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Introduction

Luc-Alain Giraldeau and Michael Kosfeld

Why do some individuals invest effort and time in making a resource available, while others simply wait and exploit the fruits of this effort? Why do some people cooperate in joint production and public goods provision while others free ride and abstain from contributing to aggregate welfare?

This phenomenon—the exploitation of others' investments, the free riding in the presence of others' cooperation—is studied by many scientists, including biologists, anthropologists, public health scientists, and economists. For one of us (Luc-Alain Giraldeau), as a starting PhD student in biology, it became the main theme of his research career some 36 years ago, when he stumbled onto a case of investor–exploiter interactions in pigeons.

At that time, Luc-Alain was trying to document how pigeons learned simple food discovery skills while foraging in groups, but after months of trials, this paragon of Skinner's operant conditioning seemed largely unable to learn even the humblest of tasks, like flipping lids or pecking on sticks to find food. To figure out why, Luc-Alain invested hours of painstaking observation, staring again and again at black and white videotapes. What he discovered was that the few pigeons that did learn allowed non-learning exploiters to feed off of their discoveries. Exploitation, it seemed, was the non-learners stumbling block to learning.

It did not take Luc-Alain long to realize that this form of exploitation had innumerable other consequences: on behavioral diversity within groups, on the efficiency of the group at discovering resources, aggression, food defense, spatial preferences, interspecific relationships, sociality, and social learning. As a biologist, he understood that exploitation was at the root of a wide range of phenomena and that it was remarkably ubiquitous. As the saying goes: "Once you see it, you just can't unsee it." Thus the rest of his research career was devoted to exploring the factors that governed the prevalence of exploitation within groups, mostly of birds. It quickly became obvious to him that animal exploiters might share commonalities with human exploitation or free riding in the economic world. He saw endless analogies between animal and human exploitation: Generic pharmaceutical companies exploit the discoveries of other pharmaceutical companies. Parents take advantage of other parents'

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investment in vaccinating their children and may decide not to vaccinate. Commercial fishing vessels use the success of others to decide where to fish.

As a biologist, he wondered whether these incidences simply bore a superficial resemblance to each other, or whether there was something more fundamental to link these human and animal systems? Could knowledge of animal systems inform researchers concerned with human affairs? Might discoveries in biology be useful to economists and public health policies? Might biologists improve their models of exploitation by incorporating advances developed by economists?

After spending a lifetime of research in the world of animal behavior, Luc-Alain was eager to learn whether this work could be translated to other fields, such as economics and public health. Equally, he was curious to see whether such translation could be multidirectional. So he approached the Ernst Strüngmann Forum to ask for their help.

Joining him in proposing this theme was another biologist, Philipp Heeb, who was instrumental in working on the initial proposal. Both served as cochairpersons of the Forum as well as members of the Program Advisory Committee, together with Alex Kacelnik, Michael Kosfeld, Julia Lupp, and Frédéric Thomas. Yet what brought Michael Kosfeld, an economist, to this discussion?

When Michael was initially approached to interact on this theme, the overall topic and objectives of the Forum immediately caught his attention. He well remembered how once, as a PhD student in economics with a prior training in mathematics, he had stumbled across one of the most famous games in economics: the so-called prisoner's dilemma. Originally discovered by Al Tucker to illustrate the potential nonsocial desirability of Nash equilibria, the game immediately fascinated him. On one hand, it was "theoretically obvious" that noncooperation is the only individually optimal strategy in this game, yet on the other, it seemed equally "empirically obvious" that cooperation is not simply a failure of human decision making but rather a very intuitive and natural behavior that is observed across many different contexts and situations. Since then, this game—in one form or the other—has influenced Michael's research, not only as a game theorist but also, in particular, as an experimental and behavioral economist.

Michael remembered the invigorating discussions that took place at the former Dahlem Konferenzen, during its 2002 meeting on "The Genetic and Cultural Evolution of Cooperation," chaired by Peter Hammerstein. There Michael engaged, as a postdoc, in a fascinating discussion of the "puzzle of cooperation" in both the human and animal world, together with a group of anthropologists, biologists, and economists. Because the Ernst Strüngmann Forum had resurrected the work of the Dahlem Konferenzen, Michael was truly excited to be involved in setting up a new interdisciplinary discourse that would scrutinize cooperation, this time from the perspective of exploitation.

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Together, the members of the Program Advisory Committee created a framework for evolutionary ecologists, economists, anthropologists, and public health scientists to examine collectively whether there is some generality in the phenomenon of investment and exploitation as it manifests itself across a broad range of species and systems. Might understanding of this phenomenon, studied for decades along separate research traditions, be deepened through this interdisciplinary exchange? Could we come away from this discourse with new insights to tackle problems related to renewable resource management, public health, and institutional design?

The answer to both, of course, is a resounding yes…and no.

Challenges Posed by Interdisciplinary Traditions

An Ernst Strüngmann Forum is no stroll through the park. Intelligent, hard-working scientists with years of accumulated knowledge, reputation, and authority in a discipline are suddenly thrust together in the same space to discuss the very subject of their expertise with others who clearly haven't the faintest idea of who they are. Not an easy starting point for a group of career scientists!

As with any interdisciplinary exchange, initial interactions often aim at explaining, as simply as possible, one's own approach while listeners smile politely, often thinking: "This is pure gibberish." In French, such interactions are called *un dialogue de sourds* [a dialogue between the deaf]. The analogy is appropriate. Just as some noisy occupations make a number of their workers tone deaf, so too can scientists (as they become experts in their own discipline) become discipline deaf. This deafness stands as the main obstacle to any interdisciplinary exchange, and the Ernst Strüngmann Forum is no exception.

Speaking louder or yelling is of no help whatsoever at a Forum. One has only a short week to overcome one's hearing impairment, and this is no small task. However, given the Forum's experienced leadership and guidance, we are relieved to report that many were able to get past their sensory deficits in the course of this successful Forum.

Disciplinary deafness is not an act of bad faith. It is the result of accumulated hidden assumptions about the world which make up a field, determine its most important target questions, thus allowing everyone within it to understand each other. It can, in fact, even be a productive driver of within-discipline scientific excellence. As you read through these chapters, you will no doubt detect tension between biologists and economists. Zones of overlap and divergence between economists and evolutionary biologists appear much more clearly than they did back in November 2015, when we first met in Frankfurt.

In what follows, we highlight some of the issues that seem to be at the heart of this tension. Perhaps the best way to view them is as conceptual discontinuities between the fields which need to be exposed, so that areas of disciplinary deafness can be turned into a productive interdisciplinary dialogue.

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Populations versus Individuals

Economists and evolutionary biologists both study exploitation and investment, but they clearly have different criteria for what constitutes a satisfying answer. Put simply, evolutionary biologists find solace in population-level answers whereas economists seek individual-level explanations. For example, for an evolutionary biologist, there is no point asking why some individuals choose to invest: investors simply must exist, otherwise there would be no species. If no agent within a group ever invested in searching for food, then no one would ever eat and the whole group would die, and there would be nothing left to study. Investors, evolutionarily speaking, just have to be: end of story.

Economists, on the other hand, have a hard time accepting this population-level argument. They admit that if all members of a population free ride, then the collective outcome is worse, but in most economic examples the population will not die off or become extinct. Economists approach the issue from an individual level, and not just any kind of individual: one that is smart and has the capacity to plan ahead. For an economist, the real puzzle is: Why would anyone choose to invest in any costly effort, given that others will benefit as a result? In other words, economists develop models and experiments to address a question that evolutionary ecologists consider already answered.

Intriguingly, John Nash laid out this "duality" of a population- versus individual-level perspective in his original PhD thesis when he introduced the concept of (Nash) equilibrium in noncooperative games, a solution concept that has since influenced research in economics and other social sciences, probably like no other. Unfortunately, the population-level perspective, or mass action interpretation as Nash called it, was mostly forgotten during the rise of game theory in economics, while it became truly fundamental to biologists and is reflected in concepts such as evolutionary stability, developed by John Maynard Smith and George Price. Only in the early 1990s did evolutionary game theory begin to partly enter economic modeling, but it seems true to say that it has never become part of mainstream economic thinking.

Producer–Scrounger versus Cooperation

Both evolutionary ecologists and economists agree that a population composed of all investors and no exploiters would typically be the best general outcome possible. Because evolutionary biologists do not concern themselves with the investor strategy, all of their work focuses on the causes of exploitation (free riding). Their models reflect this bias, typified most notably by the "producer–scrounger" game, which searches for the factors that govern the frequency of exploitation within a population: the way resources are distributed, their overall abundance, whether resources can be defended or not, and whether agents are equal or unequal in strength.

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For economists, to ask why free riding exists is a no-brainer: it is economically beneficial. The crux of the issue, then, is to find the conditions under which rational economic agents would choose to use the more costly but socially profitable alternative: invest. The games that place the emphasis on investment, such as the prisoner's dilemma game or public goods games, are framed in a perspective of cooperation, not exploitation. Hence the target questions in both disciplines are different and as a consequence so too is the terminology, and the models are framed in different traditions: exploitation in one, cooperation in the other.

Genes versus Learning and Culture

Evolutionary biologists focus on a wide range of species, many of which have no brains and little in terms of cognition. These species behave, nonetheless, and their behavior is far from irrational or erratic. Biologists, therefore, assume nothing about the thinking power of the agents they are studying. They simply take for granted that natural selection has endowed an agent with the necessary behavioral decision mechanism to make the best possible choice under a given set of circumstances. As a result, evolutionary ecologists employ game theory to study the interaction between organisms such as plants and their pollinators, without being the least bit concerned about the details of their decision mechanism. To evolutionary ecologists, the human brain, despite its complexity and immense capabilities in terms of culture and cultural transmission, must also be seen as an adaptive choosing device, nothing more. Accordingly, they assume that they do not need to concern themselves with the details of individual decisions, because a population will behave as expected by natural selection, on average.

Economists view the brain and humans quite differently from evolutionary biologists. As social scientists who focus exclusively on humans, the details of a decision are of paramount importance, and thus social scientists invoke (bounded) rationality, culture, social norms, legal and political institutions, enforcement rules, and reputation in their quest for answers. All of these, and much more, factor into their models and play a prominent role in the formulation of hypotheses. In addition, economists make a clear distinction between preferences and behavior. It may be rational for an individual to cooperate if s/he expects to be punished otherwise (say, by the police or by the courts), even though in general the individual prefers unilateral defection to joint cooperation. In contrast, an individual may rationally decide not to cooperate, even though s/he prefers joint cooperation to unilateral defection, if s/he believes that other players will defect as well (and there is no punishment). Exactly for these reasons, institutions—legal, social, or economic—are so important for economists, because they fix incentives, affect beliefs, and thus determine the explicit and implicit "rules of the game." The idea that evolutionary ecologists

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need not concern themselves with these factors can easily appear foolish and unrealistic to any economist.

Taxonomic Generality versus Specificity

Evolutionary biologists face a daunting task: they want to explain the behavior of a diverse set of taxa that adopt an unmanageable number of different behaviors. As a result, they tend to lump everything into a general, perhaps more superficial model that ignores specific cases but is useful in all circumstances. To do this, naturally, they must ignore a lot of what economists would consider to be important variables. The producer–scrounger game model provides a great example: it requires very few parameters, makes limited assumptions about the agents as well as the type of resource and so on. The model is meant to apply whenever a group of agents searches for a resource which, once found, can be shared. The game can be applied to bacteria-producing siderophores as well as whales hunting for patches of krill. Ecologists take great pleasure in knowing that their model can be applied widely to a broad set of species and problems.

The task faced by economists is equally daunting. They wish to account for decisions within a wide range of economic, social, and cultural settings in a single, but rather complex species: humans. Thus, they might not find it advantageous to change their models just to account for the behavior of another species, as their goal is to explain the behavior of humans in a given set of circumstances. To ecologists, economists thereby appear sometimes like compulsive hairsplitters: instead of coming up with one or two general models, they prefer to dig into institutional details, devising different games to capture more realistically all of the characteristics of the situation under study. Hence, while the behavioral ecologist keeps coming back with the general producer–scrounger game, the economist replies with a plethora of games, each for a slightly different way in which an exploitation situation can arise: the prisoner's dilemma, the linear or nonlinear public goods game, the common-pool resource game, and so on. Furthermore, economists get excited about the ways in which a given game can be modified even further (such that, e.g., individual incentives become aligned with social efficiency), for example, by writing legally binding contracts or by changing more generally underlying economic and legal institutions. This allows them to incorporate human-specific, and perhaps even cultural-specific, complexities to improve their predictions, but they do so at the price of taxonomic generalization.

The Structure of the Book

Whether you are an economist or an evolutionary ecologist, you will certainly appreciate the tension that loomed behind our discussions. However, you also need to understand the philosophy that underpinned our debate. Put simply,

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at an Ernst Strüngmann Forum hidden agendas are not tolerated, consensus is never a goal, and questions are viewed to be as important as answers. Within the confines of this intellectual retreat, participants are always encouraged to expose their individual and collective disciplinary ignorance, otherwise referred to as "gaps in knowledge." Once these become visible, the next challenge is then to brainstorm with colleagues on how such gaps could be filled.

This book is a summary of our debate and is structured around four main themes:

- Ecological and economic conditions of parasitic strategies
- Governance of natural resources
- Impact on human health
- Consequences for individual behavior, social structure, and design of institutions

Each section contains background information on fundamental concepts, which the Program Advisory Committee believed necessary for a fecund interdisciplinary discussion. Written before the Forum, these chapters were subsequently revised based on formal reviews as well as input received from the participants. As such, these chapters provide a glimpse of what economists, health scientists, or biologists initially considered important and may expose the disciplinary divides that exist. The final chapter in each section is a summary of each group's discourse. Drafted during the Forum by a heroic individual (the rapporteur) and written in collaboration with all group members, these chapters strive to overcome disciplinary deafness. Here you will find an economist trying to use the exploiter–investor terminology and a behavioral ecologist attempting to use economical terminology, e.g., in the characterization of resources in terms of rivalry and exclusivity. Genuine effort was made to bridge the gulf that separates disciplinary pursuit on the phenomenon of exploitation and here we wish to highlight the editorial efforts of Philipp Heeb and Julia Lupp who greatly helped us in trying to achieve this goal.

In this book you will find novel avenues for future research to address problems of sustainable use of renewable resources, the design of institutions, public health policies, and even medicine. Importantly, this volume represents the beginning of a further conversation that needs to be pursued between evolutionary biologists and economists, if we are to gain a better grasp of the factors that either govern the persistence of exploitation within social groups or which limit the use of cooperative investor strategies.

We are forever in debt to the Ernst Strüngmann Foundation and its Scientific Advisory Board for having afforded us this opportunity and providing the starting point for future interdisciplinary exchange. Let the dialog begin.

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