Sophie A. O. Armitage, and Paul Schmid-Hempel. "Social Immunity." *Current Biology* 17, no. 16 (August 21, 2007): R693–702. https://doi.org/10.1016/j.cub.2007.06.008.
4) Dimensions - Link to generate Fig. 2
5) Pull, Christopher D., and Dino P. McMahon. "Superorganism Immunity: A Major Transition in Immune System Evolution." *Frontiers in Ecology and Evolution* 8 (2020). https://doi.org/10.3389/fevo.2020.00186.
6) Pradeu, Thomas. *The limits of the self: immunology and biological identity*. Oxford University Press, 2011.
7) Pradeu, Thomas (2013) Immunity and the emergence of individuality. [Published Article or Volume] URL: http://philsci-archive.pitt.edu/id/eprint/10048 (accessed 2021-08-22).
8) Cotter, S.C., and R.M. Kilner. "Personal Immunity versus Social Immunity." *Behavioral Ecology* 21, no. 4 (July 1, 2010): 663–68. https://doi.org/10.1093/beheco/arq070.
9) López-Uribe, Margarita M., Warren B. Sconiers, Steven D. Frank, Robert R. Dunn, and David R. Tarpy. "Reduced Cellular Immune Response in Social Insect Lineages." *Biology Letters* 12, no. 3 (March 31, 2016): 20150984. https://doi.org/10.1098/rsbl.2015.0984.
10) Kennedy, P., G. Baron, Qiu Bitao, D. Freitak, H. Helanterä, Edmund R. Hunt, F. Manfredini, Thomas, Oshea-Wheller, S. Patalano, Christopher D Pull, Takao Sasaki, D. Taylor, C. Wyatt and S. Sumner. "A new dawn in social insect research: small solutions for big problems in biology." (2019).
11) Rueppell, O., M. K. Hayworth, and N. P. Ross. "Altruistic Self-Removal of Health-Compromised Honey Bee Workers from Their Hive." *Journal of Evolutionary Biology* 23, no. 7 (2010): 1538–46. https://doi.org/10.1111/j.1420-9101.2010.02022.x.
12) Pull, Christopher D, Line V Ugelvig, Florian Wiesenhofer, Anna V Grasse, Simon Tragust, Thomas Schmitt, Mark JF Brown, and Sylvia Cremer. "Destructive Disinfection of Infected Brood Prevents Systemic Disease Spread in Ant Colonies." Edited by Diethard Tautz. *ELife* 7 (January 9, 2018): e32073. https://doi.org/10.7554/eLife.32073
13) Van Meyel, Sophie, Maximilian Körner, and Joël Meunier. "Social Immunity: Why We Should Study Its Nature, Evolution and Functions across All Social Systems." *Current Opinion in Insect Science* 28 (August 2018): 1–7. https://doi.org/10.1016/j.cois.2018.03.004
14) Körner, Maximilian. "The role of social and individual pathogen defense in an insect with facultative family life: insights into the early evolution of group living." PhD diss., 2019.
15) Nuotclà, Jon A., Peter H. W. Biedermann, and Michael Taborsky. "Pathogen Defence Is a Potential Driver of Social Evolution in Ambrosia Beetles." *Proceedings of the Royal Society B: Biological Sciences* 286, no. 1917 (December 18, 2019): 20192332. https://doi.org/10.1098/rspb.2019.2332.
16) Biedermann, Peter Hw, and Marko Rohlfs. "Evolutionary Feedbacks between Insect Sociality and Microbial Management." *Current Opinion in Insect Science* 22 (August 2017): 92–100. https://doi.org/10.1016/j.cois.2017.06.003.
17) Evans, H. C. "Entomogenous Fungi in Tropical Forest Ecosystems: An Appraisal." *Ecological Entomology* 7, no. 1 (1982): 47–60. https://doi.org/10.1111/j.1365-2311.1982.tb00643.x.
18) Heine, Daniel, Neil A. Holmes, Sarah F. Worsley, Ana Carolina A. Santos, Tabitha M. Innocent, Kirstin Scherlach, Elaine H. Patrick, et al. "Chemical Warfare between Leafcutter Ant Symbionts and a Co-Evolved Pathogen." *Nature Communications* 9, no. 1 (June 7, 2018): 2208. https://doi.org/10.1038/s41467-018-04520-1
19) Fernández-Marín, Hermógenes, David R. Nash, Sarah Higginbotham, Catalina Estrada, Jelle S. van Zweden, Patrizia d'Ettorre, William T. Wcislo, and Jacobus J. Boomsma. "Functional Role of

Phenylacetic Acid from Metapleural Gland Secretions in Controlling Fungal Pathogens in Evolutionarily Derived Leaf-Cutting Ants." *Proceedings of the Royal Society B: Biological Sciences* 282, no. 1807 (May 22, 2015): 20150212. https://doi.org/10.1098/rspb.2015.0212
20) Yek, Sze H., Jacobus J. Boomsma, and Morten Schiøtt. "Differential Gene Expression in Acromyrmex Leaf-Cutting Ants after Challenges with Two Fungal Pathogens." *Molecular Ecology* 22, no. 8 (2013): 2173–87. https://doi.org/10.1111/mec.12255
21) Vung, Nguyen Ngoc, Yong Soo Choi, and Iksoo Kim. "High Resistance to Sacbrood Virus Disease in Apis Cerana (Hymenoptera: Apidae) Colonies Selected for Superior Brood Viability and Hygienic Behavior." *Apidologie* 51, no. 1 (February 2020): 61–74. https://doi.org/10.1007/s13592-019-00708-6.
22) Vung, Nguyen, Iksoo Kim, Man Lee, Hye Kim, Dong Kim, and Yong Choi. "Controlling Sacbrood Virus Disease in Apis Cerana Colonies with Biological Methods in Korea." *Journal of Apiculture* 33 (November 30, 2018): 283–95. https://doi.org/10.17519/apiculture.2018.11.33.4.283
23) Lanan, Michele Caroline, Pedro Augusto Pos Rodrigues, Al Agellon, Patricia Jansma, and Diana Esther Wheeler. "A Bacterial Filter Protects and Structures the Gut Microbiome of an Insect." *The ISME Journal* 10, no. 8 (August 2016): 1866–76. https://doi.org/10.1038/ismej.2015.264
24) Kaltenpoth, Martin, and Tobias Engl. "Defensive Microbial Symbionts in Hymenoptera." *Functional Ecology* 28, no. 2 (2014): 315–27. https://doi.org/10.1111/1365-2435.12089.
25) Woodhams, Douglas C., and Robert M. Brucker. "Disease Defence through Generations: Leaf-Cutter Ants and Their Symbiotic Bacteria." *Molecular Ecology* 22, no. 16 (2013): 4141–43. https://doi.org/10.1111/mec.12431.
26) Esparza-Mora, M. Alejandra, Hannah E. Davis, Stefania Meconcelli, Rudy Plarre, and Dino P. McMahon. "Inhibition of a Secreted Immune Molecule Interferes With Termite Social Immunity." *Frontiers in Ecology and Evolution* 8 (2020): 75. https://doi.org/10.3389/fevo.2020.00075.
27) Cremer, Sylvia. "Social Immunity in Insects." *Current Biology* 29, no. 11 (June 3, 2019): R458–63. https://doi.org/10.1016/j.cub.2019.03.035.
28) Milutinović, Barbara, Miriam Stock, Anna V. Grasse, Elisabeth Naderlinger, Christian Hilbe, and Sylvia Cremer. "Social Immunity Modulates Competition between Coinfecting Pathogens." *Ecology Letters* 23, no. 3 (2020): 565–74. https://doi.org/10.1111/ele.13458.
29) Millard, Alan Gregory. "Exogenous Fault Detectionin Swarm Robotic Systems," n.d., 224. Ph.D. diss. 2016
30) Beechler, Brianna R., Heather Broughton, Austin Bell, Vanessa O. Ezenwa, and Anna E. Jolles. "Innate Immunity in Free-Ranging African Buffalo (Syncerus Caffer): Associations with Parasite Infection and White Blood Cell Counts." *Physiological and Biochemical Zoology* 85, no. 3 (May 1, 2012): 255–64. https://doi.org/10.1086/665276.
31) Wampold, Bruce E. "Healing in a Social Context: The Importance of Clinician and Patient Relationship." *Frontiers in Pain Research* 2 (2021). https://doi.org/10.3389/fpain.2021.684768.
32) Caldararo, Niccolo. "Evolutionary Aspects of Disease Avoidance: The Role of Disease in the Development of Complex Society." *SSRN Electronic Journal*, February 7, 2012. https://doi.org/10.2139/ssrn.2001098.

Beyond

The difference in mind between man and the higher animals, great as it is, certainly is one of degree and not of kind.

– Charles Darwin

The female with "equal rights" never evolved; she was invented, and fought for consciously with intelligence, stubbornness, and courage.

– Sarah Blaffer Hrdy

These two thoughts (that I first came across in books I read over the summer) have been engraved in my mind and are sure to shape my thinking in the future. The same can be said of this reading and writing project with Dr. Gadagkar. It has helped me become a better writer, gain perspective, and it's sure to shape my thinking and work as a future scientist.

I have thoroughly enjoyed reading these amazing books and exploring in depth different aspects of animal behaviour and evolution. Perhaps it would have been helpful to augment this with more readings on current topics and ideas in animal behaviour, and learn about the more technical aspects of the field as well. Along with the focus on writing, the scope of the project could be broadened to include science communication in other forms, such as presentations or chalk talks.

Through the readings and writings, I have sampled from different topics, and even different taxa, in animal behaviour. In the future, the beyond, I would love to explore the growth of biological thought in animal behaviour – the interplay and exchange of ideas between the fields of evolution, ecology and animal behaviour through the last two centuries. It would be very interesting to trace the historical development of the field through the writings of prominent thinkers, anecdotes of specific studies, and interviews with scientists in the field.

In conclusion, I would like to thank Dr. Gadagkar for this wonderful opportunity. I look forward to working with him in the future.

Acknowledgements

I wouldn’t have reached this juncture without the help and support of several people. I’m grateful to my family, who patiently listened to all my ramblings about what I was reading; friends and colleagues who read my first drafts and gave their feedback; and the members of Gadagkar Lab, who welcomed me and made me feel like I was a part of the team. Finally, I would like to thank Dr. Raghavendra Gadagkar for his writings, which are a joy to read and led me to this project, and for the sustained, involved interactions over the summer.

Appendix

List of all the articles that have cited Cremer and Sixt (2009) –

1) Mohamed, Nancy. "Gc-Ms Analysis and Antimicrobial Effect of Ootheca of The Egyptian Pygmy Mantis, Miomantis Paykullii (Order: Mantodea)." *Egyptian Academic Journal of Biological Sciences. C, Physiology and Molecular Biology* 13, no. 1 (April 19, 2021): 123–32. https://doi.org/10.21608/eajbsc.2021.167837. [M]
   a) Fungi and bacteria can be successful environmental selection agents for the presence of parental eggs in insects since many animals develop their eggs in organic substrates or in the soil, where they are constantly in contact with spores, fungi, and mold. Costa (2006), Cremer and Sixt (2009), Trumbo (2012), and Reber and Chapuisat (2012) are just a few examples.

2) Wampold, Bruce E. "Healing in a Social Context: The Importance of Clinician and Patient Relationship." *Frontiers in Pain Research* 2 (2021). https://doi.org/10.3389/fpain.2021.684768. [S], [U], [Medicine]
   a) Honeybees utilize a "social fever" when an infection is present in the colony, induced by the bees fanning their wings, which raises the temperature of the hive.
   b) In social species, natural healing mechanisms at the organism level have social healing analogs, which evolved to promote group fitness: "At the interface between social and individual immunity, several findings indicate that a strong social defense may replace to a certain extent the need for a sophisticated individual immune system"

3) Maák, István, Eszter Tóth, Magdalena Lenda, Gábor Lőrinczi, Anett Kiss, Orsolya Juhász, Wojciech Czechowski, and Attila Torma. "Behaviours Indicating Cannibalistic Necrophagy in Ants Are Modulated by the Perception of Pathogen Infection Level." *Scientific Reports* 10, no. 1 (October 21, 2020): 17906. https://doi.org/10.1038/s41598-020-74870-8. [M], [Ants]
   a) However, even if handling infected individuals could increase the risk of horizontal transmission, low-level infections acquired through contact with an infected nestmate may even boost the individual immunity system.
   b) This may be one of the reasons why the workers transported many of the corpses representing lower infection threat (contaminated with spores and hyphae) to the nests, where they were probably consumed. During consumption, these sources of pathogens can actively immunize the workers, which can achieve higher protection and survival.
   c) However, even if handling infected individuals could increase the risk of horizontal transmission, low-level infections acquired through contact with an infected nestmate may even boost the individual immunity system.

4) Spivak, Marla, and Robert G. Danka. "Perspectives on Hygienic Behavior in Apis Mellifera and Other Social Insects." *Apidologie* 52, no. 1 (February 1, 2021): 1–16. https://doi.org/10.1007/s13592-020-00784-z. [M], [Bees]
   a) Workers that destructively eliminate already infected or infested individuals protect the colony, or superorganism, in a similar way to immune cells that protect an organism from pathogen spread throughout the body.

5) Phillips, Zachary I. "Emigrating Together but Not Establishing Together: A Cockroach Rides Ants and Leaves." *The American Naturalist* 197, no. 1 (January 1, 2021): 138–45. https://doi.org/10.1086/711876. [M], [Ants]
   a) Host development can have a profound effect on transmission. If this general relationship extends to the scale of the superorganism (i.e., coevolved society of individuals), we can expect host colony development to influence the between-colony transmission of symbionts.

6) **Pull, Christopher D., and Dino P. McMahon. "Superorganism Immunity: A Major Transition in Immune System Evolution." *Frontiers in Ecology and Evolution* 8 (2020). https://doi.org/10.3389/fevo.2020.00186. [S], [T], [Individuality vs Sociality], [Evolution]
   a) Later, Cremer and Sixt (2009) took the immunity analogy further, pointing out the many ways in which social immunity in superorganisms plays a functionally equivalent role to metazoan immunity.
   b) Although originally considered in early examinations of colony-level immune systems, the role of immune policing and the immunological delineation of the individual have been largely neglected in recent discussions of social immune systems, which is likely due to a research focus on microbial pathogens.
   c) Germline parasites that hijack host reproduction are not, as far we are aware, known in metazoan organisms, but exist in colonial organisms.
   d) Given their strong, evolutionary convergences, organismal and superorganismal immune system evolution likely followed similar patterns.

7) Goes, Aryel C., Mariana O. Barcoto, Pepijn W. Kooij, Odair C. Bueno, and Andre Rodrigues. "How Do Leaf-Cutting Ants Recognize Antagonistic Microbes in Their Fungal Crops?" *Frontiers in Ecology and Evolution* 8 (2020). https://doi.org/10.3389/fevo.2020.00095. [M], [Ants], [Fungi]
   a) In this context, group members collaborate to avoid, control, or eliminate pathogens, thus acting as parts of an immune system.

8) Vung, Nguyen Ngoc, Yong Soo Choi, and Iksoo Kim. "High Resistance to Sacbrood Virus Disease in Apis Cerana (Hymenoptera: Apidae) Colonies Selected for Superior Brood Viability and Hygienic Behavior." *Apidologie* 51, no. 1 (February 2020): 61–74. https://doi.org/10.1007/s13592-019-00708-6. [M], [Bees]
   a) Among the social immunity of honey bees, the hygienic behavior, which may exist in all eusocial insects, plays an important role in the reduction of the loads and transmission rates of pathogens in colonies.

9) Zhao, Xingying, Long Liu, Wei Zhou, Qing Cai, and Qiuying Huang. "Roles of Selenoprotein T and Transglutaminase in Active Immunization against Entomopathogenic Fungi in the Termite Reticulitermes Chinensis." *Journal of Insect Physiology* 125 (August 2020): 104085. https://doi.org/10.1016/j.jinsphys.2020.104085. [M], [Fungi], [Termites]
   a) Due to the ubiquity of epidemics, social insects have developed sophisticated disease defenses at both individual and colony levels.

10) Dziechciarz, P., Borsuk, G., and Olszewski, K. "Prospects and Validity of Laboratory Cage Tests Conducted in Honeybee Research Part Two: New Possibilities for Use of Laboratory Cage Tests in Response to Challenges Revealed at the Turn of the 20 and 21 Centuries." *Journal of Apicultural Science* 64, no. 1 (July 2, 2020): 5–13. https://doi.org/10.2478/jas-2020-0002. [M], [Bees]
   a) Bees can be infected with pathogens when taking or sharing infected food.

11) Liu, Long, Xing-Ying Zhao, Qing-Bo Tang, Chao-Liang Lei, and Qiu-Ying Huang. "The Mechanisms of Social Immunity Against Fungal Infections in Eusocial Insects." *Toxins* 11, no. 5 (May 2019): 244. https://doi.org/10.3390/toxins11050244. [S], [Fungi]
   a) In addition to the infection at the level of individuals, a similar phenomenon also occurs at the level of colonies in social insect societies. Social insects in their colony are similar to cells in a body, communicate with each other and collectively work as a superorganism.
   b) Similarly, when the social insects' colonies like superorganisms are infected, their 'social immune systems' are activated. Societal members perform the defensive functions as the body cells do, including pathogen recognition, chemical communication, killing pathogens by burial ('social encapsulation') and/or antifungal secretions (similar to humoral immunity) and active social exclusion ('social apoptosis').
   c) Lastly, both solitary and social insects take a special care of their high value cells or individuals, germ lines or queens, to prevent pathogen infections.

12) Bos, Nick, Viljami Kankaanpää-Kukkonen, Dalial Freitak, Dimitri Stucki, and Liselotte Sundström. "Comparison of Twelve Ant Species and Their Susceptibility to Fungal Infection." *Insects* 10, no. 9 (September 2019): 271. https://doi.org/10.3390/insects10090271. [M], [Ants]
   a) To cope with the challenges an increased pathogen pressure poses, ants employ a variety of strategies to prevent infections from becoming established. These range from individual behavioral and physiological responses, to collective behaviors that convey disease control, referred to as "social immunity".

13) Nuotclà, Jon A., Peter H. W. Biedermann, and Michael Taborsky. "Pathogen Defence Is a Potential Driver of Social Evolution in Ambrosia Beetles." *Proceedings of the Royal Society B: Biological Sciences* 286, no. 1917 (December 18, 2019): 20192332. https://doi.org/10.1098/rspb.2019.2332. [M], [Evolution], [Beetle]
   a) This idea relates to the concept of superorganismality, where a whole nest of social insects is regarded as a single reproducing entity (the 'super organism'). Groups of nest members take on specialized roles, which corresponds to the differentiated cell tissues of a multicellular organism.

14) Cappa, Federico, Iacopo Petrocelli, Francesca Romana Dani, Leonardo Dapporto, Michele Giovannini, Jeferson Silva-Castellari, Stefano Turillazzi, and Rita Cervo. "Natural Biocide Disrupts Nestmate Recognition in Honeybees." *Scientific Reports* 9, no. 1 (February 28, 2019): 3171. https://doi.org/10.1038/s41598-019-38963-3. [M], [Bees], [Perception]
   a) Social insects have evolved a number of behavioural adaptations to restrict the diffusion of diseases inside the colony, which go under the name of social immunity.

15) Garrido, Claudia, and Antonio Nanetti. "Welfare of Managed Honey Bees." In *The Welfare of Invertebrate Animals*, edited by Claudio Carere and Jennifer Mather, 69–104. Animal Welfare. Cham: Springer International Publishing, 2019. https://doi.org/10.1007/978-3-030-13947-6_4. [M], [Bees], [Perception]

a) A superorganism represents a reproductive, self-organised unit: reproductive animals (queens and drones) and workers depend on each other. Queens and drones monopolise reproduction, while the workers' tasks are brood care, defence and foraging.
b) The social structure of honey bee colonies adds a level of complexity to the response against parasites. As a superorganism, the colony as a whole has mechanisms to fight diseases, usually referred to as "social immunity"; using immunity in the general sense of combat parasites.
c) This means that in addition to physiological, individual responses (e.g. humoral responses, wound healing, etc.), the workers cooperate to exclude or fight diseases in the colony. These mechanisms have been paralleled with those of long-lived vertebrates and can be considered at three levels: 1) Border defences, 2) Soma defences, 3) Germ line defences.
d) Honey bee colonies can discriminate between self and non-self, which is based on the "colony odour".

16) Pérez-Lachaud, Gabriela, Franklin H. Rocha, Javier Valle-Mora, Yann Hénaut, and Jean-Paul Lachaud. "Fine-Tuned Intruder Discrimination Favors Ant Parasitoidism." *PLOS ONE* 14, no. 1 (January 17, 2019): e0210739. https://doi.org/10.1371/journal.pone.0210739. [M], [Ants], [Perception]

a) Despite the aggressive behavior and sophisticated defense strategies of most ant species, many organisms (termed in general myrmecophiles) have managed to deal with ant aggressiveness and bypass their defense strategies. In response, ants have evolved a suite of physiological, immunological and behavioral defensive responses to counter exploitation by micro- and macro-parasites both at the individual and the colony level.

17) Fouks, Bertrand, Emily G Robb, and H Michael G Lattorff. "Role of Conspecifics and Personal Experience on Behavioral Avoidance of Contaminated Flowers by Bumblebees." *Current Zoology* 65, no. 4 (August 1, 2019): 447–55. https://doi.org/10.1093/cz/zoy099. [M], [Bees], [Perception]

a) Colony life can, therefore, prove advantageous as it provides the unique opportunity for group-level defenses (social immunity), with each individual member of the colony collaborating to reduce the transmission of parasites within their colony.

18) Silva, Luiza Helena Bueno da, Ives Haifig, and Ana Maria Costa-Leonardo. "Facing Death: How Does the Subterranean Termite Coptotermes Gestroi (Isoptera: Rhinotermitidae) Deal with Corpses?" *Zoology* 137 (December 1, 2019): 125712. https://doi.org/10.1016/j.zool.2019.125712. [M], [Termites]

a) The colonies of social insects have adaptations to reduce the impact of infectious diseases and increase their fitness. Moreover, in social colonies, selection acts in the individual and social levels and shaped parallel evolutionary solutions in immune responses.

19) Kashyap, Dipti, Harshita Pandey, Kamal Jaiswal, and Suman Mishra. "Fungal Diseases of Honey Bees: Current Status and Future Perspective." In *Recent Developments in Fungal Diseases of Laboratory Animals*, edited by Arti Gupta and Nagendra Pratap Singh, 7–27. Fungal Biology. Cham: Springer International Publishing, 2019. https://doi.org/10.1007/978-3-030-18586-2_2. [M], [Bees], [Fungi]

a) Apart from individual immunity, social immunity also plays an important role, such as colony-level pathogen protection; thus, cooperative behavior helps reduce the parasitic load.

20) Hroncova, Zuzana, Jiri Killer, Josef Hakl, Dalibor Titera, and Jaroslav Havlik. "In-Hive Variation of the Gut Microbial Composition of Honey Bee Larvae and Pupae from the Same Oviposition Time." *BMC Microbiology* 19, no. 1 (May 24, 2019): 110. https://doi.org/10.1186/s12866-019-1490-y. [M], [Bees], [Microbiome]
  a) As suggested by Cremer et al., foods could be enriched with regard to specific non-pathogenic potentially probiotic microbes, which can inhibit pathogen growth.

21) "Prospects and Validity of Laboratory Cage Tests Conducted in Honeybee Research Part Two: New Possibilities for Use of Laboratory Cage Tests in Response to Challenges Revealed at the Turn of the 20th and 21st Centuries - ProQuest." Accessed June 30, 2021. https://www.proquest.com/openview/1cfa9b5304ba2c9253b74bec411219fa/1?pq-origsite=gscholar&cbl=2026566. [M], [Bees]
  a) Bees can be infected with pathogens when taking or sharing infected food.

22) Körner, Maximilian. "The role of social and individual pathogen defense in an insect with facultative family life: insights into the early evolution of group living." PhD diss., 2019. [C], [U], [Evolution], [Individuality vs Sociality]
  a) Since the coining of the term of social immunity over ten years ago (Cremer et al., 2007), a major proportion of the work investigating the phenomenon has been targeting its occurrence and mechanisms in eusocial insects.
  b) The many insights into social immunity in a eusocial context have greatly advanced our understanding on how these complex structures evolve and are maintained.
  c) The discovery of social immunity rapidly led to major advances in our understanding of why and how eusocial insects are efficiently protected against pathogens.
  d) The central idea of this[eusocial] framework is that social immunity mimics the individual immunity of multicellular organisms when the unit of selection has shifted from the individual to the colony.

23) Casillas Perez, Barbara E. "Collective defenses of garden ants against a fungal pathogen." PhD diss., 2019. [M], [Ants]
  a) In vertebrates, there are cells specialized in patrolling, detecting threats and recruiting a larger cellular response. Besides this, individual cells can signal their own status. Similarly social insects are known to patrol and detect threats.

24) *Kennedy, P., G. Baron, Qiu Bitao, D. Freitak, H. Helanterä, Edmund R. Hunt, F. Manfredini, Thomas, Oshea-Wheller, S. Patalano, Christopher D Pull, Takao Sasaki, D. Taylor, C. Wyatt and S. Sumner. "A new dawn in social insect research: small solutions for big problems in biology." (2019). [S], [T]

a) It [social immunity] is thereby analogous to the physiological immune system of multicellular organisms, and could provide insights into the evolution of immune defences across these domains.

25) *Cremer, Sylvia, Christopher D. Pull, and Matthias A. Fürst. "Social Immunity: Emergence and Evolution of Colony-Level Disease Protection." *Annual Review of Entomology* 63, no. 1 (2018): 105–23. https://doi.org/10.1146/annurev-ento-020117-043110. [S], [T], [Evolution]
   a) In 2009, Cremer & Sixt conceptualized the remarkable number of similarities between social immunity and the organismal immunity of a multicellular body, arguing that, in effect, social immunity functions as the immune system of the colony.

26) Boomsma, Jacobus J., and Richard Gawne. "Superorganismality and Caste Differentiation as Points of No Return: How the Major Evolutionary Transitions Were Lost in Translation." *Biological Reviews* 93, no. 1 (2018): 28–54. https://doi.org/10.1111/brv.12330. [M], [Evolution], [Individuality vs Sociality]
   a) The following offers a reasonable summary [of examples of superorganismal colony-level adaptations]: (*i*) honeybee dance language for efficient foraging, (*ii*) nest-building and foraging routines, including the complex communication mechanisms involved, (*iii*) thermoregulation and other forms of active nest environment control, (*iv*) additional morphological differentiation of helpers when evolutionarily derived soldier castes or additional nursing castes evolve, and (*v*) social immunity strategies.

27) *Pull, Christopher D, Line V Ugelvig, Florian Wiesenhofer, Anna V Grasse, Simon Tragust, Thomas Schmitt, Mark JF Brown, and Sylvia Cremer. "Destructive Disinfection of Infected Brood Prevents Systemic Disease Spread in Ant Colonies." Edited by Diethard Tautz. *ELife* 7 (January 9, 2018): e32073. https://doi.org/10.7554/eLife.32073. [S], [T], [Perception], [Ants]
   a) These defences are performed collectively by the workers to form an emergent layer of protection known as social immunity that, like the immune system of a body, protects the colony from invading pathogens.
   b) Hence, social immunity is characterised by a care-kill dichotomy, where colony members should be cared for when possible but sacrificed if necessary, both of which benefit the colony.
   c) Whilst the role of ant poison as a topical disinfectant by ants and other animals (i.e. 'anting' behaviour in birds) is well characterised, its use as an internal disinfectant within the body of others during destructive disinfection is a novel and a rare example of the kill-component of social immunity.
   d) Eliminating infected kin to protect the rest of the group, observed in termites and honeybees as well, requires an unconditional level of altruism that is expected to be absent or at least rare in other forms of sociality (e.g. aggregations, non-superorganismal family groups and communal breeders, but has parallels to the immune system of the metazoan body.
   e) Both the immune system and social immunity have first lines of defences that reduce the risk of infection: pathogens that enter the body are met with mechanical and chemical defences, such as ciliated cells in the lung that move pathogens trapped in mucus out of the body, and in ants, sanitary care plays an analogous role.
   f) Since the loss of both somatic cells and individual insect workers can be tolerated with negligible effects on fitness, these convergent strategies have likely evolved at both the multicellular and superorganismal levels of biological organisation, as an effective way to clear infections and avoid any further damage to the body and colony, respectively.

g) This [need to remove infected individuals] seems to be a general principle in disease defence, as cells are also rapidly detected and destroyed shortly after infection to prevent pathogen spread in multicellular organisms.
h) Studying the similarities and differences between organismal immunity and social immunity could therefore potentially lead to new insights about how disease defences evolve.
i) In contrast, the results of our study suggest that equivalent selection pressures during the major evolutionary transitions from unicellularity to multicellularity in the metazoans, and from sociality to superorganismality in the social insects, have resulted in convergent defences that protect multicellular organisms and superorganismal insect societies from systemic disease spread, by ensuring the survival of the whole over its parts.

28) Heine, Daniel, Neil A. Holmes, Sarah F. Worsley, Ana Carolina A. Santos, Tabitha M. Innocent, Kirstin Scherlach, Elaine H. Patrick, et al. "Chemical Warfare between Leafcutter Ant Symbionts and a Co-Evolved Pathogen." *Nature Communications* 9, no. 1 (June 7, 2018): 2208. https://doi.org/10.1038/s41467-018-04520-1. [M], [Fungi], [Ants], [Evolution]
    a) Ant colonies have nested levels of immune defense encompassing a lower level (individual ants) and a higher collective level that is usually referred to as social immunity.

29) *Van Meyel, Sophie, Maximilian Körner, and Joël Meunier. "Social Immunity: Why We Should Study Its Nature, Evolution and Functions across All Social Systems." *Current Opinion in Insect Science* 28 (August 2018): 1–7. https://doi.org/10.1016/j.cois.2018.03.004. [C], [T], [Evolution]
    a) The discovery of social immunity rapidly led to major advances in our understanding of why and how eusocial insects are efficiently protected against pathogens.
    b) The central idea of this framework is that social immunity mimics the individual immunity of multicellular organisms when the unit of selection has shifted from the individual to the colony.

30) Biganski, Sarah, Christoph Kurze, Matthias Y. Müller, and Robin F. A. Moritz. "Social Response of Healthy Honeybees towards Nosema Ceranae-Infected Workers: Care or Kill?" *Apidologie* 49, no. 3 (June 1, 2018): 325–34. https://doi.org/10.1007/s13592-017-0557-8. [M], [Bees]
    a) Social immunity is characterised by a low benefit for the individual bee but an increased fitness advantage for the entire colony.

31) Ravaiano, Samira Veiga, Wagner Faria Barbosa, Lúcio Antônio Campos, and Gustavo Ferreira Martins. "Variations in Circulating Hemocytes Are Affected by Age and Caste in the Stingless Bee Melipona Quadrifasciata." *The Science of Nature* 105, no. 7 (July 19, 2018): 48. https://doi.org/10.1007/s00114-018-1573-x. [M], [Bees]
    a) In addition, social immunity may acts as an important barrier to infections, similar to that observed in other superorganisms.

32) Straus, Samantha, and Leticia Avilés. "Effects of Host Colony Size and Hygiene Behaviours on Social Spider Kleptoparasite Loads along an Elevation Gradient." *Functional Ecology* 32, no. 12 (2018): 2707–16. https://doi.org/10.1111/1365-2435.13225. [M], [Spider]

a) This type of colony organization has been referred to as a “superorganism", with parallels drawn between colony-level immunity and the individual-level immunity of multicellular organisms.

33) Aanen, Duur K. “Social Immunity: The Disposable Individual.” *Current Biology* 28, no. 7 (April 2, 2018): R322–24. https://doi.org/10.1016/j.cub.2018.02.050. [M]
   a) Like the vertebrate immune system, the social immune system of the colony is comprised of various layers of defence.

34) Smith, Dylan. "Effects of pesticide exposure on the morphological development of the bee brain and the consequences for learning performance." PhD diss. (2018). [M], [Bees], [Cognition]
   a) Eusociality has also been suggested to buffer against parasite infection, a term known as social immunity (group-level, behavioural immune responses), through behaviours such as allogrooming of infected individuals.

35) Kennedy, Patrick, Gemma Baron, Bitao Qiu, Dalial Freitak, Heikki Helanterä, Edmund R. Hunt, Fabio Manfredini, et al. “Deconstructing Superorganisms and Societies to Address Big Questions in Biology.” *Trends in Ecology & Evolution* 32, no. 11 (November 2017): 861–72. https://doi.org/10.1016/j.tree.2017.08.004. [S], [T]
   a) It [social immunity] is thereby analogous to the physiological immune system of multicellular organisms, and could provide insights into the evolution of immune defences across these domains.

36) Simone-Finstrom, Michael. “Social Immunity and the Superorganism: Behavioral Defenses Protecting Honey Bee Colonies from Pathogens and Parasites.” *Bee World* 94, no. 1 (January 2, 2017): 21–29. https://doi.org/10.1080/0005772X.2017.1307800. [S], [Bees]
   a) Analogies can be made between mechanisms of individual and social immune defense, which also sheds light on the superorganism concept.
   b) Due to the connections between individual, physiological immunity and colony-level social immune mechanisms, common terminology for how these traits are expressed is also being adopted.

37) Boomsma, Jacobus J. “Forum The Global Ant Genomics Alliance (GAGA),” n.d., 7. [M], [Ants]
   a) Over more than 100 million years of history, the ants have been impressive social innovators. They evolved advanced division of labor; assembly line processing of food resources; mass-raiding predatory columns; seed-harvesting and storage; sophisticated chemical, acoustic and visual communication systems; fungus-farming for food; herding aphids as livestock for meat and honeydew; practicing biological and chemical pest control; and social immune systems akin to efficient public health systems.

38) Gómez-Moracho, Tamara, Philipp Heeb, and Mathieu Lihoreau. "Effects of Parasites and Pathogens on Bee Cognition." *Ecological Entomology* 42, no. S1 (2017): 51–64. https://doi.org/10.1111/een.12434. [M], [Bees], [Cognition]
   a) In recent years, there has been growing evidence that parasites and pathogens also affect the behaviour of insects, either through a negative impact on their neural system and cognitive abilities, or as a response to reduce further risks of contamination.

39) Vung, Nguyen, Iksoo Kim, Man Lee, Hye Kim, Dong Kim, and Yong Choi. "Controlling Sacbrood Virus Disease in Apis Cerana Colonies with Biological Methods in Korea." *Journal of Apiculture* 33 (November 30, 2018): 283–95. https://doi.org/10.17519/apiculture.2018.11.33.4.283. [M], [Bees], [Medicine]
   a) As social insects, honeybees have evolved novel physiological, behavioral and organizational adaptations as individual and social immunity to combat diseases.

40) Harpur, Brock Alexander. "Population Genomic Approaches to Understanding the Genetics and Evolution of Social Insects," PhD diss., April 10, 2017. https://yorkspace.library.yorku.ca/xmlui/handle/10315/33586. [M], [Evolution], [Genetics]
   a) Social organisms can combat pathogens through individual innate immune responses or through social behaviours that limit transmission within groups — called social immunity.

41) Quevillon, Lauren E. *The Ecology, Epidemiology, and Evolution of Parasites Infecting Ants (Hymenoptera: Formicidae)*. PhD diss., The Pennsylvania State University, 2018. [S], [Ants], [Evolution]
   a) The social and spatial segregation of workers most susceptible to encountering infectious agents is often cited as a mechanism of disease prophylaxis in social insect colonies.
   b) Static social network analyses complement these findings; in addition to engaging in more trophallaxis events (higher degree), foragers (active and inactive) exchange food with a greater number of unique individuals (Table D.3), indicating that their contact redundancy is lower than theory would predict.

42) Pull, Christopher. "Disease defence in garden ants." PhD diss., Institute of Science and Technology Austria, Klosterneuburg, Austria, 2017. [M], [Ants]
   a) In 2009, Cremer and Sixt conceptualized the remarkable number of similarities between social immunity and the organismal immunity of a multicellular body, arguing that, in effect, social immunity functions as the immune system of the colony.

43) Lanan, Michele Caroline, Pedro Augusto Pos Rodrigues, Al Agellon, Patricia Jansma, and Diana Esther Wheeler. "A Bacterial Filter Protects and Structures the Gut Microbiome of an Insect." *The ISME Journal* 10, no. 8 (August 2016): 1866–76. https://doi.org/10.1038/ismej.2015.264. [M], [Microbiome], [Bacteria]
   a) In general, the composition of gut microbiomes is known to be structured through diet, gut physiology and compartmentalization, avoidance of parasites through hygienic behavior, physical barriers (for example, peritrophic matrix (Hegedus et al., 2009)) and innate immune systems.

44) Pradeu, Thomas. “Organisms or Biological Individuals? Combining Physiological and Evolutionary Individuality.” *Biology & Philosophy* 31, no. 6 (November 1, 2016): 797–817. https://doi.org/10.1007/s10539-016-9551-1. [M], [U], [Individuality vs Sociality], [Evolution]

a) Other examples include the immunological delineation in social insects where, sometimes, the immunological unit is the “superorganism”.

45) *López-Uribe, Margarita M., Warren B. Sconiers, Steven D. Frank, Robert R. Dunn, and David R. Tarpy. “Reduced Cellular Immune Response in Social Insect Lineages.” *Biology Letters* 12, no. 3 (March 31, 2016): 20150984. https://doi.org/10.1098/rsbl.2015.0984. [S], [Individuality vs Sociality]

a) Insect societies also confront and respond to strong selective pressures from diseases, worsened by the high genetic relatedness among nest-mates that enables pathogens and parasites to easily sweep through a host insect colony.

46) Leclerc, Jean-Baptiste, and Claire Detrain. “Ants Detect but Do Not Discriminate Diseased Workers within Their Nest.” *The Science of Nature* 103, no. 7 (July 30, 2016): 70. https://doi.org/10.1007/s00114-016-1394-8. [M], [Ants], [Perception]

a) This spontaneous isolation that was also found in fungus-infected *Temnothorax* ants, *Camponotus aethiops* as well as in honey bees *A. mellifera* appears as a simple way for the infected individual to increase its inclusive fitness, by minimizing contacts with related individuals and by preventing the pathogen to potentially devastate the colony.

47) Otani, Saria, Nick Bos, and Sze H. Yek. “Transitional Complexity of Social Insect Immunity.” *Frontiers in Ecology and Evolution* 4 (2016). https://doi.org/10.3389/fevo.2016.00069. [M], [Evolution]

a) The distinction and manifestation of personal and social immunity had been reviewed extensively elsewhere.

48) Millard, Alan. "Exogenous fault detection in swarm robotic systems." PhD diss., University of York, 2016. [M], [U], [Robotics]

a) For example, in social insect colonies, odour likely plays an important role in the detection of parasitic infections, for which there is no direct artificial analogue.

49) Eguaras, Martín J. “Effect of Propolis Oral Intake on Physiological Condition of Young Worker Honey Bees, Apis Mellifera L.” *Journal of Apicultural Science* 61, no. 2 (December 12, 2017): 193–202. https://doi.org/10.1515/jas-2017-0023. [M], [Bees]

a) When hundreds of individuals interact, the response at a colony level has analogous properties to the complex humoral and cellular immune systems.

50) Gallagher, Joe Dominic. "Gregarious immunisation in the mealworm beetle, Tenebrio molitor." PhD diss., University of Sheffield, 2016. [M], [Beetle], [Evolution]
   a) Kin selection is likely to be a stronger selective force in highly related populations, favouring group-level defences that reduce the risk of pathogenesis for all members of the group and should yield high inclusive fitness benefits. This has likely allowed for the evolution of complex 'social' immune defences in the eusocial insects, such as self-grooming, allogrooming and antimicrobial secretion.

51) Quevillon, Lauren E., Ephraim M. Hanks, Shweta Bansal, and David P. Hughes. "Social, Spatial and Temporal Organization in a Complex Insect Society." *Scientific Reports* 5, no. 1 (August 24, 2015): 13393. https://doi.org/10.1038/srep13393. [S], [Ants]
   a) The social and spatial segregation of workers most susceptible to encountering infectious agents is often cited as a mechanism of disease prophylaxis in social insect colonies.
   b) Static social network analyses complement these findings; in addition to engaging in more trophallaxis events (higher degree), foragers (active and inactive) exchange food with a greater number of unique individuals (SI Table 2), indicating that their contact redundancy is lower than theory would predict

52) Liu, Long, Ganghua Li, Pengdong Sun, Chaoliang Lei, and Qiuying Huang. "Experimental Verification and Molecular Basis of Active Immunization against Fungal Pathogens in Termites." *Scientific Reports* 5, no. 1 (October 13, 2015): 15106. https://doi.org/10.1038/srep15106. [M], [Termites], [Fungi]
   a) At the colony level, social insects employ behavioural and social immunity to defend against pathogens, including allogrooming, trophallaxis, isolation and cannibalism.
   b) Long-lived insect societies generally face high risks from the same pathogens during their lifespan and could thus benefit from the long-lasting protection of active immunization against pathogens rather than the temporary protection of passive immunization.

53) Fernández-Marín, Hermógenes, David R. Nash, Sarah Higginbotham, Catalina Estrada, Jelle S. van Zweden, Patrizia d'Ettorre, William T. Wcislo, and Jacobus J. Boomsma. "Functional Role of Phenylacetic Acid from Metapleural Gland Secretions in Controlling Fungal Pathogens in Evolutionarily Derived Leaf-Cutting Ants." *Proceedings of the Royal Society B: Biological Sciences* 282, no. 1807 (May 22, 2015): 20150212. https://doi.org/10.1098/rspb.2015.0212. [M], [Ants], [Fungi]
   a) Larger social groups tend to have higher burdens of disease, requiring compensatory measures for prophylaxis and control.

54) Pérez-Lachaud, Gabriela, Juan Carlos Bartolo-Reyes, Claudia M. Quiroa-Montalván, Leopoldo Cruz-López, Alain Lenoir, and Jean-Paul Lachaud. "How to Escape from the Host Nest: Imperfect Chemical Mimicry in Eucharitid Parasitoids and Exploitation of the Ants' Hygienic Behavior." *Journal of Insect Physiology* 75 (April 2015): 63–72. https://doi.org/10.1016/j.jinsphys.2015.03.003. [M], [U], [Ants]
   a) Social insects have evolved a suite of physiological, immunological and behavioral defensive responses to counter exploitation by micro- and macro-parasites both at the individual and the colony level.

55) Appler, R. Holden, Steven D. Frank, and David R. Tarpy. “Within-Colony Variation in the Immunocompetency of Managed and Feral Honey Bees (Apis Mellifera L.) in Different Urban Landscapes.” *Insects* 6, no. 4 (December 2015): 912–25. https://doi.org/10.3390/insects6040912. [M], [Bees]

a) While group living has been highly successful ecologically, it also introduces certain costs that can challenge insect societies. Perhaps most notably is the increased likelihood of harboring and enabling the spread of disease-causing agents, placing a premium on different mechanisms of physiological immunity (at the individual level) and “social immunity” (at the colony level).

56) **Caldararo, Niccolo. "Social behavior and the superorganism: Implications for disease and stability in complex animal societies and Colony Collapse Disorder in Honeybees." *Interdisciplinary Description of Complex Systems: INDECS* 13, no. 1 (2015): 82-98. [S], [U], [Bees]

a) This is particularly interesting in the context of Cremer & Sixt review of the analogies in the evolution of individual and social immunity. A successful response to infection requires identification of pathogen and an appropriate response at both the level of the individual in a biological immune response and a socially defensive behavioural response.

57) Ulrich, Yuko, and Paul Schmid-Hempel. “The Distribution of Parasite Strains among Hosts Affects Disease Spread in a Social Insect.” *Infection, Genetics and Evolution* 32 (June 2015): 348–53. https://doi.org/10.1016/j.meegid.2015.04.002. [M]

a) Social insect colonies are also interesting entities for the study of host-parasite interactions in general, because they are highly integrated and function to a large extent as a single organism when it comes to anti-parasitic defenses.

58) Powell, J. Elijah, Vincent G. Martinson, Katherine Urban-Mead, and Nancy A. Moran. “Routes of Acquisition of the Gut Microbiota of the Honey Bee Apis Mellifera.” *Applied and Environmental Microbiology* 80, no. 23 (December 1, 2014): 7378–87. https://doi.org/10.1128/AEM.01861-14. [S], [Bees], [Microbiome]

a) Thus, exposure to nurses appears to limit bacterial numbers in the gut, potentially indicating social immunity.

59) Kaltenpoth, Martin, and Tobias Engl. “Defensive Microbial Symbionts in Hymenoptera.” *Functional Ecology* 28, no. 2 (2014): 315–27. https://doi.org/10.1111/1365-2435.12089. [M], [Microbiome], [Bees], [Ants], [Bacteria]

a) As social insects live in large colonies that facilitate the transmission of pathogens and thereby increase susceptibility to infections, many social taxa have evolved specialized mechanisms to prevent pathogens from spreading within their colonies, which are collectively referred to as ‘social immunity’. Hygienic behaviours, like allogrooming, control of individuals entering the nest, separating groups with different tasks and infection risks, and waste control reduce the risk of pathogen infestation in the colony.
b) In addition to the gut of a single bee, the entire hive can be a source of symbionts providing resistance or defence.

60) Boos, Stefan, Joël Meunier, Samuel Pichon, and Mathias Kölliker. “Maternal Care Provides Antifungal Protection to Eggs in the European Earwig.” *Behavioral Ecology* 25, no. 4 (July 1, 2014): 754–61. https://doi.org/10.1093/beheco/aru046. [M], [Fungi]
   a) Fungi and bacteria may be key ecological agents of selection for parental egg attendance in insects, as many species raise their clutch of eggs on organic substrates or in burrows/tunnels in the soil where they are continuously in contact with bacteria, fungi, and mold.
   b) Across animal species and taxa, a broad variety of mechanisms are known to help individuals limit their risks of infection by parasites and microbial pathogens. These mechanisms include parasite avoidance, self-grooming, or specific and nonspecific immunological responses.

61) Nicodemo, Daniel, Euclides Braga Malheiros, David De Jong, and Regina Helena Nogueira Couto. “Increased Brood Viability and Longer Lifespan of Honeybees Selected for Propolis Production.” *Apidologie* 45, no. 2 (March 2014): 269–75. https://doi.org/10.1007/s13592-013-0249-y. [M], [Bees]
   a) [M, i] Simone-Finstrom and Spivak (2010) reported that social immunity is a promising area of study in social insect biology. Among the behaviors controlled by colony needs, resin collection and production of propolis, which have antimicrobial properties, reduce microbe levels in the honeybee colony and may help in disease resistance.

62) Leonhardt, Sara D., and Martin Kaltenpoth. “Microbial Communities of Three Sympatric Australian Stingless Bee Species.” *PLOS ONE* 9, no. 8 (August 22, 2014): e105718. https://doi.org/10.1371/journal.pone.0105718. [M], [Microbiome], [Bees]
   a) In this context, the microbial community associated with social bees has received considerable attention, and previous studies found a consistent core microbiota across honeybees and bumblebees. While some of these symbiotic microbes have been hypothesized to aid in nutrient acquisition, others play an important role for the social immunity of bee colonies.

63) Stürup, M., B. Baer, and J. J. Boomsma. “Short Independent Lives and Selection for Maximal Sperm Survival Make Investment in Immune Defences Unprofitable for Leaf-Cutting Ant Males.” *Behavioral Ecology and Sociobiology* 68, no. 6 (June 1, 2014): 947–55. https://doi.org/10.1007/s00265-014-1707-x. [S], [Ants], [Evolution]
   a) Leaf-cutting ants have some of the longest lived colonies with queen life spans up to 20 years, but males die on the day they leave the colony in which they hatched, having lived as adults for just a few weeks under constant protection by their worker sisters who provide sophisticated social immunity against external parasites and pathogens.
   b) Our results suggest instead that the extent to which eusocial males have independent lives outside their colony of origin is crucial, which implies the prediction that long-lived patrolling males of bumblebees should upregulate their immune defences if they would contract infections after leaving their colony. This ability would then likely be linked to a higher need to express immune defences also before leaving the nest, as annual bumblebee colonies live with their diseases, whereas perennial ant colonies are able to almost entirely exclude them through advanced social immunity mechanisms.
   c) Yet, similar to established termite reproductives, these ergatoid males never operate without having nursing workers nearby, so their operational immune defences will likely depend on the efficiency of the social immunity that workers can provide.

64) *Ho, Eddie K. H., and Megan E. Frederickson. “Alate Susceptibility in Ants.” *Ecology and Evolution* 4, no. 22 (2014): 4209–19. https://doi.org/10.1002/ece3.1291. [S], [Ants]
   a) Immunological defenses, however, are not distributed uniformly among colony members. For example, workers likely enact most social immunity behaviors and, in many species, males lack metapleural glands. This variation in immunity among castes may result from selection pressures acting on, and potentially trading-off between, individual ants and whole ant colonies.
   b) Rolff (2002) did not examine how selection might act on males and females in colonies of ants or other eusocial insects. Because of the interdependency of ant castes for survival and reproduction, the colony as a whole is the primary unit of selection.

65) Gao, Qi. "Social immunity and the expression of immune-related genes in the Eastern subterranean termite." (2014). Phd diss., The University of Western Ontario. *Electronic Thesis and Dissertation Repository*. 2493. https://ir.lib.uwo.ca/etd/2493 [M], [Termites], [Genetics]
   a) Social group members derive great benefit from these cooperatively or mutually performed behaviors that allow for task specialization and parallel processing of those tasks.
   b) Similarly, the removal of dead adults from the nest by undertaker specialists helps to control disease in social insect colonies. All these typical behavioral adaptations provide the social members an extra protection beyond the individual-level from disease contamination.
   c) In eusocial society, maintaining relatively constant density (number of individuals) and caste composition (ratio) is the essential basis for the performance of the colony-level tasks, such as foraging, parental care, nest maintenance, and defensive behaviors.

66) Fouks, Bertrand Joseph Jean-Baptiste. "Behavioural and social immunity in a eusocial insect, the bumblebee Bombus terrestris." (2014). PhD diss., Martin-Luther-University Halle-Wittenberg. [M], [Bees]
   a) The broader definition of social immunity allows for the opening of a new scope into the altruism and cooperation evolution paradigm, while the more narrow definition of social immunity allows considering the colony as a “superorganism”, to integrate the parasite pressure into the evolution of social structures and the possibility to investigate convergent evolution between individual and social immunity.
   b) Social insects reduce the parasite spread within a colony using a wide range of behaviours. This is the case for grooming behaviour which can be increased or decreased, depending on the species, if an individual gets infected, social fever in bees and hygienic behaviour. Some of these processes can be correlated with immune mechanisms in vertebrates when considering insect colonies as superorganisms.
   c) This change of thermoregulatory behaviour has a direct effect on the immune response and can be seen as an induced fever similar to the homeotherms immune response.
   d) Coming back to the social immunity and the concept of the superorganism, analogies in the evolution of individual and social immunity have been reviewed by Cremer & Sixt (2009).
   e) Indeed, social fever, the reduction of social contacts with infected individuals, the increase of grooming behaviour to remove parasites, which also can lead to some immune memory, and the structure of colony/ social organization can be connected with individual immunity of vertebrates.

67) Zhukovskaya, Marianna, Aya Yanagawa, and Brian T. Forschler. “Grooming Behavior as a Mechanism of Insect Disease Defense.” *Insects* 4, no. 4 (December 2013): 609–30. https://doi.org/10.3390/insects4040609. [M]

a) Few studies have examined the role of behavior in insect disease defense. However, the role of insect grooming and hygienic activities is gaining recognition in the field of insect pathology.

68) Johansson, Helena, Kishor Dhaygude, Stafva Lindström, Heikki Helanterä, Liselotte Sundström, and Kalevi Trontti. "A Metatranscriptomic Approach to the Identification of Microbiota Associated with the Ant Formica Exsecta." *PLOS ONE* 8, no. 11 (November 18, 2013): e79777. https://doi.org/10.1371/journal.pone.0079777. [M], [Microbiome], [Ants]
    a) Furthermore, and in contrast to solitary insects, social insects also have social immunity, i.e. individuals mount immune responses for the benefit of others.

69) Yek, Sze H., Jacobus J. Boomsma, and Morten Schiøtt. "Differential Gene Expression in Acromyrmex Leaf-Cutting Ants after Challenges with Two Fungal Pathogens." *Molecular Ecology* 22, no. 8 (2013): 2173–87. https://doi.org/10.1111/mec.12255. [M], [Fungi], [Ants], [Genetics]
    a) Both these defences are expressed by individual ants, but may become collective social defences by the ways in which they are applied, and it is generally believed that collective defences of this kind have very significant functions across the social insects.

70) Fernández-Marín, Hermógenes, Gaspar Bruner, Ernesto B. Gomez, David R. Nash, Jacobus J. Boomsma, and William T. Wcislo. "Dynamic Disease Management in Trachymyrmex Fungus-Growing Ants (Attini: Formicidae)." *The American Naturalist* 181, no. 4 (April 1, 2013): 571–82. https://doi.org/10.1086/669664. [M], [Fungi], [Ants]
    a) Studies of eusocial insects are especially relevant to understanding trade-offs in antimicrobial strategies. Colony sizes range from a few related individuals to tens of thousands or even millions, living in crowded conditions favorable for pathogen transmission.

71) Pradeu, Thomas. "Immunity and the emergence of individuality." *From groups to individuals: Evolution and emerging individuality* 16 (2013): 77. [M], [U], [Individuality vs Sociality], [Evolution]
    a) In a majority of cases, the immune response in social insects occurs at the level of the individual insect. Yet colony level immunity may exist as well in some species. Indeed, in some cases, it appears that being part of a colony makes an important difference in the capacity to mount an immune response.

72) *Woodhams, Douglas C., and Robert M. Brucker. "Disease Defence through Generations: Leaf-Cutter Ants and Their Symbiotic Bacteria." *Molecular Ecology* 22, no. 16 (2013): 4141–43. https://doi.org/10.1111/mec.12431. [S], [Microbiome], [Ants], [Bacteria]
    a) A bloom of *Pseudonocardia* bacterium soon after hatching suggests vertical transmission within ant colonies. Because *Pseudonocardia* is considered protective, this also supports the social immunity concept in which greater investment of immune factors is concentrated at more critical colony 'organs'.

73) Tragust, Simon. "Social immune defence in ants-Different aspects of hygienic behaviour and the infestation with Laboulbeniales in Lasius neglectus ants." PhD diss., 2013. [M], [Ants]
   a) The innate immune system is only the last line of defence, with boundary defences such as the cuticle and behavioural adaptations such as avoidance behaviour preceding them.

74) Medzhitov, Ruslan, David S. Schneider, and Miguel P. Soares. "Disease Tolerance as a Defense Strategy." *Science* 335, no. 6071 (February 24, 2012): 936–41. https://doi.org/10.1126/science.1214935. [M], [Medicine]
   a) Social insects also have well-documented avoidance behaviors that help minimize colony exposure to pathogens.

75) Beechler, Brianna R., Heather Broughton, Austin Bell, Vanessa O. Ezenwa, and Anna E. Jolles. "Innate Immunity in Free-Ranging African Buffalo (Syncerus Caffer): Associations with Parasite Infection and White Blood Cell Counts." *Physiological and Biochemical Zoology* 85, no. 3 (May 1, 2012): 255–64. https://doi.org/10.1086/665276. [M], [U]
   a) Empirical studies in ecoimmunology have focused largely on birds and invertebrates, extending strong foundations in lifehistory theory in these taxa. Transferring these approaches to free-living mammal species has only recently begun.

76) Martinson, Vincent G., Jamie Moy, and Nancy A. Moran. "Establishment of Characteristic Gut Bacteria during Development of the Honeybee Worker." *Applied and Environmental Microbiology* 78, no. 8 (April 15, 2012): 2830–40. https://doi.org/10.1128/AEM.07810-11. [M], [Microbiome], [Bees]
   a) In many social insects, larvae are only fed adult-processed foods, which could be altered to inhibit microbial growth or enriched for a certain subset of nonpathogenic/probiotic microbes, thus insulating the young from opportunistic pathogens.

77) Konrad, Matthias, Meghan L. Vyleta, Fabian J. Theis, Miriam Stock, Simon Tragust, Martina Klatt, Verena Drescher, Carsten Marr, Line V. Ugelvig, and Sylvia Cremer. "Social Transfer of Pathogenic Fungus Promotes Active Immunisation in Ant Colonies." *PLOS Biology* 10, no. 4 (April 3, 2012): e1001300. https://doi.org/10.1371/journal.pbio.1001300. [M], [Fungi], [Ants]
   a) Society members act collectively, similar to cells in a body, and work as a superorganism in multiple aspects, including anti-pathogen defence.
   b) Social immunisation may not be limited to the highly eusocial insect societies but could similarly occur in other societies or at the family level. If also detected in vertebrates, the underlying mechanisms may be very different, as vertebrates have the additional adaptive/acquired immune component and do not rely solely on the innate immune system that characterises invertebrate immunity.
   c) The long-lived societies of social insects are at especially high risk of re-encountering the same pathogens multiple times during their lifespans, and could greatly benefit from a persistent, rather than transient, social immunisation, particularly against common pathogens such as the fungus *Metarhizium*.

78) De Roode, Jacobus C., and Thierry Lefèvre. "Behavioral Immunity in Insects." *Insects* 3, no. 3 (September 2012): 789–820. https://doi.org/10.3390/insects3030789. [M]

a) In this review, we will categorize insect behaviors as behavioral immunity, regardless of whether they increase the direct or indirect fitness of the individuals displaying the behaviors. Although this view is often overlooked in studies on behavioral responses to diseases, the field of social immunity in insects has recently received interest, and has clearly demonstrated that individuals can increase their inclusive fitness by protecting themselves (behavioral self-immunity), their offspring (behavioral trans-generational immunity) or other relatives (social immunity).

79) Bos, N., T. Lefèvre, A. B. Jensen, and P. D'ettorre. "Sick Ants Become Unsociable." *Journal of Evolutionary Biology* 25, no. 2 (2012): 342–51. https://doi.org/10.1111/j.1420-9101.2011.02425.x. [M], [Ants]

a) In response to parasite (broadly defined here to include both macroparasites and microparasites such as fungi) pressure, group living organisms have evolved several lines of defence. In addition to their individual physiological immune mechanisms, they are able to engage in a group-level immunity consisting of a series of behaviours that reduce the risk of infection or minimize the parasite-induced fitness losses.

80) Conte, Y. Le, C. Alaux, J.-F. Martin, J. R. Harbo, J. W. Harris, C. Dantec, D. Séverac, S. Cros-Arteil, and M. Navajas. "Social Immunity in Honeybees (Apis Mellifera): Transcriptome Analysis of Varroa-Hygienic Behaviour." *Insect Molecular Biology* 20, no. 3 (2011): 399–408. https://doi.org/10.1111/j.1365-2583.2011.01074.x. [M], [Bees], [Genetics]

a) Such social immunity includes grooming, the use of antimicrobial materials for nest construction (eg resin), social fever and nest hygiene. Since their description, many studies have explored the behavioural mechanisms of these collective immune defences against pathogens, but the molecular basis and pathways remain largely unknown.

81) Shorter, J. R., and O. Rueppell. "A Review on Self-Destructive Defense Behaviors in Social Insects." *Insectes Sociaux* 59, no. 1 (February 1, 2012): 1–10. https://doi.org/10.1007/s00040-011-0210-x. [S]

a) Another field to draw conceptual lessons from may be immunology. In return, understanding self-destructive defensive behaviors in social insects can inform other fields of research. Parallels between individual disease defense and social immunity in insect societies exist, but social insect colonies are experimentally much more accessible.

82) Baracchi, David, Antonio Fadda, and Stefano Turillazzi. "Evidence for Antiseptic Behaviour towards Sick Adult Bees in Honey Bee Colonies." *Journal of Insect Physiology* 58, no. 12 (December 1, 2012): 1589–96. https://doi.org/10.1016/j.jinsphys.2012.09.014. [M], [Bees]

a) Multicellular organisms and insect societies face the same organizational problems and the same intense selective pressures from pathogens and parasites leading to a series of analogies in their anatomy and social anatomy, physiology and social physiology, immunity and social immunity.

83) Chouvenc, Thomas, and Nan-Yao Su. “When Subterranean Termites Challenge the Rules of Fungal Epizootics.” *PLOS ONE* 7, no. 3 (March 28, 2012): e34484. https://doi.org/10.1371/journal.pone.0034484. [M], [Termites], [Fungi]
   a) [M, d] Social insect colonies have been considered superorganisms in which the social immunity was compared by analogy to the individual immunity of higher vertebrates.

84) Andersen, Sandra B., Matthew Ferrari, Harry C. Evans, Simon L. Elliot, Jacobus J. Boomsma, and David P. Hughes. “Disease Dynamics in a Specialized Parasite of Ant Societies.” *PLOS ONE* 7, no. 5 (May 2, 2012): e36352. https://doi.org/10.1371/journal.pone.0036352. [M], [Ants], [Fungi], [Evolution]
   a) The high density of continuously interacting individuals within colonies implies that infection risks are high, but also that selection for efficient prophylactic defences has been strong. Recent reviews have emphasized that behavioural forms of social immunity are normally very efficient, so that ant parasites pose a limited threat for escalating epidemics within colonies.

85) Gruber, Monica Alexandra Maria. "Genetic factors associated with variation in abundance of the invasive yellow crazy ant (Anoplolepis gracilipes)." PhD diss., Victoria University of Wellington (2012). [M], [Ants], [Genetics]
   a) Pathogen spread is facilitated by the social organisation of these insects, owing to aggregations of close relatives. Consequently, social insects employ a number of behavioural and physiological mechanisms to enhance disease resistance.

86) Caldararo, Niccolo Leo. "Evolutionary aspects of disease avoidance: the role of disease in the development of complex society." *Available at SSRN 2001098* (2012). [S], [U], [Evolution]
   a) Mass induced behavior by disease has been considered for over 100 years in humans, especially regarding remarkable examples from the Black Plague of the 14th century C.E. and other forms of stereotyped disease avoidance customs have been noted by several researchers. This is particularly interesting in the context of Cremer & Sixt (2009) review of the analogies in the evolution of individual and social immunity.

87) Nish, Simone, and Ruslan Medzhitov. “Host Defense Pathways: Role of Redundancy and Compensation in Infectious Disease Phenotypes.” *Immunity* 34, no. 5 (May 27, 2011): 629–36. https://doi.org/10.1016/j.immuni.2011.05.009. [M], [U], [Medicine]
   a) The honeybees have effective social immunity mechanisms, such as pathogen avoidance, social grooming, and nest hygiene, which are absent in the nonsocial insects including fruit flies and mosquitoes.

88) Rosengaus, Rebeca B., Courtney N. Zecher, Kelley F. Schultheis, Robert M. Brucker, and Seth R. Bordenstein. “Disruption of the Termite Gut Microbiota and Its Prolonged Consequences for Fitness.” *Applied and Environmental Microbiology* 77, no. 13 (July 1, 2011): 4303–12. https://doi.org/10.1128/AEM.01886-10. [M], [Microbiome], [Termites], [Evolution]
   a) Symbionts, whether parasitic, commensal, or mutualistic, pose important selective pressures on their hosts. These host-microbe interactions likely influence the evolution of multiple host life

history traits, including longevity, behavior, reproductive biology, immunity, and evolution and maintenance of sociality.

89) Abramowski, D., C. R. Currie, and M. Poulsen. “Caste Specialization in Behavioral Defenses against Fungus Garden Parasites in Acromyrmex Octospinosus Leaf-Cutting Ants.” *Insectes Sociaux* 58, no. 1 (February 1, 2011): 65–75. https://doi.org/10.1007/s00040-010-0117-y. [M], [Ants], [Fungi]
   a) Parasite defenses in social insects include immune systems in individuals, mechanisms of social immunity, the application of gland or bacteria-derived antibiotics, and behavioral parasite removal.

90) Vojvodic, Svjetlana, Annette B. Jensen, Bo Markussen, Jørgen Eilenberg, and Jacobus J. Boomsma. “Genetic Variation in Virulence among Chalkbrood Strains Infecting Honeybees.” *PLOS ONE* 6, no. 9 (September 22, 2011): e25035. https://doi.org/10.1371/journal.pone.0025035. [M], [Bees], [Genetics]
   a) Evolutionary studies tend to predict intermediate virulence levels, with exact levels for any system depending on transmission mode and the frequency of multiple infection. While this has been shown to some degree in bumblebees, it has also become clear that these inferences may not necessarily apply for all social insect hosts when prophylactic social behaviours interact with disease defences at the level of individual larvae.

91) Chouvenc, Thomas, Paul Bardunias, Hou-Feng Li, Monica L. Elliott, and Nan-Yao Su. “Planar Arenas for Use in Laboratory Bioassay Studies of Subterranean Termites (Rhinotermitidae).” *Florida Entomologist* 94, no. 4 (December 2011): 817–26. https://doi.org/10.1653/024.094.0413. [M], [Termites]
   a) In the current study, the colonization of the cellulose pad by *S. marcescens*, a known termite pathogen, which occurred in the Petri dishes but not in the arenas, suggests that the sand and the rich microbial community associated with the tunnel system provides termites with a buffering environment against outbreaks of opportunistic parasitic or pathogenic organisms.

92) Dobata, S., T. Sasaki, H. Mori, E. Hasegawa, M. Shimada, and K. Tsuji. “Persistence of the Single Lineage of Transmissible ‘Social Cancer’ in an Asexual Ant.” *Molecular Ecology* 20, no. 3 (2011): 441–55. https://doi.org/10.1111/j.1365-294X.2010.04954.x. [M], [Ants], [Evolution]
   a) In the cooperation of cell ‘societies’, allograft immunity usually rejects the migration of cells between multicellular organisms, which also inhibits the spread and persistence of cancer cells. However, some cancer cells have evolved the capability of migration (or transmission) among organisms, and this has been confirmed recently in some mammals.

93) Vitikainen, Emma, and Liselotte Sundström. “Inbreeding and Caste-Specific Variation in Immune Defence in the Ant Formica Exsecta.” *Behavioral Ecology and Sociobiology* 65, no. 5 (May 1, 2011): 899–907. https://doi.org/10.1007/s00265-010-1090-1. [M], [Ants]
   a) Social life nonetheless also carries hazards, in particular, as societies form dense aggregations of closely related individuals, which facilitates the spread of pathogens among society members. Indeed, social insects are ridden with a range of parasites and pathogens and have evolved a

range of behavioural and physiological adaptations to mitigate the potential harm caused by these.

94) Armitage, Sophie A. O., Jens F. Broch, Hermogenes Fernández Marín, David R. Nash, and Jacobus J. Boomsma. “Immune Defense in Leaf-Cutting Ants: A Cross-Fostering Approach.” *Evolution* 65, no. 6 (2011): 1791–99. https://doi.org/10.1111/j.1558-5646.2011.01241.x. [M], [Ants]
    a) Other complexities arise when different levels of selection are involved, for example when defenses at the group level partly compensate for individual immunity. Although sterile workers are in some ways comparable to somatic cells in multicellular organisms, and as such are disposable to a degree, they have highly effective immune defenses to protect the propagation of the germline.

95) Poulsen, Michael, Janielle Maynard, Damien L Roland, and Cameron R Currie. “The Role of Symbiont Genetic Distance and Potential Adaptability in Host Preference towards Pseudonocardia Symbionts in Acromyrmex Leaf-Cutting Ants.” *Journal of Insect Science* 11, no. 1 (January 1, 2011). https://doi.org/10.1673/031.011.12001. [M], [Ants], [Fungi], [Evolution]
    a) Self-recognition and antagonism towards non-self is a crucial component of social insect biology, where recognition of, and response to, colony members and individuals from other nests are governed by colony members learning and constantly updating their reference of self from the collective colony odor. This is largely analogous to immune system responses, in which non-self components within an insect or vertebrate body are targeted and suppressed or removed.
    b) However, because many non-self components are beneficial (i.e., mutualistic and commensal symbionts), mechanisms that allow for the immune system to distinguish between dangerous and beneficial non-self are crucial.

96) Gherman, Bogdan I., Liviu Al MĂRGHITAŞ, Daniel S. Dezmirean, and Robin FA Moritz. "Disease and Behavior in Honeybees." *Bulletin UASVM Animal Science and Biotechnologies* 68 (2011): 1-2. [M], [Bees]
    a) The individual members of an insect society cooperate to ensure colony growth, survival and reproduction. There is reproductive division of labor such that one or a few individuals, the queens and their mates, produce the colony offspring, while the majority of individuals, the workers, perform tasks such as foraging, nest construction and maintenance, and caring for offspring.

97) Simone-Finstrom, Michael, and Marla Spivak. “Propolis and Bee Health: The Natural History and Significance of Resin Use by Honey Bees.” *Apidologie* 41, no. 3 (May 1, 2010): 295–311. https://doi.org/10.1051/apido/2010016. [M], [Bees]
    a) Social immunity, which describes how individual behaviors of group members effectively reduce disease and parasite transmission at the colony level, is an emerging field in social insect biology.
    b) Particularly with respect to this entombment behavior, the use of propolis by bees can be described analogously to individual immune function. If we consider a honey bee colony as one entity or “superorganism”, then this behavior would be equivalent to cellular encapsulation of foreign microbes or parasites seen at the individual level.

98) Evans, Jay D., and Marla Spivak. “Socialized Medicine: Individual and Communal Disease Barriers in Honey Bees.” *Journal of Invertebrate Pathology* 103 (January 1, 2010): S62–72. https://doi.org/10.1016/j.jip.2009.06.019. [M], [Bees]

a) Accordingly, we discuss the dynamics of hygienic behavior and other group-level behaviors that can limit disease. These group-level dynamics, labeled ‘social immunity’, provide an underappreciated benefit of living in crowded social groups with respect to reduction of disease.
b) When hundreds or thousands of individuals within a honey bee colony interact, the social immune responses at the colony-level have analogous properties to the complex humoral and cellular immune systems within a multicellular organism. Social immune responses have been described recently for a number of social insects.

99) Hamilton, Casey, Brian T. Lejeune, and Rebeca B. Rosengaus. “Trophallaxis and Prophylaxis: Social Immunity in the Carpenter Ant Camponotus Pennsylvanicus.” *Biology Letters* 7, no. 1 (February 23, 2011): 89–92. https://doi.org/10.1098/rsbl.2010.0466. [M], [Ants]

a) These insects have evolved a variety of adaptations to cope with pathogenic pressures, including behavioural, biochemical and immunological responses. While individual immune responses involve cellular immunity and the humoral production of effector molecules, group behaviour in social insects can also prevent infection and disease transmission and achieve adaptive social immunity.
b) Trophallactic exchanges from reproductives and/or workers to brood may also contribute to trans-generational immune priming in social insects. Few studies have investigated the externalization of such immune factors in social insects.

100) Cotter, S.C., and R.M. Kilner. “Personal Immunity versus Social Immunity.” *Behavioral Ecology* 21, no. 4 (July 1, 2010): 663–68. https://doi.org/10.1093/beheco/arq070. [C], [Individuality vs Sociality]

a) Our definition of social immunity is significantly broader than the current use of the term.
b) Specifically, it [the term 'social immunity'] describes immune defenses that are mounted by a collective for the benefit of themselves and others.
c) …Our broader definition of social immunity makes it possible to study the evolution of social immune function in greater depth than would otherwise be possible. For example, there are remarkable parallels between the social immune responses shown by social insects and personal immunity exhibited by multicellular organisms.

101) Rueppell, O., M. K. Hayworth, and N. P. Ross. “Altruistic Self-Removal of Health-Compromised Honey Bee Workers from Their Hive.” *Journal of Evolutionary Biology* 23, no. 7 (2010): 1538–46. https://doi.org/10.1111/j.1420-9101.2010.02022.x. [S], [T], [Bees]

a) The most significant context for altruistic self-removal is presumably the prevention of disease transmission by infected workers because many pathogens can quickly spread through and devastate a colony once they are established.
b) Surrogate treatments that realistically simulate serious disease but do not affect the animal in other ways are needed to provide evidence for adaptive self-removal as an immune defence strategy of social insects at the colony level.
c) Altruistic self-removal presents a new form of altruistic suicide that differs from direct suicidal colony defence because it serves a pre-emptive function, similar to the suicidal entrance closure by *Forelius* ants. However, it may also be interpreted as a special form of hygienic behaviour.
d) Altruistic self-removal can only be understood as an adaptation at the colony level because isolated colony members do not normally survive away from their nest. This process shows a

functional similarity to programmed cell death of compromised cells in multi-cellular organisms. In both cases, selection at the higher level of biological organization has resulted in altruistic suicide of lower level units. Thus, altruistic self-removal strengthens the view of a colony as an integrated superorganism.

102) *Elliot, Simon L., and Adam G. Hart. “Density-Dependent Prophylactic Immunity Reconsidered in the Light of Host Group Living and Social Behavior.” *Ecology* 91, no. 1 (2010): 65–72. https://doi.org/10.1890/09-0424.1. [M], [Individuality vs Sociality], [Evolution]

a) As the studies cited above have generated a body of empirical data on group-living (but nonsocial) insects, a number of papers have, particularly recently, explored the defenses employed by social insects to combat disease, concluding that individuals have increased resistance when in groups and employ diverse behavioral resistance mechanisms such as hygienic behaviors, increased brood care, waste management, behavioral fever, exclusion of infected individuals, and avoidance behaviors performed by infected individuals.
b) Finally, larger social groupings will have the potential for more sophisticated (thus potentially more effective and lower cost) responses to disease through cooperative behaviors.

103) Schulenburg, Hinrich, Joachim Kurtz, Yannick Moret, and Michael T Siva-Jothy. “Introduction. Ecological Immunology.” *Philosophical Transactions of the Royal Society B: Biological Sciences* 364, no. 1513 (January 12, 2009): 3–14. https://doi.org/10.1098/rstb.2008.0249. [M]

a) Parasite avoidance behaviours are widespread among animals and are particularly common among social organisms.
b) Indeed, animal societies have evolved several mechanisms to protect the community from parasite attack, ranging from specific behaviours against parasite-rich material or infected members of the society, structure and organization of the nest, as well as a systemic society-wide activation of physiological immunity, as discussed in this issue's review by Cremer & Sixt (2009).

104) Swanson, Jodi A. I., Baldwyn Torto, Stephen A. Kells, Karen A. Mesce, James H. Tumlinson, and Marla Spivak. “Odorants That Induce Hygienic Behavior in Honeybees: Identification of Volatile Compounds in Chalkbrood-Infected Honeybee Larvae.” *Journal of Chemical Ecology* 35, no. 9 (September 1, 2009): 1108–16. https://doi.org/10.1007/s10886-009-9683-8. [M], [Bees], [Perception]

a) Antiseptic behaviors are analogous to the cellular and humoral immune responses within an individual because they involve detection and recognition of the foreign pathogen or parasite, and subsequent initiation of an appropriate defensive response.

105) Walker, Tom N., and William O. H. Hughes. “Adaptive Social Immunity in Leaf-Cutting Ants.” *Biology Letters* 5, no. 4 (August 23, 2009): 446–48. https://doi.org/10.1098/rsbl.2009.0107. [M], [Ants]

a) Such group-level defences can be regarded as a form of ‘social immunity’. The social immune response may even be transferable, with the resistance of naive individuals being increased by interacting with individuals that have been exposed to a parasite.

106) Yao, M., J. Rosenfeld, S. Attridge, S. Sidhu, V. Aksenov, and C. D. Rollo. “The Ancient Chemistry of Avoiding Risks of Predation and Disease.” *Evolutionary Biology* 36, no. 3 (September 1, 2009): 267–81. https://doi.org/10.1007/s11692-009-9069-4. [M], [U], [Perception]

a) Nestmate recognition in bees involves multi-channel signaling that includes oleic, linoleic, palmitoleic linolenic acids, methyl esters, and diverse hydrocarbons.
b) Interestingly, bees may recognize infected individuals and guards may bar their entry.

107) Schluns, Helge, and Ross H. Crozier. "Molecular and chemical immune defenses in ants (Hymenoptera: Formicidae)." *Myrmecological News* 12 (2009): 237-249. [M], [Ants]
a) Collective defenses are defined by the fact that an individual animal cannot perform them on its own, e.g., allogrooming or necrophoric behavior.
b) Colony level defenses in social insects receive increasing attention and several reviews on this topic have been published, some of them very recently.