

Investigating Wasp Societies
A Historical and Epistemological Study

by

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ABSTRACT

The study of wasp societies (family Vespidae) has played a central role in advancing our knowledge of why social life evolves and how it functions. This dissertation asks: How have scientists generated and evaluated new concepts and theories about social life and its evolution by investigating wasp societies? It addresses this question both from a narrative/historical and from a reflective/epistemological perspective. The historical narratives reconstruct the investigative pathways of the Italian entomologist Leo Pardi (1915-1990) and the British evolutionary biologist William D. Hamilton (1936-2000). The works of these two scientists represent respectively the beginning of our current understanding of immediate and evolutionary causes of social life. Chapter 1 shows how Pardi, in the 1940s, generated a conceptual framework to explain how wasp colonies function in terms of social and reproductive dominance. Chapter 2 shows how Hamilton, in the 1960s, attempted to evaluate his own theory of inclusive fitness by investigating social wasps. The epistemological reflections revolve around the idea of investigative framework for theory evaluation. Chapter 3 draws on the analysis of important studies on social wasps from the 1960s and 1970s and provides an account of theory evaluation in the form of an investigative framework. The framework shows how inferences from empirical data (bottom-up) and inferences from the theory (top-down) inform one another in the generation of hypotheses, predictions and statements about phenomena of social evolution. It provides an alternative to existing philosophical accounts of scientific inquiry and theory evaluation, which keep a strong, hierarchical distinction between inferences from the theory and inferences from the data. The historical narratives in this dissertation show that important scientists have advanced

our knowledge of complex biological phenomena by constantly interweaving empirical, conceptual, and theoretical work. The epistemological reflections argue that we need holistic frameworks that account for how multiple scientific practices synergistically contribute to advance our knowledge of complex phenomena. Both narratives and reflections aim to inspire and inform future work in social evolution capitalizing on lessons learnt from the past.

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PREFACE

In a time when most efforts go into the one-sided production of big data as well as into the development of tools to handle them, this dissertation reminds us that multiple experimental, observational, conceptual and theoretical practices support the production of scientific knowledge. It develops two interconnected arguments. The first shows how important scientists in the past have advanced our knowledge of complex biological phenomena by constantly interweaving empirical, conceptual and theoretical work. The second argues that we need holistic, epistemological frameworks that account for how multiple scientific practices synergistically contribute to advance our knowledge of complex phenomena.

Small and seemingly unimportant objects have often played a pivotal role in the advancement of our understanding of important and complex questions. This is the case of the role that wasp societies have played in advancing our understanding of how social life functions and why it evolves. The evolutionary biologist and scholar of wasps M.J. West-Eberhard once wrote to philosopher R. M. Burian: “Wasps are not ... important as a ‘test organism’ like *Drosophila*, phage, garden peas, or white rat, although they have sometime been used that way. They are important as an ‘idea generator’, and I think there are things about wasps that makes this so” (Burian 1991, p. 334). This dissertation asks: How have scientists *generated* and *evaluated* new concepts and theories about social life and its evolution by *investigating* wasp societies?

Social insects, especially Hymenoptera, bees, wasps and ants, exhibit a bewildering variety of social organizations (Gadau and Fewell 2009; Hölldobler and Wilson 2009). Most social systems involve cooperation and division of labor. Eusocial

systems also show reproductive division of labor (Wilson 1971). This includes the presence in the colony of one or more individuals that are in charge of reproduction and other individuals that instead are not able to reproduce and take care of other duties.

The wasp family Vespidae is one of the few insect families in which diverse genera and species span a full spectrum of levels of organization, including solitary life, pre-social life, simple sociality, and several forms of complex sociality (Gadagkar 2009; Hunt 2007; Turillazzi and West-Eberhard 1996). Many genera of the Vespidae family, such as the most famous *Polistes*, are primitively eusocial (West 1967). They are organized in flexible social hierarchies, do not show morphological caste differentiation and have high degrees of flexibility in social roles (Pardi 1942, 1946; Rau 1939).

This dissertation aims to capture how the study of wasp societies, especially *Polistes*, has supported both the generation and the evaluation of new theories, concepts and hypotheses about immediate and evolutionary causes of social life. It follows two main lines of inquiry, a narrative and a reflective one. Both lines provide an entrance point to address broader issues about the historical, methodological and conceptual foundations of our understanding of social life and its evolution.

Narratives. Reconstructing Investigative Pathways

The works of the Italian entomologist Leo Pardi (1915-1990) and the works of the British evolutionary biologist William Donald Hamilton (1936-2000) represent the beginning of two important lines of inquiry, respectively on the immediate (e.g. Pardi 1942, 1946, 1948) and on the evolutionary understanding of social behaviors in wasps (e.g. Hamilton 1964a, 1964b, 1972).

In animal physiology (Röseler 1985; Röseler et al. 1984), evolutionary developmental biology (West-Eberhard 1996) and, more recently, in molecular sociobiology (Patalano et al. 2015), scientists have openly acknowledged the importance of Pardi's groundbreaking contributions. Hamilton's empirical work on wasps often did not reach the stage of publication (Wilson 1971; Grafen 2004). Yet, it influenced the way many scientists started looking for empirical evidence in order to understand whether abstract theories and models of social evolution could help explain why social life evolved (Wilson 1971; West-Eberhard 1975, 1978a, 1989; Strassmann 1979, 1981a).

Chapter 1 and Chapter 2 reconstruct how Pardi and Hamilton evaluated whether their own concepts, i.e. social dominance and social hierarchy in Pardi's case, and theories, i.e. inclusive fitness theory in Hamilton's case, applied to real biological situations. The main historiographical approach that informed these reconstructions is F. Holmes's idea of *investigative pathway* (Holmes 2004). According to Holmes, an investigative pathway is the "research trail ... [or] personal trajectory of individual scientists within the larger investigative movements in which they take part" (Holmes 2004, p. xvi). The metaphor of the pathway, Holmes writes: "suggests that one proceeds step-by-step, each step guided by those taken previously and by uncertain intimations about what lies ahead" (Holmes 2004, p. xvi). Holmes further characterized the pathway as a trail that: "... changes direction but does not loses continuity" (Holmes 2004, p. xvii).

Following the step-by-step development of Pardi's and Hamilton's investigative pathways helps understand how, within certain historical, cultural and scientific contexts, the two scientists dealt with the uncertainties of evaluating if new concepts and theories

would apply to real biological phenomena. It shows how these two scientists engaged in the evaluation of their ideas against empirical evidence over time, and how in this process they interwove experimental, observational, conceptual and theoretical reflections.

The idea of the pathway applies to the reconstruction of Pardi's and Hamilton's works on wasps in different ways. The Italian entomologist devoted the first 15 years of his career to the study of *Polistes* wasps, his main object of study. Thus, Chapter 1 reconstructs Pardi's investigative pathway between 1939 and 1952 in its entirety. Differently from Pardi's case, social wasps were not Hamilton's primary object of investigation. Hamilton chose wasps as they presented puzzling behaviors, which did not easily fit explanations in terms of his theory of inclusive fitness. Thus, focusing on Hamilton's empirical work on wasps, Chapter 2 provides a perspective that complements existing narratives about Hamilton's work that have mainly focused on more theoretical dimensions of his scientific production (e.g. Grafen 2004; Segerstrale 2013).

Chapter 1 asks: How did Pardi come up with new concepts and explanations of how social life is organized and regulated in *Polistes* wasps? And how did he go about evaluating whether such concepts actually apply to the complexity and diversity of wasp social life? The chapter details how Leo Pardi in the 1940s first showed that societies of the genus *Polistes* are organized in a linear social hierarchy that relies on reproductive dominance and on the physiological and developmental mechanisms that regulate it, i.e. on the status of ovarian development of single wasps (Pardi 1946a).

The reception of Pardi's work has relied mostly on broad reviews the Italian scientist wrote summarizing the main findings of his work in the English language (Pardi 1948). With some exceptions (e.g. Turillazzi 1996, 2014; West-Eberhard 1969), most

scientists after Pardi did not read or mention the many papers in German and in Italian where the Italian scientist published the results of his detailed investigations. Yet, these works are essential if we want to understand how Pardi generated and evaluated the concepts of social hierarchy and social dominance in the investigation of *Polistes*.

Chapter 1 relies on the analysis of published works that have not received proper attention and makes heavy use of material stored both in Pardi's house in Tuscany and in the Biology Department at the University of Florence. This material consists of personal and professional correspondence, notebooks, and notes for the preparation of lectures.

This material shows how Pardi's work emerged at the intersection of several scientific and national traditions, such as: Italian histology and cytology; American animal sociology; Austro-German ethology and physiology; and the French school of entomology. The numerous letters from and to many scientists around the world document Pardi's struggles in bringing together methods and concepts from behavioral, comparative and naturalistic approaches with physiological and mechanistic studies of social life in order to evaluate whether his concepts of social dominance and social hierarchy could help explain how *Polistes* societies actually work.

Chapter 2 asks: How did Hamilton attempt to evaluate whether inclusive fitness theory could help explain why social life evolved in concrete bio-social systems? As well as: What role did the empirical study of social wasps play in these attempts? Though mostly known for his important theoretical contributions (e.g. Grafen, 2004), Hamilton maintained that scientists should always pay close attention to concrete biological phenomena, with their complexity and even with their perversity (Hamilton 1996b).

Chapter 2 deals with Hamilton's empirical work in the 1960s and early 1970s. It details Hamilton's investigations of social wasps, mainly between 1963 and 1968.

In the early 1960s, with his theory of inclusive fitness, Hamilton introduced a neo-Darwinian approach based on population genetics in the study of social evolution (Hamilton 1964a, 1964b; Wilson 1971, 1975). The theory summarized the conditions favoring the evolution of so-called altruistic behaviors, say of behaviors that are detrimental to the individuals performing them and beneficial to those receiving them (Charnov 1977). Paradigmatic examples of altruistic behaviors are the self-sacrificing behaviors of workers in societies of ants, wasps and bees of the order Hymenoptera. Hamilton's inclusive fitness theory pointed out the importance of measuring the level of relatedness between actors and recipients of an altruistic action as well as costs and benefits in terms of fitness of those actions (Hamilton 1963).

Hamilton's biographers have pointed out his naturalistic passions and the wide knowledge Hamilton possessed of the biological world, especially of insects and plants (e.g. Grafen 2004; Segerstrale 2013). However, existing narratives do not show the interplay of empirical and theoretical work characterizing Hamilton's groundbreaking contributions in the 1960s. The step-by-step reconstruction of Hamilton's investigative pathway in those years records how he actually interwove empirical investigations and theoretical elaborations, in the attempt to provide theoretically sound and empirically grounded explanations of why social behaviors evolved.

In order to evaluate the theory, Hamilton wanted to measure both ecological (i.e. costs and benefits) and genetic (i.e. relatedness) factors driving the evolution of social life. Yet, in the 1960s and 1970s, there was no way to actually quantify these factors

(Hamilton 1972; Strassmann 1979, 1981a). Hamilton's notebooks and correspondence with entomologists and evolutionary biologists stored in The W.D. Hamilton Archive at the British Library in London show how the British scientist embarked, though not always systematically, in theory evaluation using a wide variety of empirical practices—from comparative analyses to observations and, at times, experimental manipulations. They also help document how Hamilton's empirical work inspired the work of many scientists after him who attempted to produce empirical evidence about why social life evolved (e.g. Wilson 1971; West 1967; West-Eberhard 1973, 1975; Strassmann 1979, 1981a; Strassmann and Orgren, 1983).

Reflections. Theory Evaluation and its Investigative Framework

Both Pardi's and Hamilton's investigative pathways show how these two scientists struggled in the attempt to evaluate new concepts (i.e. Pardi's idea of social dominance) and theories (i.e. Hamilton's inclusive fitness theory) against empirical evidence. The third chapter of this dissertation transitions from the reconstruction of *investigative pathways* to a reflection on the *investigative framework* that informs theory evaluation in the field of social evolution in the 1960s and 1970s.

Though Chapter 3 deals with theory evaluation specifically in social evolution, similar conclusions might apply to the way concepts, such as Pardi's idea of social hierarchy, and mechanisms, such as Pardi's explanations of the connection between social and reproductive dominance, can be evaluated against empirical evidence. Chapter 3 specifically asks: How does theory evaluation work in social evolution and how can we account for the main epistemological features of this process?

Since the late 1800s, entomologists had tried to reconstruct the main steps leading to the evolution of social life (e.g. Wheeler 1923; Richards 1971; Evans 1958).

Evolutionary biologists had asked how natural selection could produce behaviors that lower the fitness of the individuals performing them, such as the self-sacrificing behaviors of workers and auxiliaries in social insects (Fischer 1930; Haldane 1932). In the early 1960s, with its focus on both ecological (i.e. costs and benefits) and genetic (i.e. relatedness) factors, Hamilton's inclusive fitness theory raised new challenges, and opened new lines of empirical research in the study of social evolution (Wilson 1971; West-Eberhard 1975).

In the 1960s and 1970s, Hamilton's theory was new and contentious (e.g. Alexander 1974; Lin and Michener 1972; West-Eberhard 1975, 1978a). It was unclear whether or not it would point out the appropriate parameters (i.e. relatedness, costs and benefits) to understand why social behaviors evolved and "... whether there is evidence that it [the theory] does work effectively in nature" (Hamilton 1964b, p. 17). Some scientists strongly embraced the theory (e.g. Wilson 1971, 1975). Other scientists questioned it (e.g. Lin and Michener 1972). Yet, many scientists engaged in its evaluation using empirical methods (West-Eberhard 1975).

Chapter 2 already shows how Hamilton attempted to provide empirical evidence in order to evaluate inclusive fitness theory by studying wasps. Chapter 3 draws on Hamilton's work as well as on the work of two important scholars of wasps and evolutionary biologists from the 1960s and 1970s who greatly contributed to advance the field of social evolution: Mary J. West-Eberhard (1969, 1973, 1975, 1978a) and Joan E. Strassmann (1979, 1981a, 1981c). It focuses on the diverse and varied set of practices

these scientists used in the evaluation of inclusive fitness theory, at a time when the theory was new and data were scarce and hard to obtain.

Drawing on an analysis of the works of Hamilton, West-Eberhard and Strassmann in the 1960s and 1970s, Chapter 3 presents an account of theory evaluation in the form of an *investigative framework*. This framework provides an account of theory evaluation grounded in scientific practice. It makes use of a broad definition of investigative practice, which encompasses empirical, conceptual, and theoretical aspects of scientific work (e.g. Rouse 1996; Soler et al. 2104). Relying on the historical narratives, the framework argues that, in the production of knowledge about the evolution of complex bio-social systems, all such practices are not only interconnected, but they also constantly inform one another.

Existing accounts of scientific inquiry and theory evaluation keep a hierarchical distinction between inferences from empirical data and inferences from theories and models. On the one hand, *theory/model-first* accounts understand theory evaluation as a *top-down* process that starts with the derivation of hypotheses from the theory or models and ends with the *confirmation* or *falsification* of such hypotheses through empirical data (e.g. Earman 1983; Hempel 1965; Giere 2004, 2010). These accounts have neglected the constructive role of empirical investigations in the generation of hypotheses.

On the other hand, *experiment-first* accounts explain how empirical practices produce knowledge about phenomena, mainly as a *bottom-up* process (e.g. Bogen and Woodward 1988; Hacking 1983; Rheinberger 1997; Woodward 1989, 2011). Such accounts have pointed out that experiments play more creative roles and that a variety of assumptions and techniques for data gathering and analysis are, at least partially,

independent of high-level theories or models (Bogen and Woodward 1988; Woodward 1989, 2011).

Both kinds of accounts hierarchically separate (top-down) inferences from theories and models from (bottom-up) inferences from empirical data in the generation of statements and hypotheses about phenomena. Yet, Chapter 3 shows that it is hard to keep this hierarchical separation when we look, for instance, at how scientists have actually investigated social wasps in the evaluation of inclusive fitness theory. An analysis of theory evaluation in scientific practice makes clear that, inferences from the theories and inferences from the data have informed one another in the generation of hypotheses, statements, and predictions about phenomena of social evolution. Therefore, differently from both *theory/model-first* and *experiment-first* accounts, the *investigative framework for theory evaluation* in this dissertation argues that, if we want to understand how knowledge is produced about complex, evolutionary phenomena, it is important to account for how inferences from theories—and models—as well as inferences from empirical data inform one another.

The framework articulates how statements about phenomena of social evolution, the hypotheses and predictions about why social behaviors have evolved, emerge at the interface of top-down inferences from abstract theories (e.g. the theory of inclusive fitness) and bottom-up inferences from empirical (i.e. comparative, experimental, and observational data). Therefore, it provides a *holistic* and *integrated* perspective on scientific research. This perspective is holistic because it goes beyond the account of specific practices (e.g. modeling and experimentation) in the investigation of complex evolutionary phenomena. It shows how different practices are always interconnected and

never exist in isolation in the process of knowledge production. This perspective is integrated because it shows how different practices actually inform one another, for instance how inferences from the data and inferences from theories and models support one another in the production of scientific knowledge. This holistic and integrated perspective provides an account of theory evaluation that cannot be reduced to either theory/model-first or experiment-first accounts of scientific research.

Both the narrative and the reflective lines of inquiry in this dissertation address broad issues about the historical, methodological and conceptual foundations of our scientific understanding of social life. The narratives show how scientists have advanced our knowledge of complex biosocial systems and their evolution. Abstracting from the details, the reflections provide a framework that account for the synergistic use of multiple practices in the process of knowledge production about complex phenomena of social evolution. Both narratives and reflections aim to inspire future work in social evolution capitalizing on successful scientific endeavors and lessons learnt from the past.

CHAPTER 1

UNDERSTANDING SOCIETIES FROM INSIDE THE ORGANISMS

LEO PARDI' S WORK ON SOCIAL DOMINANCE IN POLISTES WASPS (1937- 1952)

1.1 Introduction¹

The Museum of Comparative Zoology at Harvard University once hosted a small gallery of the leading world scholars on social insects. On June 2, 1972, E.O. Wilson, one of the intellectual fathers of sociobiology, wrote to the Italian ethologist Leo Pardi asking for a picture to put in the gallery. Since then, Pardi sits in the Pantheon of social insects scholars. Leo Pardi was born in San Giuliano Terme, a small town near Pisa, in 1915 and died in Rignano sull'Arno in 1990. During fifty years of active scientific research, he gave groundbreaking contributions to the understanding of social life in insects, especially *Polistes* wasps, and about orientation mechanisms in sandhoppers (Pardi 1946b, 1948; Pardi and Papi 1952; Pardi 1954). This article reconstructs Pardi's work on *social dominance* in *Polistes* at the intersection of European ethology and American animal sociology between 1937 and 1952. It shows that a focus on Pardi's physiological and mechanistic approach enriches and complements existing narratives of the historical foundations of our understanding of animal behavior (e.g. Burkhardt 2005; Mitmann 1992).

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Social dominance and social hierarchy are widely recognized as essential features of insect societies, especially in many wasps and in several species of ants and bees (e.g. Wilson 1971; Hölldobler and Wilson 2009). Before Pardi, animal sociologists and psychologists had talked about humans and other vertebrate societies in terms of dominance and hierarchies (Schjelderup-Ebbe 1922; Allee 1931). In the early 1940s, Leo Pardi was the first to introduce these two concepts in the study of an invertebrate society (Pardi 1942, 1946a). He showed that societies of *Polistes* wasps are organized in a linear social hierarchy and that, in this genus, social dominance relies on reproductive dominance and on the physiological and developmental mechanisms that regulate it, i.e. on the status of ovarian development of single wasps (Pardi 1946a). Pardi's ideas have been recognized as a groundbreaking contribution not only in sociobiology but also in physiology (e.g. Röseler 1985; Röseler et al. 1984), evolutionary developmental biology (e.g. West-Eberhard 1996) and in recent studies in molecular sociobiology (e.g. Patalano et al. 2015; Gadau, 2015).

In his research, Pardi developed a peculiar style of ethology that brought together the observational approach of natural history, the comparative style of morphology (with a focus on internal organs) and experimental methods from embryology and physiology (Pardi 1972). In an obituary that he wrote after the death of the Nobel Prize Karl von Frisch (1886-1982), Pardi defined the Austrian scientist as a *physiologist of behavior* because of his attention to physiological mechanisms in the study of the complex patterns of social life (Pardi 1983). Von Frisch's attention to the physiological underpinnings of animal behavior became a scientific model for the young Italian scientist, as Pardi pointed out in many occasions (Pardi 1946a, 1948). Beside Karl von Frisch, the

American animal sociologist Warder Clyde Allee (1885-1955) had a major influence on the development of Pardi's ideas. Allee's studies on the hormonal underpinnings of social behaviors in vertebrates inspired Pardi's confidence in the possibility to mechanistically explain the causes of social life (Pardi 1948). In later years, inspired by both von Frisch and Allee, Pardi talked about his own approach as *etho-physiology* (Pardi 1996) or *natural experimentation* (Pardi 1972).

Existing narratives have usually dealt separately with the history of European ethology (e.g. Burkhardt 2005) and American animal social thought (e.g. Mitman 1992). These narratives have neglected the importance of physiological and mechanistic studies in shaping our current understanding of animal behavior. Pardi's work focused on physiological and mechanistic understanding of social life in animals and, at the same time, unfolded at the intersection European ethology and American animal sociology. Pardi's early etho-physiological investigations are an early example of disciplinary and methodological integration for the understanding of complex behaviors, such as the ones characterizing social life in *Polistes*. Numerous letters stored in Pardi's office reveal his active exchanges with scientists inside and outside of Italy, in the American, German and French speaking world. His correspondence shows Pardi's commitment in bringing together behavioral, comparative and naturalistic approaches with physiological and mechanistic studies of social life. Leo Pardi's etho-physiological work on *Polistes* as well as, in following years, Pardi's collaboration with his colleague and friend Floriano Papi (1926-) on orientation mechanisms (Pardi and Papi 1952) contributed to the emergence of a school of ethological research in the Italian peninsula (Papi 1991).

This article follows Pardi's investigations on *Polistes* from 1937, the year of his graduation at the University of Pisa, to 1952, the year of Pardi's last publication on social wasps before his return to the scene of sociobiology in the early 1970s. Pardi's investigative pathway in the early years of his scientific activity consists of four main stages, which show a progressive articulation of his ideas about social hierarchies and social dominance in *Polistes* (see Holmes, 2004). The first stage goes from 1937 to 1941. During these years, Pardi honed his skills in the histological and physiological investigation of insects working in Pisa with the Italian protistologist Leopoldo Granata (1885-1940) and, later, in Munich with Karl von Frisch. In the second stage, he explored *Polistes* wasp societies and recognized that *Polistes* societies were organized in a linear hierarchy. In the third stage, between 1942 and 1950, the idea of social dominance became the conceptual and analytical framework for the understanding of social life in wasps explaining the emergence and maintenance of social hierarchy. In the fourth stage, after an initial enthusiastic consensus, the French entomologist Édouard-Philippe Deleurance (1918-1990) in March 1950 attacked Pardi's work in an international meeting at the CNRS in Paris. Deleurance's attack compelled Pardi to design a conclusive experiment where he showed that his ideas were correct. The controversy also had a negative effect, as afterward Pardi decided to abandon the field of animal sociology for about 20 years. Pardi returned to the study of wasp societies in the late 1960s, during the heydays of sociobiology.

1.2 *Polistes* Societies in Historical Context

Wasps of the genus *Polistes*, commonly known as paper wasps, are one of the most important social systems in sociobiology (e.g. Jandt et al. 2014). Scientists have studied *Polistes* to understand both mechanistic and evolutionary factors underpinning social life in animals (e.g. Pardi 1942, 1946; West-Eberhard 1969). *Polistes* is a primitively eusocial genus and differs from highly eusocial insects such as most ants and bees (Wilson 1971). Highly eusocial insects are characterized by distinct morphological castes, which means that it is possible to distinguish queens and workers, say reproductive and non-reproductive castes, just by looking at their morphology. In primitively eusocial species, such as *Polistes*, this is not possible as the only differences between the castes are behavioral and all females are potential breeders (e.g. Marchal 1896; Rouboud 1916).

The genus *Polistes* is a cosmopolitan genus, found both in temperate and tropical regions (e.g. Richards 1951; Hamilton 1964; Eberhard 1969). Over the course of the year, each colony goes through a series of stages that constitute its life cycle. Fertilized queens overwinter in crevices or under bark (e.g. Rau 1938; Pardi 1942). In temperate climates in early spring, they start building a new colony either singly or jointly with other auxiliary foundresses. When several females participate to the foundation of a new colony, scientists talk of polygynic foundation. Out of the founding females, one becomes the leader and the others become auxiliaries or leave. The founding females are very aggressive when interacting with each other: bites, antennal clashing, clasping the other wasps are some of the behaviors characterizing colony foundation (Rau 1939). From these fights and aggressive interactions, a social hierarchy emerges (Pardi 1942, 1946a).

After the foundation, in late spring or early summer, the first larvae hatch giving rise to sterile workers. This phase is usually referred to as the workers phase. At a later time, reproductive females emerge. The new adults are either haploid males or females that will become the new potential foundresses (e.g. Heldmann 1936; Pardi 1942). The reproductive phase lasts until late summer or mid fall when the wasps disperse from their natal nest. Between colony decline and their entry into the hibernacula, the sites where *Polistes* hibernate, males and non-worker potential gynes mate. The fertilized females re-emerge after hibernation in the spring and start founding a new nest. During the founding and worker phase, individuals differentiate into reproductive castes (Heldmann 1936; Pardi 1942).

By the time Pardi started working on *Polistes* wasps in the late 1930s at the University of Pisa, there were more questions than answers surrounding wasps and their social life. Some scientists, also not professional entomologists, had observed wasp nests and made important conjectures about the mechanisms underpinning their organization (e.g. Rau 1938; Marchal 1896; Rouboud 1916). From the observation of the larvae-adult interactions, many authors had focused on the role of nutrients and on feeding behaviors for the understanding of social relationships in wasp colonies (Marchal 1896; Rouboud 1916). Yet, there was not a unifying framework that could make sense of the complex social systems of wasp colonies, their constructive activities and their yearly life cycle.

The German entomologist Georg Heldmann in “Über das Leben auf Waben mit mehreren überwinterten Weibchen von *Polistes gallica*” (Heldmann 1936) first rigorously dealt with the emergence of reproductive division of labor in the early stage of colony life. In this article, Heldmann, at the time curator and director of the Hessisches

Landes Museum in Darmstadt, defined one of the females coming out of the foundation as Nestmutter, mother of the nest, and observed that this wasp stays on the nest and lays most eggs (Heldmann 1936). He dubbed the rest of the wasps Hilfsweibchen, auxiliary females. These wasps, Heldmann found out, are mostly engaged with food collection as well as in building activities (Heldmann 1936). Heldmann's work openly raised the question that later became the main focus of Pardi's work. He asked if the polygyny at the foundation was real (*reell*) or fictitious (*scheinbar*). He observed that only one of the foundresses is able to lay eggs and, therefore, argued that the foundation is actually monogynic, although it might seem to be polygynic at a first sight (Heldmann 1936).

1.3 Apprenticeship Years (1937-1941)

When a student in Pisa at the Institute for Zoology and Comparative Anatomy, Pardi worked under the supervision of Leopoldo Granata, an eminent protistologist who had also carried out interesting research in cytology (Granata 1925). His work with Granata was at first about the main morphological features and physiological functions of the mesointestin in scorpions (Pardi 1936b). Still an undergraduate, Pardi published a series of short notes about his cytological and histological research in important Italian scientific journals of the time (Pardi 1936a, 1936b, 1937).

Granata had studied the function of fat bodies in amphibians (Granata 1925) and directed the young Pardi towards the investigation of these important, but still mostly unknown, internal bodies. In particular, Granata invited his young student to study position, role and physiological functions of fat bodies in several insects. In the manuscript for the speech delivered when he was awarded the Balzan Price in 1989,

Pardi described the work that Granata assigned him in this way: “The task given to me by my mentor at that time [Granata] was to pick up the larvae and dissect them in order to study the histological transformation of their fat bodies during larval life and beyond. To do this, I had to know the age of the larvae and some information about the biology of the colony”.

Pardi’s work on fat bodies under the supervision of Granata culminated a few years later in an impressive monograph, *I Corpi Grassi degli Insetti*, published by *Redia* in 1939. In this volume, Pardi detailed the role of fat bodies in storing proteins and lipids in the body and as a main source of energy for the growth and functioning of adult insects (Pardi 1939). Already in two short articles from 1937 and 1938, Pardi reported his preliminary observations about the function of fat bodies in *Polistes*. The two articles document Pardi’s encounter with his beloved wasps. This encounter happened from inside the organism, as Pardi’s focus was not directed to the understanding of the complex behavioral patterns of *Polistes* colonies, but rather on the physiological role that internal organs play in relation to colony life cycle, colony growth, reproduction and the provision of energy during extended non-feeding periods (Pardi 1939).

After graduating at the University of Pisa, Pardi was awarded a special fellowship by the Pisa Rotary Club to spend some months doing research abroad. Pardi did not use the fellowship right away and waited until 1941, when he decided to visit the lab of the future Nobel Prize Karl von Frisch. In the fall of 1941, Pardi spent about 2 months working with von Frisch and with his students in Munich. During his stay, Pardi actively helped in the activity of von Frisch’s lab. The research to which Pardi contributed was

published in 1942 in *Die Naturwissenschaften* with the title “Die Werbetänze der Bienen und ihre Auslösung” (Von Frisch 1942).



Figure 1. Leo Pardi, Karl von Frisch and Floriano Papi (from 1952)

Right after von Frisch’s death in 1983, Pardi delivered a speech for the *Accademia Nazionale di Entomologia*. He wrote that von Frisch had been for him: “... a perennial model, a constant point of reference” (Pardi 1983, p. 3). Pardi saw in von Frisch a scientific model because of the way the Austrian scientist conceived of the appropriate goals and methods in the study of animal behavior. Pardi described von Frisch’s work as an: “[...] harmonious synthesis between passionate and careful naturalistic observation [...], which accurately formulates the problem, and the simple and rigorous experimentation, which aims to solve it” (Pardi 1983, p. 6). Since his meeting with von Frisch, this harmonious synthesis would become Pardi’s own way of operation.

In a hasty note that he used for the preparation of some lectures, Pardi sketched out the main difference between K. Lorenz and Von Frisch's investigative styles. Pardi's sketch shows why he saw von Frisch's approach as a scientific model. Pardi defined Lorenz's style with the following words: *historical, comparative anatomy, qualitative, theoretical*. When describing von Frisch's investigative approach, Pardi used diametrically opposite terms: *experimental, physiology, quantitative* and *cautious with theoretical speculations*. The two Nobel Prizes, according to Pardi, differed in every respect. Whereas Lorenz had a 'historical' approach, von Frisch used an 'experimental' approach. Lorenz made use of comparative anatomy as the main tool for the investigation of animal behavior, while von Frisch used physiological experiments. Also, Lorenz was prone to speculate and von Frisch was extremely cautious in the elaboration of general hypotheses and in the interpretation of experimental results. Finally, von Frisch's approach was 'quantitative' and Lorenz's way of investigating animal behavior was mostly 'qualitative'.

Yet, the attributes of their investigative styles were not all that mattered to Pardi. He also pointed out the different personalities of the two scientists. Under Lorenz's name, he wrote the words 'exhibitionist' and 'chatty'. Under von Frisch's name, on the opposite, Pardi wrote the words 'discreet' and 'taciturn'. From what his students, colleagues and family members report, Pardi's personality was definitely closer to the latter than to the former. Both the man and the scientist Karl von Frisch came to represent an exemplar model for the young Pardi.

1.4 Social Hierarchies and Social Dominance (1941-1942)

After his encounter with von Frisch, social behaviors in *Polistes* societies became Pardi's main topic of investigation. In his first studies of *Polistes* social behavior, Pardi focused on the initial stage of nest foundation and on the process of differentiation between reproductives and non-reproductives observable in this early stages of the colony life cycle (Pardi 1940, 1941). The idea of social dominance emerged during these years, although still at an embryonic stage (Pardi 1942). In three short notes that appeared between 1940 and 1941, Pardi addressed Heldmann's hypothesis that polygyny is actually fictitious and not real (Pardi 1940, 1941). Contrary to earlier studies, which relied above all on behavioral observations, Pardi brought together the observation of behavior with results from the investigation of the physiological development of the wasps (Pardi 1940).

Pardi's observations of behaviors agreed with Heldmann's hypothesis about the fictitious nature of polygyny at nest foundation (Pardi 1940). Yet, his histological analysis of internal bodies did not. Pardi researched wasps' fertility by dissecting their ovaries and looking into the metabolic functions of other internal bodies, such as fat bodies, which he knew extremely well from his previous work. He confirmed that all the wasps captured and dissected at nest foundation were fecundated, with well-developed ovaries and with complete vitellogenesis. In 1941, relying on his dissections, Pardi argued that the foundresses contributing to the foundation of a new nest were actually equivalent. Nonetheless, the monogyny at the foundation was, according to him, real and not fictitious, as the behavioral observations seemed to show and as Heldmann had argued. However, Pardi explicitly admitted that he could not say yet how the process of

differentiation actually takes place. He wrote: “division of labor emerges only with the emergence of social life and due to mechanisms that are not clear yet” (Pardi 1941).

In the spring of 1942, Pardi performed numerous observations of colonies both in captivity and in the wild. He used mostly cages put on the roof of the Zoology department in Pisa and wasps found in the countryside. Pardi published his findings in a long article, “La poliginia iniziale di *Polistes gallicus*” (Pardi 1942). Here, Pardi reported the main features of the social Hierarchy that emerges during the foundation of the colony. Before Pardi, studies about social Dominance had only focused on vertebrates, mostly birds (Heinroth 1911; Schjelderup-Ebbe 1922). The Norwegian zoologist Thorleif Schjelderup-Ebbe (1894-1976) was the first to provide an extensive description of social Hierarchies and dominance relationships in hens. His paper “Beiträge zur Sozialpsychologie des Haushuns” from 1922 soon became a classic for scientists in the field of animal psychology and animal sociology (Mitman 1992). Schjelderup-Ebbe had described the existence of a linear hierarchy, a despotic one, in chickens and hens (Schjelderup-Ebbe 1922). In this kind of hierarchy, the alpha hen dominates with her aggressive behavior all the other individuals in the group. Also, beta is dominated by alpha, but dominates the individuals underneath her in the hierarchy. Alpha will have nutritional as well as reproductive advantage over all the rest of the colony members. The lowest ranking individuals, instead, will be disadvantaged in comparison to all the rest. Schjelderup-Ebbe’s ideas inspired many other works of this kind in the following years (Mitman 1992).

In 1942, Pardi found out that social Hierarchy in *Polistes* is also linear. He detailed the fights at nest foundation that precede the establishment of the hierarchy as

well as the aggressive interactions between dominant and subordinate wasps (Pardi 1942). Numerous letters show the existence of a dense intellectual conversation between Schjelderup-Ebbe and Pardi. The correspondence between the two scientists show Pardi's commitment to understand how his description of Social Hierarchies in wasps could relate, and maybe find confirmation, in studies on other taxa. Beside him the Norwegian scientist had worked also on some invertebrates, such as some species of ants, and helped Pardi to think through the difficulties of applying concepts used for humans and higher vertebrates to describe an insect society. In his 1946, Pardi was still puzzled by the striking similarity of social organization in taxa so different from one another. He wrote: "The statistical analysis of the behavior of single individuals in societies of a Vespidae (*Polistes gallicus*), revealed since 1942 a surprising correspondence with the facts observed in such taxonomically distant social groups. I do not want to extend my observations to all social insects, but I think this similarity is worth to point out and present here" (Pardi 1946b, p. 9)

In "La poliginia iniziale", Pardi also hypothesized that the main factors driving differentiation among the founding wasps had to be found in the mechanisms underpinning potential fecundity. Still awaiting a full blown experimental confirmation, Pardi's tentative explanation of the mechanisms of differentiation relied on two main factors, an organic difference among the foundresses and some secondary causes that can be traced back to work castration, the more traditional hypothesis elaborated by Marchal (1896). About the primitive and organic differences, Pardi wrote: "I think that, likely from the very beginning, among the associated females there exists physiological or anatomical differences, that determine their behaviors. Today I cannot say for sure what

are these differences [...]. As for now, I will just hint at the possibility that one of the main differences is represented by the potential fecundity, which can be measured with some degree of approximation by comparative, histological analysis of their ovaries” (Pardi 1942, p. 88).

Trying to explain how equivalent females can acquire different roles during the foundation of a colony, Pardi started reflecting on the idea of dominance. He gave his first definition of dominance in this short passage: “I have named ‘Dominance’ that characteristic behavior of an ‘active female’ ” (Pardi 1942, p. 44). Here, social dominance is still a feature of some specific individuals, not an overarching regulatory framework. Dominance is at this point a kind of activity performed by the Nestmutter or leading wasp on the nest, which becomes the only egg-laying females and shows a dominant, aggressive behavior (Pardi 1942). Yet, Pardi started finding a place for social dominance by weighing it against other possible phenomena typical of a polygynic colony foundation. In particular, he compared social dominance with the idea of trophic advantage and work castration. Such explanations, according to Pardi, were correct, but they were not sufficient to explain the establishment of social hierarchies in a *Polistes* colony (Pardi 1942).

1.5 Doing Science and Networking in War Times (1942/1946)

In “La Poliginia iniziale” Pardi’s ideas about social hierarchy and social dominance were still hypothetical and not fully supported by evidence. Between 1942 and 1946, he transformed those hypotheses into an explanatory framework supported by detailed observations. An account of his research on *Polistes* eventually appeared in two

important articles “La ‘Dominazione’ e il ciclo ovarico annuale in *Polistes gallicus*” (Pardi 1946a) and “Sui fenomeni di Dominazione nelle società degli animali” (Pardi 1946a, 1946b).

In the early 1940s, doing science in Italy was a difficult enterprise. World War II hit the Italian peninsula and, as a consequence, academic production dropped in most fields. In 1944 Tuscany, where Pardi lived and worked at the time, became one of the main fronts of the battle between the Allies and the Nazis. The river Arno in Pisa was the border dividing the Nazis and the allies for months. During the years of the war, Pardi took most of the equipment from the lab, as well as many of the books in the department, and stored them outside the city with the hope that they would not be destroyed. He also participated, although not in a prominent position, to the movement of partisan resistance to Nazi’s occupation (Pardi 1991). On top of the difficulties brought by the war, in 1946, the flood of the Arno in Pisa destroyed part of the facilities of the Zoology department, as reported by Pardi in a footnote in one of his 1946 papers (Pardi 1946a). A long certificate stored in the archives of the University of Pisa documents and recognizes Pardi’s involvement in keeping the department active and in minimizing the damage of the war.

In those years, Pardi consistently looked for help in rebuilding the library and trying to attract attention to the harsh situation of Italian scientists. He got in touch with scientists at the forefront of animal sociology both in Germany and in the United States. Numerous letters from these years are still stored in his office. In these letters, Pardi asked for help to rebuild the library in Pisa, mostly focusing on contributions that could be of interest for his personal research, as well as for the research of some of his colleagues. He asked for volumes and printed copies of both articles published in the last

years and articles destroyed because of the war or of the flooding of the Arno. In a letter from November 11, 1945 to the famous Chicago animal sociologist W.C. Allee, Pardi wrote: “Dear Sir, the war has destroyed most part of our library. We have great difficulties to reconstitute the destroyed or damaged collections of scientific periodics. Therefore, we would appreciate it very much if you would kindly send to our institute reprints of your articles and the ones of your co-workers.” This is followed by a long list of articles.

While trying to bring back material and attention to Italian science, Pardi wanted to make his work known outside of Italy. In an undated letter, written on a paper letter from the Red Cross, Pardi reported to Allee the main ideas that he was working on at the time. He talked about his recognition of a social hierarchy in an invertebrate society, but did not mention the idea of social dominance: “From 1942 until now I have made some studies concerning the Vespidae *Polistes gallicus* L. which I think will be of interest to you. The main conclusion of this studies follow: My observations prove conclusively that in this social Vespidae a social hierarchy exists. This hierarchy is very similar to the hierarchy you observed in birds and other vertebrates, and the workers of the same nest are far from being equivalent. I studied very carefully the structure and modifications of this social hierarchy.”

Later on, in a letter from April 23 1946, Pardi asked W.C. Allee if he knew about any American journals that would be willing to publish an article about his work on social hierarchy in *Polistes*. Allee’s response to Pardi was enthusiastic. He wrote: “I would welcome an article by you concerning the social hierarchy in wasps [...] You can have a considerable leeway in constructing your paper, giving new facts and weaving

them in with other material known to you, particularly with other materials that have been published in your part of the country within the last few years.” Although the invitation to write the article came in 1946, the publication got delayed because, as Pardi wrote: “[...] some other duties and first of all the work of repairing the institute, have diverted me from the research. I hoped to send to you the results of my experiences and observations [...] but the researches have not come to a decisive point and I want another season in order to perform them” (May 6, 1947). The publication that Pardi and Allee are talking about appeared in 1948 in *Physiological Zoology* with the title “Dominance Order in *Polistes* Wasps” (Pardi 1948). This article was a review summarizing conceptual and experimental advances presented in Pardi’s 1946 articles (Pardi 1946a, 1946b).

“Dominance Order in *Polistes* Wasps” became Pardi’s most cited contribution until today, mostly because it was written in English and because it summarized work previously published only in Italian and German.

In the same years, after Pardi had published mostly in Italian journals, the Swiss zoologist H. Hediger and the future Nobel Prize Niko Tinbergen invited him to write a contribution for the newly created international journal *Behavior*. The contribution, this time in German, was also published in 1948 with the title “Beobachtungen über das interindividuelle Verhalten bei *Polistes gallicus*” (Pardi 1948). In a letter from March 30, 1946, Hediger wrote to Pardi: “If you have new papers ready for publication, we shall be glad to have them for the new journal.” And a few months later, after receiving Pardi’s response, in a Letter from May 14, 1946, Hediger enthusiastically wrote: “... we should be extremely glad to have your manuscript about the social hierarchy in the Vespidae, in

any language whatever. As far as I know, your work would be the first publication concerning social hierarchy in invertebrate animals.”

1.6 Social and Reproductive Dominance (1946-1950)

Pardi's experimental work between 1942 and 1946 mostly focused on the organic processes that influence and determine the establishment and maintenance of a social hierarchy in *Polistes*. In 1942 Pardi had already pointed out the connection between the place occupied by a single individual in the social hierarchy and her reproductive potential. The relationship between social status and reproductive dominance led Pardi to look for the organic basis of social interactions in the level of physiological development of the ovaries, the organs deputed to the fulfillment of reproductive functions.

As Pardi clearly stated in 1946: “ ... dominance has a definite relation to the developmental status of the ovaries” (Pardi 1946a, p. 45). Already before the 1942 publication, but more consistently afterward, between 1942 and 1946, Pardi engaged in detailed dissections of internal bodies of wasps. Although he focused mostly on ovaries, he also paid attention to the physiological and development status of other internal bodies, such as corpora allata and fat bodies. Between 1940 and 1945 Pardi performed more than 450 dissections of ovaries (Pardi 1946a).



Figure 2. Pardi working with a Microscope (from 1943)

In 1946, Pardi elaborated an Index of Ovarian Development that allowed him to provide a quantitative analysis of the developmental status of ovaries. In order to develop this index, Pardi, measured the diameter of the eggs closest to the oviduct in each ovariol. As there are 3 ovarioles for each side, for each individual Pardi would obtain 6 measurements. He would then simply calculate the arithmetical mean of the 6 measurements. Beside performing measurements of this kind and developing his index of ovarian development, Pardi focused on the differences in physiological function of the ovaries at different developmental stages. He observed that the relationship between the status of ovaries is not only a function of how big they are, but it also depends on the physiological conditions of the ovaries, say on whether the ovaries are growing or they are regressing (Pardi 1946a).

Parallel to the *index of ovarian development*, Pardi developed an index for the measurement and assessment of social dominance. He used a definition of social hierarchy similar to the one formulated by Schjelderup-Ebbe (1922) and added a statistical characterization to the concept. A social hierarchy can be established by looking at the statistical mean value of all the possible encounters among the individuals in a group (Pardi 1946a, p. 10). By looking at all the interactions among the different individuals on the nest, Pardi created a Dominance Index. This index was meant to allow for the measurement and assessment of dominance interactions. Pardi would measure the Dominance Index by multiplying the number of individuals dominated for 100 and then divide the result by the total number of individuals met: $I = (N \text{ dominated individuals} \times 100) / N \text{ Individuals met}$.

By creating an index for ovarian development as well as a dominance index, Pardi was able to more clearly quantify the relationships between the status of internal organs and the role that different individuals play in the social hierarchy of the colony. This made possible the application of statistical analysis as well as the production of graphic representations of how the two indexes could vary in relation to each other. A diagram in “La ‘Dominazione’ e il Ciclo Ovario Annuale” shows the correlation between ovarian development and social status during the life cycle of the colony. On the X-axis Pardi put the time of the year and on the Y-axis the level of ovarian development. Each line in the diagram represents the status of development of a given wasp. At the foundation, individuals starting with a small difference in ovarian status develop suddenly in Alfa and Beta or Lower females respectively. Also, at the hatching of the larvae the individuals with most developed ovaries are the ones that end up higher in the hierarchy. The ones

with underdeveloped ovaries have a lower rank. In this way, Pardi graphically showed the existence of a correlation between ovarian development, reproductive dominance and social dominance.

Besides recognizing the existence of a correlation, Pardi pointed out further directions of research that could eventually lead to the assessment of the biological mechanisms causally connecting social and reproductive dominance. First, Pardi proposed to assess how the status of ovarian development could influence the establishment of social hierarchies; second, he wanted to understand the opposite process, say how dominant or passive behaviors can influence respectively the optimal or underdevelopment of ovaries. He recognized the need to understand both sides of the causal link and produced hypotheses, which were confirmed by important wasps scholars in the 1970s and 1980s (Röseler 1985; West-Eberhard 1969).

In the 1946 papers, Pardi hypothesized that the status of the gonads influences the behavior of single individuals and, consequently, their role in the hierarchy. Also, whereas the influence of ovarian secretion on social behavior was direct, according to Pardi, also internal secretions of other internal organs produced both by the corpora allata and by fat bodies influenced the development of ovaries and, consequently, the formation of social hierarchies (Pardi 1946a). Assessing the causal power of dominance on the development of ovaries was a more complicated endeavor. Pardi hypothesized that differences in dominance behaviors have an effect on the developmental status of the gonads, although it was still not clear to him how this could happen (Pardi 1946a, 60). Pardi's ideas on this point refer mostly to the emergence of workers in the life cycle of the colony. He tried to parse out the nutritional, environmental and workload related

factors in the production of subordinate individuals that give up their reproductive power. According to Pardi in 1946, all these factors acted jointly as a consequence of the overall dominance system (Pardi 1946a, 1947).

In “Sui fenomeni di dominazione nelle societa’ degli animali” Pardi enthusiastically observed: “In the last few years their study moved from a purely observational phase to an actual experimental phase” (Pardi 1946b, p. 9). When Pardi talked about an experimental phase, he was mostly referring to the work that W.C. Allee was doing in collaboration with his students at Chicago (Mitman 1992). Between 1937 and 1939, Allee together with his students started researching the effects of hormones on the social rank of individual hens (Allee and Collias 1940; Allee et al. 1939). Here, Allee aimed to provide a physiological explanation for the existence of social hierarchies by injecting hormones that would bring individuals higher or lower in the hierarchy. In their studies, the American scientists found out that injecting testosterone propionate in some lower ranked individuals for an extended period of time increased their aggressive behavior and gained them a higher rank. Studies on the hormonal dimension of social organizations also included estrogen, epinephrine and thyroxine (Allee and Collias 1940). Allee’s work supported Pardi’s confidence in the possibility to find the physiological and mechanistic basis of social behavior in *Polistes*.

1.7 Interpreting Social Dominance. Are mechanistic Explanations enough?

Although the work of many important scientists of the time influenced and inspired Pardi’s work on *Polistes*, Pardi’s engagement with the phenomena of social dominance, subordination and hierarchies took place within a broader reflection on the significance of

such phenomena in the animal and human world. His approach also relied on intellectual sources outside of the realm of experimental sciences of the time. Mostly, Freudian psychoanalysis and human sociology played an important role in the development and refinement of Pardi's ideas (Pardi 1945, 1946c). These reflections outside the boundaries of experimental sciences converged on one main issue: the differences among single individuals inside a society, or even inside the same caste. Although Pardi aimed to find mechanistic explanations of social behaviors, he wondered about the individualistic and egoistic differences that seemed to elude such mechanisms (Pardi 1945, 1946c).

In a passage from the article "Dominazione e gerarchia in alcuni vertebrati", Pardi made clear his doubts about the explanatory power of purely mechanistic explanations: "Today it would be hard to agree with Rabaud that for instance the individuals in an insect society, similarly to a machine that has been charged, behave in the group exactly as if they were alone, or that the social factor consists only in the interaction, or even that, if there is interaction, this latter has a very limited influence, which can be reduced to a facilitation of phenomena, which, by themselves do not have anything of social [...]" (Pardi 1950). Also, in a letter to the Italian entomologist, Guido Grandi (1886-1970), Pardi brought up the problem of how to reconcile his mechanistic tendencies and the broader picture in which his investigation found their significance. Pardi wrote: "I have thought a lot about the very short chats that we have had. I must confess that my mechanistic tendency (which you rightly recognize in me and that is difficult to eliminate) has been strongly shaken. Your words have made me think a lot." (1946, April 29)

Although it was difficult to actually do any work during the years of the war, Pardi found time to write for the newborn journal of the Italian psychoanalytic society, *Psicoanalisi*. A picture in his office also documents his presence at the first meeting of the society in October 25-26, 1946. Two articles by Leo Pardi appeared in the journal *Psicoanalisi* in 1945 and 1946: “Sul comportamento sessuale dei primati subumani” (Pardi 1945) and “La psicoanalisi e lo studio di alcuni comportamenti animali” (Pardi 1946c). Both articles ventured in the field of primate social behaviors and showed interesting ideas about the role that social dominance plays not only in *Polistes* wasps but in a wide variety of animal societies (Pardi 1945, 1946c).

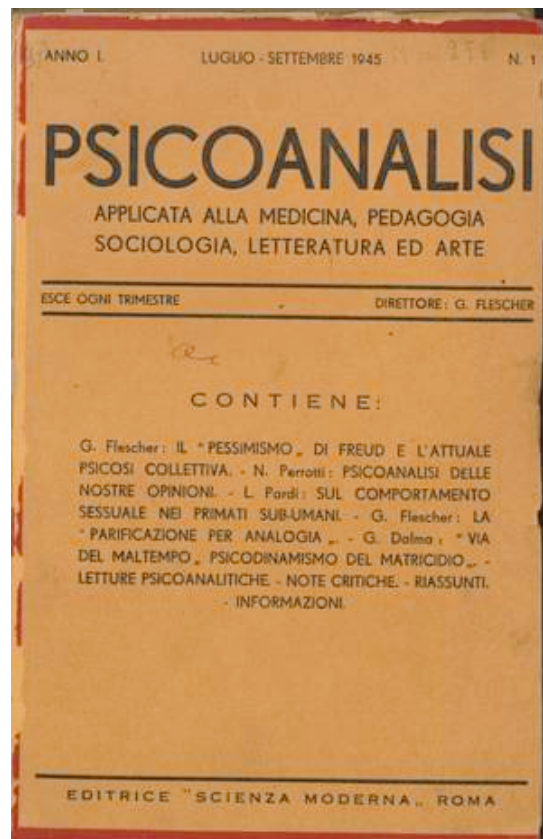


Figure 3. First Volume of *Psicoanalisi*

In “Sui Fenomeni di Dominazione”, Pardi argued that, although social behaviors in animals are ‘schematic’ if compared to the same behaviors in humans, as they follow definite rules dictated by physical/organic conditions, this does not mean that, in animals, variation among individuals disappears (Pardi 1946b, p. 14). Instead, it is essential to take into account individual variations in behaviors in order to understand social hierarchies. According to Pardi, the inter-individual differences contribute to differences in how animals in the colony can satisfy their elementary needs which is the basis for the struggle for existence characterizing nature at many levels, even within a single wasp colony. Pardi observed that dominance systems are a result of this struggle of one individual in the colony against the others. He wrote: “Dominance and social hierarchies are the result of a ‘mechanistic compromise’ between internal impulses in each individual towards the satisfaction of individual needs and the opportunity that the environment offers to satisfy them” (Pardi 1946b, p. 16).

Pardi interpreted the overall system of social dominance in Freudian terms. The mechanistic compromise between the impulse to satisfy elementary needs and the limited availability of resources that posits limits to their satisfaction is an example of the opposition of the Principle of Reality and Principle of Pleasure (Pardi 1946c). The principle of pleasure reigns supreme in unconscious processes. But the reality principle ensures the achievement of satisfactions in reality (Freud 1977). The interplay of the two principles, according to Pardi, can be seen at play in the establishment of social hierarchies in animal societies, especially but not only in wasps. On the one hand, every individual tries to satisfy its elementary needs. But, due to the lack of resources as well as to the competition for those resources inside the same colony, they cannot all achieve this

goal and have to figure out ways in which they can actually satisfy those needs. Thus, the 'mechanistic compromise', as Pardi called it, between the two impulses that gives rise to the emergence of social hierarchies (Pardi 1946b).

Beside Freudian psychoanalysis, Pardi's interpretations of social life in wasps with its regulatory features was also inspired and influenced by recent works in human sociology. Alfredo Niceforo (1876-1960), one of the first sociologists in Italy who made use of statistical analysis and empirical observations, was a major source of inspiration for Pardi. The reason why Pardi turned to Niceforo's work was again the difficulty to mechanistically explain the reasons both for individual variability and social regulation. Pardi referred to Niceforo's article "Attrazione, Repulsione e Circolazione nella Vita Sociale" (Niceforo 1935) in his main 1946 paper. Niceforo in that article stressed the differences characterizing single individuals within human societies. Although organized in social congregations, single individuals are always unique. However, these differences, according to Niceforo, can be measured. He wrote: "These differences are all measurable, and have been actually measured, so that looking at the numbers, these differences show they natural law of variability that regulates them" (Niceforo 1935, p. 190).

The claim that those differences can be measured, and therefore made object of scientific observation, were extremely appealing to Pardi. In fact, Pardi was fascinated by Niceforo's use of statistical analysis in the study of human societies. Niceforo used statistics to quantify and classify the main features of social phenomena and, more generally, of the 'collective facts', including indices of progress and the degree of civilization of social groups, peoples and different races. Niceforo's books *La misura della vita* (Niceforo 1919) and *Il metodo statistico* (Niceforo 1923) can still be found in

Pardi's office. In a letter by Niceforo to Pardi dated May 26, 1946, Niceforo praised Pardi's work on social hierarchy in wasps: "I had read the beautiful and original article that you wrote in the new journal *Historia Naturalis*. I was impressed. I found in your observations the guidelines for a ... human sociology, similar to the one that I have tried to sketch for a long time."

1.8 The Controversy with Deleurance in Paris (1950)

By 1950, Pardi had published the results of his research on both Italian and international journals, which brought his work to the attention of the international audience of animal psychologists and sociologists as well as entomologists and zoologists. In the early 1950s, Pardi's work on social wasps suddenly stopped. In these years, his career took a turn away from the study of social behaviors in wasps and towards the investigation of orientation mechanisms in the arthropod *Talitrus* (Pardi and Papi 1952; Pardi 1954). The reasons of Pardi's abandonment of the field of animal sociology can be found in his reaction to a controversy that exploded during the international conference *Structure et Physiologie des Sociétés Animales* in Paris in 1950. During this conference Pardi's work was strongly attacked by the French entomologist and neuro-physiologist Édouard-Philippe Deleurance (1918-1990).

Édouard-Philippe Deleurance, a *Polistes* expert himself, was a contemporary of Leo Pardi. He was born in 1918 and studied with Pierre-Paul Grassé (1895-1985) in the *Laboratoire d'évolution des êtres organisés* in Paris. Later, Deleurance became the director of the *Département de Comportement Animales* at the *Centre National de Recherche Scientifique* (CNRS) in Marseille. Deleurance's first publications on social

wasps seemed to agree and support Pardi's ideas. In his first short communication published in 1946 (Deleurance 1946). Deleurance reported results speaking to the problem of the inhibition of oviposition in worker wasps. Deleurance proposed that the mechanisms that lead to inhibition of egg laying are due to the presence of the founder queen on the nest and, possibly, to dominance-subordination relationships (Deleurance 1946).

After learning about the similarity of their work, the Swiss zoologist H. Hediger in 1947 put Pardi in touch with Deleurance. He wrote to Deleurance recommending him to read Pardi's publications and forwarded his letter to Pardi to let him know that 'a young French scientist' was interested in the same aspects of *Polistes* biology that Pardi had been investigating. Hediger's letter to Deleurance is still stored in Pardi's office. He wrote: "[...] In the Second Issue of *Behavior* [...] there is a very important work about observations of inter-individual behaviors in *Polistes gallicus* by Prof. Pardi, Pisa. I have no doubt that this work will be of interest to you; hence, I dare to send to you an exemplar. I also ask you to make me the big favor to send a copy of your work about your raising of the wasps to Prof. Pardi". Deleurance must have sent the results of his work to Pardi, as Pardi in a letter from May 12, 1947 acknowledged the reception of Deleurance's 1946 article. Pardi wrote to Deleurance: "Dear Colleague, I have received your nice letter from May 5 and, right afterward, your great works that you have sent me. [...] I am very happy that you, independently from me, have reached results that agree essentially with mine, and even more because you deal with a different species."

The next communication between Pardi and Deleurance took place a few years later, at least from what is possible to see from the material conserved in Pardi's office.

However, this letter was of a totally different tone. Deleurance communicated to his Italian colleague his substantial disagreement with his ideas. Between the 1947 letter and the letter expressing open disagreement, Deleurance had studied the main mechanisms that underpin the creation of a social hierarchy in *Polistes* wasps with a focus on construction activities (Deleurance 1952a, 1955a). In his 1948 contribution, Deleurance scrutinized and criticized Pardi's results about the role of ovarian development in the creation of the hierarchy (Deleurance 1948). Similarly to Pardi, Deleurance ovariectomized a small group of workers (Deleurance 1948). However, contrary to Pardi, he observed that: "the activity of the subjects that survived castration is normal [...] castration did not seem to affect social dominance" (Deleurance 1948, p. 866). In a footnote, Deleurance wrote: "Our results seem to disagree with those by L. Pardi" making explicit reference to Pardi's 1946 paper.

Deleurance warned Pardi of his disagreement before the Paris conference, as documented in Pardi's response from February 28, 1950, just a month before the Paris conference. Pardi wrote to Deleurance: "Dear Colleague, I just received your notes on *Polistes*, that you so kindly sent me. I thank you a lot for this. Also, I dare sending you two short papers. I have good reasons not to recede from my opinion about the existence of a important correlation between ovarian activity and behavior. I will make my thoughts more precise in written form."

1.8.1 Deleurance's first critique: Social dominance is not an appropriate concept

At the 1950 conference, Deleurance's general critique relied on a more general concern about the power of human language to describe animal behaviors in lower animals.

Deleurance was concerned about the use that scientists make of concepts used for humans and other vertebrates to describe behaviors of invertebrate species. Social dominance was one of those concepts. According to Deleurance, whereas the idea of social dominance might be appropriate to describe social interactions and systems in the vertebrate world, this is not the case when it comes to wasps and invertebrates. He argued that his own observations of wasp behaviors in the nest did not support the use of the idea of social dominance. The behavioral patterns that he had detailed did not fit the patterns that characterize social dominance in other animal societies, such as chickens and pigeons. Thus, these concepts could be appropriately used to describe vertebrate societies, as in Allee's studies, but not to describe and analyze invertebrate societies, as Pardi tried to do.

In this critique, Deleurance explicitly referred to the work of the founder of French physiology, Claude Bernard. Deleurance followed Bernard specifically in the way in which he conceived of the value of scientific hypotheses vis-a-vis experimental observations. The latter were concrete and constituted the concrete results of scientific investigations. The former had just a practical value. He explicitly argued: "... we refuse to abandon the level of the concrete, we only give to the Hypotheses a practical value" (Deleurance 1948). Pardi's application of the notion of social dominance to *Polistes* societies, according to Deleurance was a: "... deduction founded on the observation of correlation rather than on experimentation" (Deleurance 1952a, p. 190). By deduction here Deleurance meant the analogical reasoning that led Pardi to apply categories and concepts used in vertebrate societies to *Polistes* wasps. The idea of social dominance, according to Deleurance, was a typical example of the anthropomorphic fallacy in which:

“the analogy takes over the analysis: an explanatory system is used that does not provide any information at all on the appearance (allure) of the phenomenon”

In his response to Deleurance on this point at the Paris conference, Pardi referred to Allee’s behavioral definition of social dominance and claimed that there are no reasons why it should not be appropriate to use it in the case of wasp societies. He argued that, if a hierarchy is simply a rank-order established by the kind and number of behavioral interactions inside the nest, namely through direct fights, subordination of passive individuals and a mix of the two, then, if we observe the same patterns in wasps, it is legitimate to argue that also those systems have a dominance-subordination hierarchy. Pardi reported that: “Once we define objectively what constitutes a hierarchy based on dominance-subordination, when we look for phenomena that fit that definition, it is absolutely justified to extend this concept to other animals beside vertebrates [...] There is no difference at a biological level (or even at a psychological level) that imposes us to give in general a ‘different biological meaning’ to a fight between chickens or to a fight between wasps” (Pardi 1952, p. 193). According to Pardi, scientific investigation needs to depart from the superficial, but legitimate, use of these behavioral concepts and work on finding out the mechanisms underpinning such behaviors (Pardi 1952).

1.8.2 Deleurance’s second critique and Pardi’s final experiment

Yet, Deleurance’s attack was most importantly about Pardi’s mechanistic hypothesis. The French scientist did not agree that there is a causal connection between reproductive and social dominance. Deleurance had expressed his ideas on this point in two short articles from 1949 and 1950 (Deleurance 1949, 1950). With an interesting experimental design,

Deleurance manipulated the individuals on the nest by looking into two main factors: the presence of empty cells, used by the adults to lay their eggs, and the presence of the alpha queens on the nest. He tried to understand which of the two could determine the regression or development of the ovaries in the auxiliaries. The main idea behind Deleurance's experiment was that, if he could find that the development of the ovaries was due to the presence of the wasp on the nest, then this would support Pardi's hypothesis of a causal link that connects social and reproductive dominance. If, instead, he could show that the presence or absence of empty cells would constitute the 'sensory stimulus' (Deleurance 1946) that determines the over or under development of ovaries, then the conclusion would be against Pardi's hypothesis. Deleurance's results seemed to go against Pardi's ideas and supported the thesis that there is no causal relationship between the place of a wasp in the social structure of the colony and the developmental status of its ovaries.

At the Paris conference, Pardi defended his position against this critique, but he did not have results that could directly prove that Deleurance was wrong. Right after the Paris conference in March 1950, Pardi started working on a series of behavioral experiments on *Polistes*. The goal of these experiments was to refute Deleurance's arguments against his hypotheses (Pardi and Cavalcanti 1951). Pardi wanted to show experimentally that reproductive dominance, and not other mechanisms, such as the stimuli from empty cells reported by Deleurance, affect the under or over development of ovaries (Pardi and Cavalcanti 1951). The results of the experiments were published in the article "Esperienze sul meccanismo della monoginia funzionale in *Polistes gallicus*" in 1951 (Pardi and Cavalcanti 1951).

Pardi worked with colonies founded by three females. He used these two colonies as the control of one another. In his first experiment, Pardi took gamma in the first colony and isolated it during the day with all the cells on the nest being full. In isolation gamma did not show activity outside the nest, oophagy and built new cells. However, the gamma did not lay eggs (as there are no cells available). Pardi killed the gamma wasp and dissected its ovaries. He did the same with the beta that was used as a control, as beta had not been isolated from alpha (the dominant one). In the second colony, Pardi isolated the beta during the day and let alpha and gamma work at night. This time he killed both the beta and, after a few days, the gamma (control) and alpha in order to dissect their ovaries. In this way, he could compare the ovarian development of the different wasps to show whether the empty cells or the presence of the dominant wasp act as determining factors. So, the beta from the first colony and the gamma from the second colony have remained far from alpha but in the presence of only full cells, the beta from the second colony and the gamma from the first colony (the controls) remained with the alpha in a normal nest, say with some empty cells that could form over night.

The results of the ovarian dissections were that the ovaries of the control individuals, the ones that had stayed the whole time with alpha in a normal nest with also empty cells, did not have any eggs ready for oviposition. On the contrary the ovaries of the individuals that had been isolated from the alpha, although with no empty cells in the nest, actually had eggs ready for oviposition and more generally an index of ovarian development very close to the index of the alpha and much higher than that of the controls. Beside this experiment that shows the influence of the alpha female on the regression of the ovaries of the auxiliaries, in a second experiment Pardi also showed that

the presence of empty cells is actually not a determining and necessary factors for the reappearance of oviposition from the lower auxiliaries.

In the 1951 article, after presenting the results from his laborious experiments, Pardi categorically concluded that: “ ... the reaching of fertility from subordinates is due to the change in the social situations, say from the fact that alpha has been taken away. This means that the presence of this individual exerted before the experiments, an inhibiting action on the ovarian development of the individuals leaving on the same nest” (Pardi 1951, 252). In this way, Pardi thought to have neutralized Deleurance’s attack.

1.9 Pardi’s Abandonment of Animal Sociology and His Legacy

Still today, wasp scholars remember the vehemence of Deleurance’s attack as well as its consequences for Pardi’s career (West-Eberhard 1996). According to Pardi’s collaborators and family members, the controversy with Deleurance exhausted Pardi, a quiet and hard working scientist. He felt overwhelmed by the Paris events and decided to move on to different projects.

In the early 1970s the eminent wasp scholar Mary Jane West-Eberhard asked Pardi about the unclear reasons of his abandonment and showing her support: “I have been curious as to why you did not continue your work on *Polistes*, [...]. One time, almost ten years ago, I talked to G.P. Baerends in Ann Arbor Michigan, and he told me that you had been discouraged from continuing by those peculiar attacks from the Frenchmen (Deleurance and students). I hope not, for it is easy to see that their ‘arguments’ are not rational, and that the French work does not contradict yours in any way” (January, 10 1972). West-Eberhard curiosity relied on in depth knowledge of the

controversy, as she was able to read both French and Italian papers published by Pardi and Deleurance (Deleurance 1948, 1950, 1952b; Pardi 1942, 1946, 1951, 1952). In her doctoral dissertation on *Polistes*, which was published a few years before the letter to Pardi (West-Eberhard, 1969), West-Eberhard had pointed out that there need be no contradiction between Deleurance's and Pardi's results. Rather, from the evidence available, it was clear that more than one factor had to be involved in the control of reproduction by a single female, including both dominance – Pardi's results – and control of empty cells – Deleurance's results (West-Eberhard, 1969, pp. 20-21).

Pardi in his response to West-Eberhard's letter made clear his feelings about the controversy with Deleurance, but did not provide any clear explanation for the reasons of abandonment of the field: "Your letter has really made me happy. Your kind words about my work on *Polistes* are for me a great honor and comfort. It is true that the discussion with Deleurance and with his students (who have not always behaved correctly from a scientific perspective) had really upset me to the point where I wanted to abandon the study of this problem for a certain time. But I hope to have the opportunity to explain you better in person my position as well as theirs" (June, 1972). According to his collaborator and friend Floriano Papi, in the 1960s Pardi started thinking about going back to the study of social wasps (Papi 1991). In a letter to Mary Jane West-Eberhard from those years, Pardi also mentioned his renewed interest in wasps and his willingness to go back to their study. Referring to the controversy with Deleurance, he said: "Anyway, now, this is over and, even if in the meanwhile I have dealt with other things, I am almost old (I am 56), it pleases me to see that my work has not been un-useful. So, I decided to go back to wasps and made some observations on *Belanogaster*" (August, 1971).

Pardi's return to the study of wasps focused, not only on *Polistes* (Turillazzi and Pardi 1977), but also on forms whose social organization was either less or more primitive than the organization of *Polistes*, such as *Belonogaster* (Pardi and Marino Piccioli 1970a, 1970b, 1978a) and Stenogastrinae (Turillazzi and Pardi, 1982). Although Pardi's evolutionary interests had never been on the foreground of his investigations, he had always been aware of the important evolutionary implications of his studies on primitively eusocial species from the very beginning of his career (Pardi 1942, 1946). In the late 1960s, due to an unprecedented attention to the study of social insects in sociobiology, these studies seemed to be even more important. In studying *Belonogaster* and Stenogastrinae, Pardi's hoped to find congregations without castes. He was looking for a society of equals that might help understand the evolutionary origins of social differentiation in primitively eusocial species, but he always found caste differentiation inside those colonies (Pardi and Marino Piccioli 1970a, 1970b, 1978a).

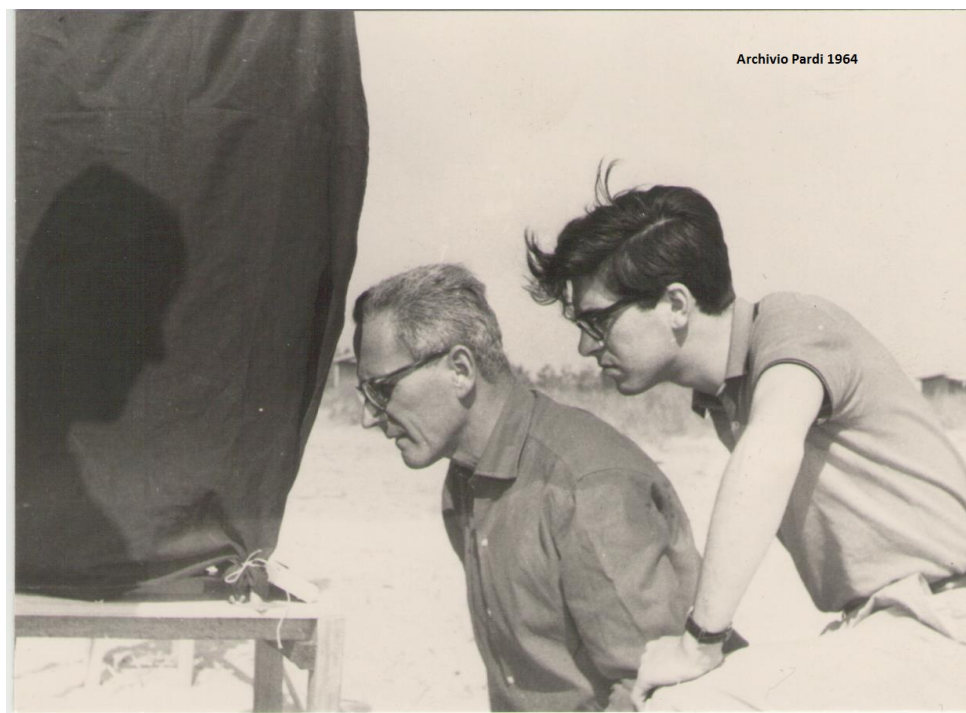


Figure 4. Leo Pardi and a collaborator observing a wasp colony

By the late 1970s and early 1980s, Pardi was back in the social insect scientific society. This time an entire cohort of students and collaborators, such as Stefano Turillazzi, Laura Beani and Rita Cervo were deepening and broadening his research on social mechanisms in wasps, looking into many aspects of this complex social system and advancing research on animals social behavior with essential publications for the field. Beside his collaborators, many scientist continued Pardi's work on social dominance in wasps looking both into the mechanistic underpinnings and the evolution of wasp social systems. Especially, Röseler and his collaborators were able to show how aggressive and subordinate behaviors influence the status of endocrine glands and other internal organs as well as how the status of these organs underpins specific behaviors of individuals in the colony (Röseler 1985; Röseler et al. 1984; Röseler et al., 1985; Röseler et al. 1986).

On the level of evolutionary causes leading to the emergence of social life, groundbreaking works in sociobiology have actually relied on Pardi's results. Importantly, Mary Jane West-Eberhard investigated the correlations between developmental/physiological processes underpinning social dominance and the evolution of social behaviors in *Polistes* wasps, relying on Pardi's studies on the relationship between social and reproductive dominance (West-Eberhard 1969, 1978a).

1.10 Conclusions

Existing narratives of the history of ethology have focused on Konrad Lorenz and Niko Tinbergen's foundational works and have portrayed the development of ethological investigations as revolving around the assessment of adaptive value and phylogenetic history (Burkhardt 2005). Following Lorenz's and Tinbergen's careers the history of ethology stressed the attempt to define intellectual and disciplinary boundaries against the narrow mechanistic approach of physiology and neuro-physiology, rather than finding a dialogue with it (Burkhardt 2005). Also, reconstructions of the development of animal sociology have focused on the origins of this discipline mostly within the context of American ecological and evolutionary thought (Mitman 1992; Mitman and Burkhardt 1991). Such reconstructions have explored the development of animal sociology within the context of a distinctive school of ecology at the University of Chicago revolving around the figures of Charles Otis Whitman, Warder Clyde Allee and Alfred Emerson (e.g. Maienschein 1988; Mitman and Burkhardt 1991; Mitman 1992).

Many important traditions in the study of animal behavior have been left out from these narratives. With a few exceptions, current narratives do not acknowledge the

importance of entomology, with its focus on comparative analysis in taxonomy and systematics, for our understanding of social behaviors and their evolution (Sleigh, 2007). Also, although von Frisch's influence on the development of ethology has been widely recognized, it has mostly been seen as tangential, rather than central, to its development (Burkhardt 1996, 2005). Finally, the role of the French school of entomology with important scientists such as P.P. Grassé, R. Chauvin and E.P. Deleurance focusing on social insects, and with neo-Lamarckian tendencies, has only received peripheral attention (Burkhardt 1994; Chavot 1994). From different perspectives, these neglected traditions have as common denominators the comparative, physiological and often mechanistic understanding of social behaviors. Although maybe not central to the establishment of a strong disciplinary approach, they have contributed to the creation of a huge reservoir of observations and to the development of investigative methods that have helped articulating our understanding of animal social behavior.

As it emerges from the reconstruction of Pardi's investigative pathway between 1937 and 1952, his approach was peculiar but not isolated from the work of other scholars. On the contrary, it progressively emerged at the intersection of Italian histological and physiological tradition, American animal sociology and Austro-German ethology and physiology. These sources of creativity influenced Pardi's research on social dominance and social hierarchy in *Polistes* wasps. They inspired his use of comparative approaches, physiological and embryonic methods, the application of quantitative analysis and, eventually, the design of experiments to test causal hypothesis about complex social behaviors. Leo Pardi's etho-physiology adds an important perspective on the varied and complex field of physiological and mechanistic approaches

to the study of animal behavior. Its detailed reconstruction complements and enriches previous historical works and invites to further explore the role that these approaches played, before, during and after the birth of sociobiology, in shaping our current understanding of social life in animals.

CHAPTER 2

“HOW COMPLEX AND EVEN PERVERSE THE REAL WORLD CAN BE”

W.D. HAMILTON’ S EMPIRICAL WORK ON SOCIAL WASPS (1964-1968)

“... a species which is highly social in a rather flexible and human way, it offers great possibilities for observation and experiment.” (Hamilton, Notebook 1; November 22, 1963; ZIX42/1/13)

“Seeing deep correspondences in seemingly unrelated things is the essence of science and is vital to mathematics and philosophy as well” (Hamilton 1996a, p. 256)

2.1 Introduction

To most scholars in the life sciences, William D. Hamilton’s name reminds them of the *theory of inclusive fitness*, the so-called *Hamilton’s rule*, and the *haplodiploidy hypothesis* (Charnov 1977; Hamilton 1963, 1964a, 1964b). Inclusive fitness theory showed how genetic relatedness of individuals affect their behavior towards one another. The rule pointed out that social behavior evolves under specific combinations of costs, benefits and relatedness (Hamilton 1963). The haplodiploidy hypothesis explained why self-sacrificing behaviors evolved in social insects of the order Hymenoptera, wasps, bees and ants (Hamilton 1964b). Rule, theory and hypothesis have dominated the attention of most scholars since the publication of “The Genetical Evolution of Social Behavior” in

1964 (e.g. Wilson 1971; Grafen 2004). This paper asks: How did Hamilton attempt to see if the theory, the rule and the hypothesis could help explain the evolution of social behavior in concrete biological systems? How did he apply theory and hypotheses to the complexity and variety of the biological world?

In some notes for the preparation of a lecture in the late 1970s, Hamilton wrote: “I feel very strongly that a theorist ought not to become too detached from the things he theorizes about—at least I find it salutary to keep reminding myself by observation and experimentation of how complex and even perverse the real world can be” (Hamilton; Undated; Z1X90/1/18). Though mostly a theorist, Hamilton maintained that scientists should always pay close attention to the complexity and even perversity of real biological phenomena. Complex and perverse features of wasp societies posed challenges to Hamilton’s theory of inclusive fitness and to the haplodiploidy hypothesis (Hamilton 1964b). In his work during the 1960s and early 1970s, though not always systematically, Hamilton addressed these challenges. This article reconstructs Hamilton’s investigations on social wasps, between 1963 and 1968. It points out the centrality of Hamilton’s work on wasps and shows how the British scientist constantly interwove theoretical and mathematical modeling with forms of observation, comparative analyses, and, at times, experimentation in the attempt to evaluate inclusive fitness theory (Hamilton 1964a, 1964b).

Social wasps obsessed Hamilton. When he assembled the first volume of his collected works, the first volume of *Narrow Roads to Gene Land*, he decided to put the image of a giant wasp on the cover of the book. Social wasps occupy a central place not only in Hamilton’s publications, but also in his dense notebooks from his various trips

and in the correspondence with colleagues, family and friends. Borrowing an expression from the evolutionary biologist M.J. West-Eberhard, wasps were for Hamilton a *microcosm* for the investigation of social life (c.f. West-Eberhard 1996).

Two are the main reasons of Hamilton's obsession for wasps. First, the human-like features of wasp societies genuinely fascinated him. For instance, Hamilton talked about the: "...incredible quality of the wasps' life itself—wayward, mysterious, almost human" (Hamilton to West-Eberhard; 5 October 1967; Z1X83/1/10). In later years, he also pointed out that wasp societies were to him: "... a world human in its seeming motivations and activities far beyond all that seems reasonable to expect from an insect: constructive activity, duty, rebellion, mother care, violence, cheating, cowardice, unity in the face of threat – all these are there" (Hamilton 1996b, vi). Hamilton looked at wasps' social behavior comparing them to other social systems, from cuckoo birds to humans (Hamilton 1996a, p. 261). He called this way of addressing biological phenomena *laterality of thinking* (Hamilton 1996a, p. 261). According to him, only by thinking laterally, by constantly comparing different social structures and behaviors, was it possible to understand the evolution of social behaviors.

The second reason for Hamilton's obsession for social wasps was that wasps provided 'touchstone puzzles' to the theory of inclusive fitness and to the haplodiploidy hypothesis (Hamilton 1996b, p. vi). According to this theory, altruistic acts, such as the self-sacrificing behavior of most workers and auxiliaries in wasp colonies, evolve because beneficiaries and self-sacrificing actors, under certain ecological conditions, share copies of the same genes (Hamilton 1964). Therefore, the self-sacrificing individuals can pass on their genes to their offspring by helping their relatives who carry

copies of the same genes (Hamilton 1963). However, most social wasps showed behaviors that tend to lower the relatedness of the individuals in a colony and therefore challenged explanations in terms of inclusive fitness (Hamilton 1964b). In order to address these challenges, Hamilton embarked in experimental and naturalistic explorations of wasp societies as well as in detailed analysis of the entomological literature (Hughes 2002; Segerstrale 2013).

This paper reconstructs Hamilton's empirical investigations in the mid 1960s focusing mostly on his work on wasp societies. It concentrates mostly on the years between 1963, when Hamilton's first publication in *The American Naturalist* came out, and 1968, when Hamilton left for his second trip to Latin America. After providing an overview of existing literature on Hamilton's work, the paper sketches out the main features of Hamilton's theory of inclusive fitness (Hamilton 1963, 1964a) and the haplodiploidy hypothesis (Hamilton 1964b). Second, it details Hamilton's attempts to conduct empirical work on wasp societies in his first trip to Latin America, from August 1964 to late summer 1965. Third, it reconstructs Hamilton's reflections about the value and meaning of his empirical investigations, between 1964 and 1968. Finally, it provides an outlook on how Hamilton thought to evaluate inclusive fitness theory with empirical evidence after 1968.

2.2 Narratives out of Balance

Most narratives about Hamilton's work have privileged the theoretical development of Hamilton's ideas and have neglected the importance of Hamilton's empirical work. The evolutionary biologist Alan Grafen expressed the usual perception of the importance of

Hamilton's achievements when he said: "Hamilton's great contributions to biology relied on an essential admixture of mathematics and modeling" (Grafen 2004, p. 129).

Philosophers of science have contributed to strengthen this theoretical reading of Hamilton's work while focusing on its further developments in connection to game theory and decision-making strategies (e.g. Sober and Wilson 1999; Godfrey-Smith 2014).

Some overarching themes have organized existing narratives. Most of the attention has focused on controversies about group selection and multi-level selection (Borrello 2011); how Hamilton's models relate to Fischer's, Wright's and Haldane's models (Grafen 2004); and the way inclusive fitness relates to kin selection and natural selection (Borrello 2011; Segerstrale 2013). Focusing on these themes, historians and biographers have reconstructed Hamilton's exchanges with major figures in the field of evolutionary biology of the time, from J. Maynard Smith (Segerstrale 2013; Harman 2010) and E.O. Wilson (Segerstrale 2013) to G. Price (Harman 2010), G.C. Williams (Segerstale, 2013), V.C. Wynne-Edwards (Borrello 2011) and R.L. Trivers (Segerstrale 2013).

Hamilton is partially to blame for the lack of serious engagement with his empirical work. A quote often used by historians frames his interest in natural phenomena as a compulsive tendency to follow his own "boyhood training" (Hamilton 1996a, p. 117). Following up on Hamilton's way of talking about his empirical work, his biographers have tended to give an image of his numerous trips to the Amazons and his explorations of the natural world as fulfilling Hamilton's need to escape formal academic environments and to feed his imaginative mind, almost depriving them of scientific

meaning. Referring to Hamilton's work in his trips to South America, Grafen for instance wrote: "The immediate intellectual fruits of these expeditions seem few and minor, but they clearly fed Bill's imagination and fulfilled a deep need. Perhaps the jungle offered a respite from etiquette and compromise." (Grafen 2004, p. 119)

One of Hamilton's last students, the entomologist and evolutionary biologist David Hughes questioned Hamilton's own depiction of his engagement with biological phenomena by asking: "Was he, as he claims, undisciplined in his observations, 'compulsively following my own boyhood training' or does the occasionally self-deprecating writing style of 'My intended burial and why' mask a more rigorous approach in his observations of the natural world?" (Hughes 2002, p. 84). Hughes encouraged us to get a closer look at Hamilton's naturalistic work, because "... an appreciation of the work of Bill Hamilton and its repercussions for evolutionary theory is aided by trying to understand the base upon which he built those ideas" (Hughes 2002, p. 84).

Although privileging Hamilton's theoretical achievements, Grafen admitted that Hamilton was able to integrate Darwin's keen observations and ability to describe the world and Fischer's mathematical modeling approach. He wrote: "Hamilton pursued this line in a way that was too mathematical for a Darwin, and too biological for a Fisher. [...] However, the nature of his achievements leaves no doubt how valuable is the combination in one individual of deep biological knowledge and commitment with mathematical skills" (Grafen 2004, p. 129).

In her recent biography, Segerstrale pointed out the importance of looking at the interaction of theoretical and empirical dimensions of Hamilton's work. She described

Hamilton as: “quickly moving between general theory and particular, careful observation.” According to Segerstrale, for Hamilton it was: “... always a question of fit, and if an organism’s behavior doesn’t seem to be explainable by existing theories, well, the theory will simply need to be changed” (Segerstrale 2013, p. 317). Yet, it is unclear how Hamilton cycled between theory and observation, mathematical models and exploration, experiments and simulations.

Already in the introduction to Part II of his 1964 paper, “The Genetical Evolution of Social Behavior”, Hamilton acknowledged that, in his attempts to apply inclusive fitness theory to biological phenomena, he would pay particular attention to organisms showing anomalous behaviors. Social wasps were one of such anomalous cases (Hamilton 1966a, 1996b). Detailing Hamilton’s work on these systems provides an entrance point to understand how he grappled with the complexity of biological phenomena, as well as the way Hamilton’s work inspired and informed empirical research on the evolution of social life in the years following the publication of “The Genetical Evolution of Social Behavior” (e.g. Strassmann, 1979, 1981a; West, 1967; West-Eberhard 1979, 1975).

Hamilton’s comparisons of social behaviors across species and taxa occupy numerous passages in notebooks, private and professional correspondence as well as in published papers and autobiographical notes. The importance of comparing social systems across taxa speaks to an important feature of Hamilton’s way of dealing with the complexity of the biological world, say his appreciation of the importance of comparative work in social evolution. Hamilton called this way of comparing natural phenomena “laterality of thinking” (Hamilton 1996a, p. 261).

For Hamilton, thinking laterally was not just a didactical or rhetorical tool. Rather it represented a useful heuristic, a way to conceptualize and understand the diversity and variety of the natural world. Hamilton's laterality of thinking was multidirectional. It went from humans to animals, from animals to humans and from animals to other animals. Hamilton also provided a more general description of his way of relating different biological systems to one another, when he wrote: "When two phenomena give me even a hint of similarity I try as a matter of course swapping modes of thought applied to them, forcing myself to contemplate each one in the light of the other" (Hamilton 1996a, p. 260).

For Hamilton, the 'hint of similarity' was not a random feature. Hamilton thought that: "In their broad features, the situations are indeed so similar as to suggest that similar trends of selection must be at work [...]" (Hamilton 1964b, p. 69). Hamilton took similarities between different phenomena to be evolutionarily relevant, as the presence of similar biological situations might imply that similar selective forces have shaped them. Hamilton's analogical and metaphorical reasoning pointed at possible biological homologies supporting his confidence to be able to unravel the selective forces underpinning the evolution of similar patterns of behavior by comparing different social systems (Hamilton 1996a).

Historians and biographers have either underemphasized or overemphasized the influence of analogical and comparative thinking in Hamilton's way of producing knowledge. One tendency has been to charge these parallels with a strong political meaning. For instance, recently Sarah Swenson has stressed the necessity of foregrounding Hamilton's political and philosophical ideas about the world and human

society as well as to take into account that Hamilton's main goal was "to produce a theory that had meaning for human societies" (Swenson 2015, p. 46). Swenson goes as far as to claim that "Rather than wasps, bees and termites, the origins of inclusive fitness appear to be connected to Hamilton's perception of human society and his concern for man's future" (Swenson 2015, p. 47).

On the opposite side, some authors have denied the importance of cultural or philosophical factors on Hamilton's scientific work. For instance, L.A. Dugatkin argued that Hamilton supported his theories and hypotheses about social evolution only "because his observations of insects had demonstrated that kin-biased altruism was real" (Dugatkin 2011, 94). According to him: "Hamilton appears to have no philosophical, political, or religious leanings that influenced his opinion about whether natural selection worked via kinship to produce altruism. [...]"(Dugatkin 2011, p. 94).

Yet, if we look at the multi-directionality of Hamilton's analogical parallels, from cuckoos to wasps and from wasps to humans or other social organisms, neither of these interpretations fits Hamilton's use of analogical and metaphorical reasoning. Rather, analogical reasoning seems to have played an important role in how Hamilton produced, corroborated and refined his ideas about social life and its evolution. According to Hamilton, reasoning laterally across different and seemingly unrelated social systems was a creative and heuristic tool to do science and produce knowledge about the biological world and its evolution.

2.3 *The Genetical Theory of Social Behavior* (1964)

Since his college years at Cambridge, Hamilton had worked strenuously on the problem of biological altruism (Hamilton 1996a; Segerstrale 2013). In order to access this problem, he had engaged earlier foundational works in evolutionary biology and population genetics, mostly Fischer's *The Genetical Theory of Natural Selection* and Haldane's *The Causes of Evolution* in the development of his theories and ideas (e.g. Grafen 2004; Segerstrale 2013; Harmann 2010).

Since 1962, Hamilton had unsuccessfully tried to publish his ideas in *Nature* (Hamilton 1996a; Segerstrale 2013). On March 7 1963, he submitted what would become his first published article (Hamilton, 1963). In a letter to *The American Naturalist* with the title "The Evolution of Altruistic Behavior", Hamilton sketched out his core ideas about the evolution of social behaviors (Hamilton 1963). The news about the publication soon reached Hamilton's friends in the American continent who had witnessed his struggle to get his research published. Later in 1963, Hamilton's friend and colleague, Colin Hudson wrote to him: "... yesterday we received a copy of your letter to The American Naturalist [...] you must be pleased to have got your chief idea into print at last. It will be interesting to see what reactions it receives [...]" (Hudson to Hamilton; Undated; ZIXUN/5).

In the letter to *The American Naturalist*, Hamilton presented his ideas about the evolution of altruistic behaviors, say those behaviors that are beneficial for the ones who receive them and detrimental for those who perform them (Hamilton 1963). He explained the conditions favoring the increase in frequency of a gene with altruistic effects in a population. According to Hamilton, under the right circumstances, it was not against

Darwinian rules that some individuals direct altruistic behaviors towards their close relatives, who are more likely to share with them the same genes. Talking from a gene's eye view perspective, Hamilton explained that a gene with altruistic effects can spread in a population if it favors the fitness of those individuals who bear copies of that same gene (Hamilton 1963). In order for a gene to transmit copies of itself in a population, it is not necessary that it be transmitted directly in the offspring of the individuals bearing it. The bearers can help members in the population that are related to them and help transmit copies identical to itself in other members of the population (Hamilton 1963).

A formula, which in the 1970s came to be called *Hamilton's rule* (Charnov 1977), condensed Hamilton's ideas about the conditions favoring the evolution of altruistic traits in a population. Hamilton wrote: "If the gain to a relative of degree r is k -times the loss to the altruist, the criterion for positive selection of the causative gene is $k > 1/r$." (Hamilton 1963, p. 355). If we substitute k with the ratio of costs and benefits ($k = b/c$) of the altruistic act, we obtain the more common formulation of Hamilton's rule: $br > c$, where r is a measure of the degree of relatedness between the altruistic actor and the recipient of the altruistic action as a result of common descent; b and c are respectively the costs in fitness to the actor and benefits in fitness to the recipient (Charnov 1977).

The publication in *The American Naturalist* boosted Hamilton's confidence that the scientific community, or at least the editors of some important journals, might be ready for his ideas. Yet, Hamilton had been working on a longer and more detailed article containing the full formulation of inclusive fitness theory in the language of population genetics (Hamilton 1996a; Segerstrale 2013). Right after the publication of the 1963 article, Hamilton's mother asked him about the "longer paper" he was working on: "And

what about your long paper? You may find people are more anxious to publish it now this letter has appeared. But it is a pity if it has to wait. I can quite see your present work makes it impossible for you to rewrite completely. And yet I agree about the need to make it more readily understandable.” (Hamilton B.M. to Hamilton; 10 December 1963; Z1XUN/5).

Already at the time of the publication of the 1963 letter, Hamilton had been working on several drafts of what would become “The Genetical Evolution of Social Behavior”, the ‘longer paper’ Hamilton’s mother was referring to in her letter (Seegerstrale 2013). Little more than a year after he had unsuccessfully submitted a manuscript of his longer paper to *Nature*, on May 14 1964, Hamilton re-submitted a revised version of the paper to the *Journal of Theoretical Biology* (Seegerstrale 2013). The reviewers, the evolutionary biologist J. Maynard Smith being one of them, accepted the article for publication, but suggested that it had to be split in two parts, the first containing the mathematical model of inclusive fitness theory and the second containing the details of how the model might apply to concrete biological situations (Hermann 2011; Seegerstrale 2013).

In 1964, Hamilton eventually published “The Genetical Evolution of Social Behavior” in two parts. In Part I, he presented a “genetical mathematical model” (Hamilton 1964a, p. 1) describing the interactions between relatives on one another’s fitness. The ‘genetical mathematical model’ represented the full formulation of inclusive fitness theory in the language of population genetics. Striving for the most general theory to explain the evolution of altruistic behaviors, in the 1964 article Hamilton presented the

mathematical model as applying to populations that are infinite in size, have overlapping generations and characterized by random mating (Hamilton 1964a).

In Part II, Hamilton discussed “whether there is evidence that it [the theory] does work effectively in nature” (Hamilton 1964b, p. 17). He presented detailed cases of how the theory would apply to specific phenomena of social life, ranging from the evolution of self-sacrificing behaviors to the evolution of distasteful properties in insects as well as of warning behaviors, fights, parental care and parasitoidism (Hamilton 1964b). Here, Hamilton also presented his famous haplodiploidy hypothesis showing how inclusive fitness might apply to the evolution of altruistic behaviors in social insects of the order Hymenoptera (Hamilton 1964b).

The haplodiploidy hypothesis became one of Hamilton’s most important and contested contributions to the field of social evolution (Wilson, 1971, 1975; Segerstrale, 2013). Hymenoptera have an unusual sex determination pattern, so called haplodiploidy. In this order, females are diploid, say they have a double set of chromosomes; whereas males are haploid, which means they have only one set of chromosomes. Haplodiploidy entails that females on average have more genes that are replicates to the genes of their sisters than of their own offspring due to common descent. On average, in case of single insemination and in absence of inbreeding, the degree of relatedness between a female and her own sister is $\frac{3}{4}$, whereas the degree of relatedness between that same female and her own offspring is $\frac{1}{2}$. Thus, the haplodiploidy hypothesis is also named the ‘ $\frac{3}{4}$ relatedness hypothesis’ (e.g. West-Eberhard, 1975).

With the haplodiploidy hypothesis, Hamilton suggested that, the frequent evolution of sterile workers in Hymenoptera might be the result of the unusually high relatedness of

hymenoptera sisters due to male haploidy, which leads to all sperm produced by a male being identical. This means that a female may well be able to get more genes into the next generation by helping the queen reproduce, hence increasing the number of sisters she will have, rather than by having offspring of her own. Through this hypothesis, the theory of inclusive fitness seemed to explain why worker sterility evolved in Hymenoptera by focusing most importantly on the $\frac{3}{4}$ relatedness between self-sacrificing workers and the brood they attend (Hamilton 1964b; Wilson 1971).

2.4. Theory Evaluation and Empirical Explorations in the First Trip to South America

2.4.1 Evaluating inclusive fitness theory in South America

As Hamilton admitted in the Introduction to Part II of “The Genetical Evolution of Social Behavior”, after he had provided a mathematical formulation of the theory, he felt the need to see whether he could support the theory with evidence from biological facts (Hamilton 1964b, p. 17). In *Narrow Roads of Gene Land*, remembering the times when he was writing his 1964 paper, he admitted that he: “... desperately needed examples [...] where both self-sacrifice and the limits to it were indisputable” (Hamilton 1996a, p. 20).

Already in 1963, Hamilton started thinking about traveling to Brazil in order to collect facts and data that could support his theory with biological evidence. Two letters stored in The W.D. Hamilton Archive at the British Library in London help understand the scientific reasons behind Hamilton’s plan. The first is a letter from July 2 1963 addressed to his department at Imperial College in London. The second is the application

for the *Darwin Fellowship*, which dates May 15 1963, the day after the submission of “The Genetical Evolution of Social Behavior” to the *Journal of Theoretical Biology*.

In the first letter, Hamilton reassured his department at Imperial College and clearly expressed the need to perform empirical work in order to support his theory with empirical data. He wrote: “The experimental work is in fact directly relevant to the theoretical work which the URC has so kindly supported in the past two years [...]” (Hamilton, Letter to Imperial College; 2 July 1963; Z1XJO/1/5). He also made clear that: “The work is, it is true, somewhat remote from problems of human population genetics and evolution, owing to the male-haploid system of sex determination in the Hymenoptera; but the theory itself is applicable to any species and if its worth can be proved for social insects this will perhaps make its relevance to human social problems seem worthy of closer attention” (Hamilton, Letter to Imperial College; 2 July 1963; Z1XJO/1/5). Here Hamilton expressed the importance of testing the theory in different taxa, as it was supposed to hold universally, from insects to humans. Thus, although he wanted to study mostly Hymenoptera, Hamilton also thought that his work on insects was relevant to general theories of social evolution and in particular to understand social evolution in humans.

In the application for the *Darwin Fellowship*, Hamilton clearly stated that in South America he wanted to concentrate mainly on social wasps and wrote: “My primary reason for choosing South America was the great variety of species of social wasps found there” (Hamilton, Application to Darwin Fellowship; 15 May 1963; Z1XJO/1/5). And then he added: “Most of them are little known but reports indicate that they have social features which are of the greatest interest to my theory (i.e. somewhat contradictory to

it)” (Hamilton, Application to Darwin Fellowship; 15 May 1963; Z1XJO/1/5). Some social features of wasp societies were ‘somewhat contradictory’ to Hamilton’s theory as they tended to lower the degree of relatedness in the colonies (Hamilton 1964b). Therefore, in Brazil, Hamilton wanted to observe wasp colonies in order to better understand to what extent such features constituted a problem for his theory. He wrote: “I want to find out something about the genetical kinship existing in colonies and swarms of these wasps by marking individuals with paint, observing their egg laying etc; also to discover whether the individuals of a colony show any discriminations based on closeness of kinship in their social behavior” (Hamilton, Application to Darwin Fellowship; 15 May 1963; Z1XJO/1/5).

The passage above resonates with a quote from Hamilton’s first notebook from his first trip to Brazil, where Hamilton expressed his appreciation for the opportunities that social wasps lent to observation and experimentation. In Notebook I, he wrote: “There is no doubt that in it is a very unusual biological situation and with a species which is highly social in a rather flexible and human way, it offers great possibilities for observation and experiment” (Hamilton, Notebook I; 22 November 1963; ZIX42/1/13).

2.4.2 Exploring wasp societies in South America

Hamilton’s first trip to Latin America lasted little longer than a year, from August 1963 to September 1964. Hamilton embarked for Brazil on August 16 1963 and spent the first months of his trip working in the lab of the famous entomologist Warwick Esteban Kerr in the Biology Department at the *Universidade Estadual Paulista* in Rio Claro, a small city close to San Paolo. Kerr was an ex-student of the evolutionary biologist Theodosius

Dobzhansky at Columbia and an expert on the evolution and behaviours of tropical bees (e.g. Kerr 1969). After his stay in Kerr's lab, Hamilton went on a tour that took him and Sebastiano Laroca, a bee scholar and Kerr's collaborator, from São Paulo through Brasília and finally to Belém. After Belém, Hamilton headed up on his own to Barbados to see his friend Colin Hudson and with him he went up to Nicaragua, Mexico and finally to the United states (Seegerstrale 2013). Hamilton and Hudson flew back to the United Kingdom from Chicago in the late summer of 1964 (Seegerstrale 2013).

Kerr's expertise in the genetics of Hymenoptera served Hamilton's goal to understand the genetic mechanisms underpinning the evolution of social life. As he wrote in his application to the *Darwin Fellowship*: "Altogether it certainly seems that professor Kerr, in being a geneticist, in being concerned with the genetics of social hymenoptera, and in having himself performed some of the very few determinations of multiple-mating in the group, could hardly be more suitably experienced for advising and assisting me in the rather unusual field I want to study" (Hamilton, Application to Darwin Fellowship; 15 May 1963; Z1XJO/1/5).

While in Rio Claro working in Kerr's lab, Hamilton interacted and worked together with many scientists. Most of them were interested in social Hymenoptera. Some of them were specifically working on wasps. Besides working in Kerr's lab, during those months, Hamilton did numerous excursions in Rio Claro and surrounding areas. Hamilton's notebooks from the trip carefully, yet chaotically, report his attempts to observe and experiment on wasps and other organisms. Most observations, drawings and pictures in four densely written notebooks and in Hamilton's correspondence to family and colleagues from the trip are about wasps (Hamilton, Notebook I, II and III;

Z1XUN/15). When reporting in Notebook I about his first day in Kerr's lab, Hamilton excitedly wrote: "Spent time walking around campus looking for *Polistes* nests that are hanging everywhere." (Hamilton, Notebook 1; 13 September 1963; ZIX42/1/13). In his months in Latin America, Hamilton reported observations about 8 genera of wasps, 8 genera of bees and 2 genera of ants. He collected and observed wasp nests of *Polistes fuscatus*, *Polistes canadiensis*, *Mischocyttarus cassanunga*, *Mischocyttarus dormans*, *Polistes cinerascens*, *Apoica pallida*, *Protopolybia minutissima* and others (Hughes, 2002).

In a report to O.W. Richards, Hamilton's friend, mentor and director of the Field Station of Imperial College London at Silwood Park where Hamilton was working at the time, Hamilton described the wasps he had observed and said: "Social wasps are very abundant here but of the polybiini the great majority are different species of *Polybia* or the very closely related genera ... *Polistes canadiensis* and *P. versicolor* are very common ... *Mischocyttarus* species are also very common" (Hamilton to Richards; 19 February 1964; ZIXUN/5). Hamilton also pointed out that he had mostly been observing *Polistes* behavior, but that he wished he had had more time to observe and study *Mischocyttarus*. He wrote: "I am rather wishing I had spent more time on the little-known behavior of M.[*Mischocyttarus*] and less on *Polistes*, which however I have found extremely fascinating" (Hamilton to Richards; 19 February 1964; ZIXUN/5). The neotropical *Mischocyttarus* belongs, like *Polistes*, to the subfamily of the Polistinae. These wasps show less aggressive behaviors and more flexibility than *Polistes* and therefore were to Hamilton very interesting for the investigation of the evolution of social life.

Hamilton did not limit his observations to wasp behaviors. Right upon arrival in Rio Claro, he learned new techniques to carefully dissect wasps in order to find out about the physiological status of their internal organs. On his third day in Rio Claro, Hamilton started dissecting wasps. He also started a very accurate Index Card System to collect anatomical and physiological observations about the wasps he had collected (Hamilton, Index Cards; Z1XUN/15). Each card was organized in 5 columns containing information about specific aspects of the biology of every wasp.

The first column was a simple number identifying the wasp. Hamilton would use this numbers in his field notes when referring to those wasps, creating in this way a complex reference system between the notes in his books and the index cards. The second category was about whether the wasp collected was a male or a female. In the case of female wasps, he always pointed out whether the ovaries were developed or underdeveloped as a sign for the possible social status of each wasp. The third column was about the status of the spermatheca and whether or not it was packed with sperm. This column was essential to Hamilton's interest in multiple mating, one of the puzzles wasp societies posed to his theory. This is why he learned specifically how to dissect the spermatheca from Kerr and his students. The status of development of the fat bodies, whether they were well developed or not occupied usually the fourth column. Previous studies in wasp physiology had described the correlation between development of fat bodies, ovarian development and social status of each wasp. Finally, the last column described wing length and length of the first legite as well as the presence and status of the hamuli on wings. This last information helped Hamilton to figure out the relationship between flight range and geographic distribution of the wasps in a given area.

Besides the numerous notes on the nests that he found, Hamilton also took many photographs and drew many pictures of nests. He said: “I was relying on these to amplify these notes. Unfortunately almost all of these were lost; some when I posted them from Belem and some when a suitcase was stolen in Nicaragua. Hence one of the more un-studious things I want to do in Brazil: to retrieve what I can of those photographs. I have the idea of collecting photographs for some sort of a semi-popular illustrated article or book on the weird and wonderful neo-tropical wasps life and its amazing architecture.” (Hamilton to West-Eberhard; 5 October 1967; Z1X83/1/10).

In some notes from his notebooks, besides reporting numerous behaviors and features relating to different aspects of wasp social life, Hamilton often drew analogies between wasp behaviors and the behavior of cuckoo birds. These analogies served Hamilton to get an overall understanding of the social dynamics characterizing wasp social life. The parallel between wasp social life and the behaviors of cuckoos even made it into Part II of “The Genetical Theory of Social Behavior”, where he wrote: “In these associative *Polistes* the great variation in the degree of association [...] the frequent abandonment of young nests, the quarrels, the manifest concern about adventive wasps combine to create an impression which is very reminiscent of the breeding affairs of the South American cuckoos [...]” (Hamilton 1964b, p. 69).

During the trip, Hamilton was still busy with the revisions of the ‘longer paper’ he had submitted to the *Journal of Theoretical Biology* before leaving for South America in August 1963. During the trip, Hamilton reworked the manuscript and split it into two parts, as suggested by the reviewers of the journal. Some of the observations he did in Brazil made their way into Part II of the 1964 article. But Hamilton was definitely not

happy to spend part of his time in South America reworking his paper. To Richards, Hamilton wrote: “Also, I am sorry to say, I am spending quite a large part of it at the moment rewriting the paper which you saw. It was accepted by the *Journal of Theoretical Biology*, but they wanted it out in two. The first half is to contain all the mathematics -- and this has now been sent off again. The second half is to have all the biological considerations in a revised version. Hope of escaping from this paper was one of the reasons for coming here but it seems that I did not succeed” (Hamilton to Richards; 19 February 1964; Z1XUN/5).

2.5 Addressing Wasps’ Puzzling Behaviors During and After the Trip

Hamilton’s observations and experiments during the trip to South America focused on features of wasp social life that could provide information about the level of relatedness within the colonies. To Hamilton, two were the most interesting and puzzling features of wasp societies. The first was *polygyny*, say the presence on the nest of multiple egg-laying and potentially unrelated females, both at nest foundation (*pleometrosis*) and during the whole colony life cycle (true polygyny) (Hamilton 1964b). The second was *polyandry* or multiple mating, say the fact that the reproductive individuals mate multiple times (Hamilton 1964b). Both polyandry and polygyny lower the degree of relatedness in colonies and therefore posed important challenges to Hamilton’s explanations of the evolution of social life in terms of inclusive fitness (Hamilton 1963, 1964a, 1964b).

As documented in his Notebooks, during his first trip to Brazil, Hamilton had started addressing the polygyny and polyandry puzzles trying to provide evidence that his theory could actually help explain why self-sacrificing behaviors evolved in Hymenoptera.

Hamilton letters to other evolutionary biologists and entomologists from the years during and immediately after the trip help clarify what Hamilton was actually trying to accomplish with the many, and often non-systematic, observations and experiments performed during the trip.

Back at field station of Imperial College at Silwood Park in the fall of 1964, besides working on important theoretical contributions to social evolution (Hamilton, 1966, 1967), Hamilton continued thinking, talking about and working on his wasps. Most of Hamilton's correspondence from these days was with scholars he had met in Brazil, especially Warwick E. Kerr and his collaborators Sebastiano Laroca, and Ronaldo Zucchi, as well as with other scholars who were working on questions of social evolution mostly in insects, most importantly Mary J. West-Eberhard.

2.5.1 Puzzles: polyandry and polygyny

In Part II of the 1964 article, Hamilton reported the problematic case of multiple mating in Hymenoptera and wrote: "Clearly multiple insemination will greatly weaken the tendency to evolve worker-like altruism" (Hamilton 1964b, p. 33). In the application to the Darwin Fellowship from 1963, Hamilton had already made clear that: "This question of multiple mating has an important bearing on my idea of how social behavior might have evolved in the group." (Hamilton, Application to Darwin Fellowship; 15 May 1963; Z1XJO/1/5). By mating with multiple males, the queen's progeny becomes very genetically diverse. Thus, multiple mating decreases the degree of relatedness among self-sacrificing workers and the queen or her brood. Therefore, according to Hamilton, the fact that colonies are made out of workers with different genetic origins made it hard

to explain why self-sacrificing behaviors evolved (Hamilton 1964b).

Working with Kerr and his collaborators, Hamilton tried to find out more about multiple mating both in wasps and in bees. One of the main reasons for him to go to Brazil and spend time in Kerr's lab was to: "... learn Kerr's technique of determining the occurrence of multiple-mating hymenoptera by sperm counts, and to apply it to a variety of social and semi-social hymenoptera" (Hamilton, Application to Darwin Fellowship; 15 May 1963; Z1XJO/1/5). In Rio Claro, using Kerr's technique of sperm counting, Hamilton attempted to rigorously investigate polyandry. To Richards he wrote: "I am spending part of my time here investigating multiple insemination of female hymenoptera -- mainly bees, solitary and semi-social—and part of it observing wasps" (Hamilton to Richards; 19 February 1964; Z1XUN/5). Hamilton recorded in his index cards most of the results obtained by using Kerr's techniques (Hamilton, Index Cards; Z1XUN/15).

Polygyny, the phenomenon of multiple egg-laying queens, was another aspect that made wasp societies somewhat contradictory to Hamilton's theory. In polygynous colonies, the workers attend a brood produced by more than one female. Workers are not attending a brood composed only by full sisters. Thus, similarly to polyandry, polygyny would lower the degree of relatedness in the colony and, rather than favoring altruistic behavior, it seemed to favor the spreading of genes causing selfish behaviors. Hamilton argued that: "Clearly this social mode presents a problem to our theory. Continuing cycle after cycle colonies can come into existence in which some individuals are almost unrelated to one another." (Hamilton 1964b, p. 36). Yet, and here is the puzzle, Hamilton further observed: "... it [polygyny] does not seem to do the colonies much harm and the species concerned are highly successful in many cases" (Hamilton 1964b, p. 36).

In Brazil, Hamilton looked into the problems raised by multiple egg-laying queens mostly in two groups of the Vespidae family: the subfamily Polybiinae and the genus *Polistes* belonging to the subfamily Polistinae (Hamilton, Notebook I, II and III; Z1XUN/15). Polybiinae are truly polygynous. This subfamily is made out of mostly swarm founding wasps and colony reproduction happens by swarming with several fertilized queens. In most species of Polybiinae, at least several queens engage in egg-laying on each nest (e.g. Richards and Richards 1951). Here, due to the high number of egg laying queens, the polygyny puzzle is extremely striking. In fact, as Hamilton noticed, in the Polybiinae, the probability was very high to obtain colonies where individuals are almost unrelated to each other.

The situation was slightly different in the partially polygynous and partially monogynous *Polistes*. Wasps of this genus show different modes of nest foundation depending on the climate and on the latitude (Richards and Richards 1951). Hamilton wrote: “The geographic distribution of the association phenomenon in *Polistes* is striking” (Hamilton 1964b, p. 37). Modes of colony foundation in *Polistes* go from mostly monogynous in colder regions to polygynous in the tropics. Polygyny at nest-foundation is usually referred to as *pleometrosis*. In temperate regions, usually, several wasps contribute to the foundation of the nest, but one of them becomes the only egg-laying and dominant one (Pardi 1942, 1948). The rest of the wasps, the auxiliaries or subordinates cannot reproduce and, if any, they succeed in laying only a few eggs. But with many of *Polistes* species, mostly in warmer climates, nest foundation is carried out by two or more fertilized queen-sized wasps (Pardi 1942, 1948).

Hamilton found it difficult to explain why some individuals would give up their reproductive success and become subordinates (Hamilton 1964b). In *Polistes* associations, non-reproductive females are engaged in rearing the offspring of sisters, which are less closely related to them ($r=3/8$) than their own offspring could be ($r=1/2$). Thus, Hamilton admitted: “Here it is the ready acceptance of non-reproductive roles by the auxiliaries that we have difficulty in explaining” (Hamilton 1964b, 65). In subsequent years, the evolutionary biologist M.J. West-Eberhard would point out that, in order to explain why social dominance evolved in *Polistes*, it was rather important to look into the cost and benefit side of Hamilton’s rule, rather than trying to find unilateral answers based on genetic relatedness, as Hamilton tended to do (West 1967; West-Eberhard 1969).

2.5.2 Addressing the puzzles: viscosity and relatedness (r)

In his first trip to Brazil, Hamilton had started thinking about possible features of population structure that would contribute to raising the degree of relatedness within colonies and help explain why self-sacrificing behaviors evolved in polygynous and polyandric wasp societies. He appealed mostly to the idea of *viscosity*. Already in Part II of “The Genetical Theory of Social Behavior”, Hamilton had fleshed out the connection between viscosity and inbreeding. There, he had claimed that: “... it does seem necessary to invoke at least a mild inbreeding if we are to explain some of the phenomena of the social insects – and indeed of animal sociability in general – by means of this theory. The type of inbreeding which we have in mind is that which results from a high viscosity of

population or from its actual subdivision into small quasi-endogamous groups” (Hamilton 1964b, p. 65).

Some years after the publication of “The Genetical Theory of Social Behavior”, Hamilton wrote to R. Zucchi that he was: “... inclined to consider such viscosity an important factor in the evolution of social behaviour” (Hamilton to Zucchi; 10 December 1967; Z1X89). Hamilton clearly explained that he chose the word viscosity inspired by an analogy with the physical definition of this term. He wrote: “I chose the word ‘viscosity’ with the idea that there was some analogy with the physicist’s conception of viscosity: the molecules of a viscous liquid cannot, I imagine, diffuse and interpenetrate so rapidly as do those of non-viscous liquids” (Hamilton to Zucchi; 10 December 10 1967; Z1X89).

Genes in viscous populations, according to this analogy with physical viscosity, do not randomly spread or ‘diffuse’. Therefore, such populations are different from populations characterized by random mating. They are also different from Sewall Wright’s idea of island, which pointed to geographical barriers contributing to speciation events and higher levels of inbreeding. Hamilton’s idea of viscosity pointed to ecological factors leading to the relative immobility of organisms in a population. Using the word viscosity, Hamilton wanted to express: “the ecological background of a kind of departure from random mating which is not caused by any special tendency to inbreed or by the population being divided into ‘islands’ (as S. Wright calls them), but by the relative immobility of the organisms” (Hamilton to Zucchi; 10 December 1967; Z1X89).

Hamilton was interested in the connection between ‘the relative immobility of the organisms’ in a population (viscosity) and inbreeding. He wrote: “If organisms do not move far, in terms of the dimensions of the area occupied by the population from their

places of birth, then this restricts the gene-flow and tends to cause a kind of diffuse inbreeding” (Hamilton to Zucchi; 10 December 10 1967; Z1X89). According to Hamilton, the immobility of a population leading to inbreeding was thus connected to a local increase in relatedness among the members of a viscous population. Explaining the concept to Zucchi, Hamilton clearly asserted: “The important thing about population viscosity from my point of view is that it leads to local inbreeding. [...]. The occurrence of inbreeding means that any two adjacent individuals, like or unlike-sexed, will have a higher coefficient of relationship than they would have in a non-viscous population [...].” (Hamilton to Zucchi; 10 December 10 1967; Z1X89).

In Brazil, Hamilton had tried, though not systematically, to understand how viscosity could lead to inbreeding, and in this way, contribute to make the degree of relatedness higher mostly investigating wasp societies. While in Rio Claro, in some homing experiments, Hamilton looked for a correlation between relatedness, flight range of the different wasps, and the distribution of the population in a certain area, in order to assess whether or not these populations were actually viscous, that is to say if they were characterized by local immobility and low dispersal. By performing these experiments, Hamilton wanted to see whether average relatedness could correlate with geographic proximity and relative immobility (Hamilton, Notebook I; ZIX55/1/3).

In these experiments, Hamilton tried to figure out whether or not the offspring would disperse slowly from their site of origin or if they would tend to stay close to the nest. He tried to test the flight range of the wasps so as to see if there were differences between the capacity to fly far away and the level of altruistic behaviors in the colonies (Hamilton, Notebook II; ZIX55/1/3). Also, Hamilton performed some transference

experiments where he would introduce wasps unrelated to the rest of the colony (or related as a control) to see the different reactions. In these experiments he tried to find out if wasps from distant localities are less likely to be accepted on a nest than wasps from nearby nests (Hamilton, Notebook II; ZIX55/1/3).

2.5.3 Addressing the puzzles: the importance of 'k'

In Part II of “The Genetical Evolution of Social Behavior”, Hamilton had argued that it was hard to explain the ready acceptance of reproductive roles by the auxiliaries in *Polistes* associations, as non-reproductive females are engaged in rearing the offspring of sisters which are less closely related to them ($r=3/8$) than their own offspring could be ($r=1/2$). In the years immediately after the publication of Hamilton’s 1964 paper, in her dissertation under the supervision of Richard Alexander at The University of Michigan, West-Eberhard used Hamilton’s inclusive fitness theory in order to address this problem (West 1967; West-Eberhard 1969).

Rather than focusing on the coefficient of relatedness, as Hamilton tended to do, West-Eberhard focused on costs and benefits, such as the difference in independent reproductive capacity between associates and the degree to which the presence of the joiner augments the presence of the joined female (West, 1967). West-Eberhard concluded that: “... dominance relations during group formation may maximize k for each individual by enhancing the likelihood that relatively inferior reproductive [...] become workers on nests of superior reproductive, which are thus free to specialize in egg laying” (West 1967, 1584).

After completing her dissertation, West-Eberhard went to Harvard for a post-doc in the Natural History Museum. At Harvard, Edward Osborn Wilson told her about Hamilton's interests in pursuing the study of wasps in South America (West-Eberhard 2009). After publishing an article in *Science* where she reported her findings about the evolution of social dominance in *Polistes*, on September 6 1967, West-Eberhard wrote to Hamilton. In her letter, she made clear her admiration for Hamilton's work and even claimed that: "Next to Huckleberry Finn they [Hamilton's articles] are the most important things I have ever read (inspired, inspiring, heuristic)" (West-Eberhard to Hamilton; 6 September 1967; Z1X83/1/10).

When Hamilton received her letter, he was already aware of West-Eberhard's work. He responded to her very quickly with a very long and detailed letter. In this letter, he admitted that: "One of the first things I had in mind to do when reopening my vespine interests was to write to you. I saw the abstract of your work in the *Bulletin of the Ecological Society of America*. I was very struck with it and certainly not only because of the rare pleasure of seeing my work referred to!" (Hamilton to West-Eberhard; 5 October 1967; Z1X83/1/10). Hamilton acknowledged the quality of West-Eberhard's work in applying the theory to the puzzling behaviors of *Polistes* association and admitted that he had in mind: "... considering whether the results accorded with the theory in rather the same sort of way as you have done" (Hamilton to West-Eberhard; 5 October 1967; Z1X83/1/10).

Already in his first letter to West-Eberhard from 1967, Hamilton openly admitted the difficulties he had encountered in trying to have his theory match the complexity of the biological world. He wrote: "I despair when I think how all this variability should

affect our expectations” (Hamilton to West-Eberhard; 5 October 1967; Z1X83/1/10). In the same letter, Hamilton also admitted the difficulty he had encountered in trying to evaluate his inclusive fitness theory with biological evidence. He wrote: “I felt rather overwhelmed by the complexity of the situation and did not realize the fairly simple criteria which I now have in mind as a result of thinking about your paper” (Hamilton to West-Eberhard; 5 October 1967; Z1X83/1/10).

The main difference between the two scientists in the use of inclusive fitness theory to explain why social behavior evolved was that, West-Eberhard would focus on the cost and benefit components of the formula, whereas Hamilton focused always on relatedness (see, West-Eberhard, 2009). For instance, when asking West-Eberhard for more information about her findings from her study of *Polistes canadiensis* and *Polistes fuscatus*, he wanted to know more about biological features that might help get a better idea of relatedness in those colonies. He asked West-Eberhard for: “... evidence that co-foundresses are usually sisters” (Hamilton to West-Eberhard; 5 October 1967; Z1X83/1/10) as well as for “... facts on mating behaviors, particularly such as affect the chance that inbreeding occurs” (Hamilton to West-Eberhard; 5 October 1967; Z1X83/1/10).

It was clear to both scientists that, in order to explain why social life evolved in concrete biological situations, it was important both to produce empirical evidence and to further develop general theories of social evolution. Yet, the two scientists investigative styles were complementary to one another. On the one hand, Hamilton strongly felt the difficulty of doing good empirical work that could support and show how his theory applied to the real world. He admitted to West-Eberhard: “I feel I must help if I can and

so sometimes get to thinking that having somehow become a theorist I should remain one—that the cobbler should stick to his last and avoid trying to be cattle farmer as well” (Hamilton to West-Eberhard; 16 September 1972; Z2X34/1/1). But he also expressed the wish to be able to master the complexity of good empirical work, when he added: “At the same time, I would much like to show that technique is not beyond me, that I do love the study the of living world, and that I can suffer the discipline of presenting work in primary journals” (Hamilton to West-Eberhard; 16 September 1972; Z2X34/1/1).

On the other side, West-Eberhard seemed to be more inclined to appreciate and perform empirical work and appreciated its long lasting value, while still acknowledging the importance of abstract theories. Responding to Hamilton’s letter in the early 1970s, she admitted: “Right now I am more in the mood to talk wasps and nests than theory—one can get saturated with theory and I sometime wonder if the contribution that one can make isn’t so transitory as to be worthless. On the other hand, even a little tidy bit of natural history is a lasting significance. (Still, every time that I read or hear something that grates against my current theoretical brain, it riles me into an argument and draws me into the theory trap once again)” (West-Eberhard to Hamilton; 1 August 1973; Z1X83/1/10).

2.5.4 Questioning the haplodiploidy hypothesis

Hamilton’s confrontation with the complexity of biological phenomena led him to question the haplodiploidy hypothesis as the main explanation of the evolution of social life in Hymenoptera, and especially in polygynous and polyandric social wasps. First, he pointed out that inbreeding might play an important role in the evolution of self-

sacrificing behavior. Also, Hamilton started thinking about how other mechanisms could help explain why self-sacrificing behaviors have evolved.

In the long response to West-Eberhard letter from 1967, Hamilton openly admitted that haplodiploidy was likely not the only factor driving the evolution of self-sacrificing behaviors in Hymenoptera. According to Hamilton, inbreeding must have also played an important role. He wrote: “I am now inclined to place relatively more weight on inbreeding as a factor raising the coefficient of relationship and so facilitating social evolution and less on the special features of male-haploid relationships than I was when I wrote those papers” (Hamilton to West-Eberhard; 5 October 1967; Z1X83/1/10).

In a letter to Kerr from after the first trip to Brazil, Hamilton updated the Brazilian scientist about the progress of his research. There he also briefly elaborated on the connection that he now saw between haplodiploid sex determination and inbreeding. In the years after the trip, Hamilton surmised that haplodiploidy would evolve in species with close inbreeding and said: “Incidentally, recent ideas of mine suggest that male-haploidy itself tends to evolve in species where there is habitual close inbreeding [...], and of course close inbreeding must lead to high relationship anyway” (Hamilton to Kerr; 6 May 1966; Z1X89). Similarly, when writing to West-Eberhard, he admitted: “Actually I have come to think that the two conditions may be remotely connected” (Hamilton to West-Eberhard; 5 October 1967; Z1X83/1/10). By ‘the two conditions’, Hamilton here meant haplodiploidy and inbreeding.

In the same letter to Kerr, Hamilton pointed out some difficulties of his haplodiploidy hypothesis. First, Hamilton pointed out that some male haploid groups have not developed social habits. Second, he noted that some groups with female-to-

female parthenogenesis, *thelytoky*, also did not develop social life, although this phenomenon contributes to raising the level of relatedness (Hamilton to Kerr; 6 May 1966; Z1X89). Therefore, according to Hamilton, although haplodiploidy still played a role in explaining why social life evolved, it might be important to use it together with other mechanisms. Therefore, Hamilton wrote: “I feel that the male-haploidy cannot be more than half the story, and that the other half must involve the classical concepts of the fabricating, provisioning, long-lived Hymenoptera, etc” (Hamilton to Kerr; 6 May 1966; Z1X89).

Yet, though Hamilton admitted that haplodiploidy might have been no “more than half the story”, according to him, haplodiploidy still played an important role in explanations of the evolution of social life. In the same letter to Kerr, while talking about multiple insemination, he reinforced his believe in the importance of haplodiploidy and claimed: “But again, I think it is clear that if there were two species with the same degree of multiple insemination; and both with habits such that a trend to social life was being mildly encouraged by selection, then if one had male-haploidy and the other didn’t the one that had it would be more likely to proceed into a social state” (Hamilton to Kerr; 6 May 1966; Z1X89).

Hamilton was therefore constantly questioning whether or not his mathematical models and hypotheses were appropriate to explain the evolution of social life. To Kerr, he openly declared the importance of being cautious about the overall value of his theoretical achievements. To the Brazilian scientist, he wrote: “I am still cautious about the value of my theory in the case of the social Hym[enoptera]—more cautious, I think, than Prof. E.O. Wilson who so generously supported it at a recent meeting of the Royal

Ent[omological] Soc[iety] [...]" (Hamilton to Kerr; 6 May 1966; Z1X89). Wilson during the meeting of the Royal Society that Hamilton mentioned in this passage had praised both Hamilton's theory of inclusive fitness and the haplodiploidy hypothesis as groundbreaking contribution to the understanding of social evolution (Seegerstrale 2013). Hamilton, differently from Wilson, was still very cautious in assessing the value and importance of his achievements.

2.6 Planning More Empirical Work and Doing More Theory

In the late 1960s, Hamilton's work had radically impacted the field of evolutionary biology (e.g. Wilson 1971; West-Eberhard 1969). During these years Hamilton worked on several publications where he refined his ideas about social evolution (Hamilton 1970, 1971a, 1971b, 1972). One of the major events of this time was Hamilton's second trip to South America from April 1968 to January 1969. During five of the nine months he spent in South America, from May to September 1968, Hamilton and his wife Christine joined an expedition of the Royal Society and National Geographic Society expedition to the Mato Grosso region in Brazil. They were both listed among the zoologists of the expedition, and more specifically among the entomologists interested in wasps (Smith 1972).

In the late 1960s and early 1970s, Hamilton also kept thinking about how to support his theoretical achievements with biological evidence. In this respect, he engaged in four important lines of inquiry. First, Hamilton planned, but only partially performed, more empirical work on social wasps focusing on the relationship between viscosity, inbreeding and the evolution of social life. Second, he discussed and reformulated,

mostly in correspondence with West-Eberhard, how to actually interpret his formula so as to match the complexity of the biological work. Third, Hamilton started working on a book on wasps together with West-Eberhard. Fourth, Hamilton further developed the mathematical model of inclusive fitness and included inbreeding in the formulation of the theory.

2.6.1 Plans for more empirical work

Hamilton's plans about his second trip to Brazil emerge both in correspondence and in materials he used to apply for funds. From material collected in Hamilton's Archive, it is not possible to confirm that Hamilton actually performed the experiments he was planning on doing. Yet, the thoughts behind his intentions show the direction in which Hamilton's ideas were developing in those years.

In a letter from 1966 addressed to a certain Dr. Martin of The Royal Society, Hamilton made clear that he wanted to go back to Brazil in order to study, first, how the multi-queened Polybiine societies regulate reproduction and, second, how changes in social organization are connected to changes in climate, from seasonal-tropical to equatorial (Hamilton to Dr. Martin; 7 December 1966; ZIX89/1/1). Both topics had already been part of Hamilton's interests in the first trip and had found their place in Part II of "The Genetical Evolution of Social Behavior" (Hamilton 1964b).

To West-Eberhard, Hamilton also expressed more in detail his plans for the upcoming trip. He wrote: "There are several other experiments that I would like to make to amplify and confirm the results I obtained last time" (Hamilton to West-Eberhard; 5 October 1967; Z1X83/1/10). Hamilton listed three kinds of experiments he was interested

in performing: 1. Transference experiments; 2. Homing experiments; and 3. Collection of biometrical data. All of them were related to the interest he had developed in the connection between viscosity, inbreeding and relatedness. He wrote: “I would like to make more careful series of transference experiments with adequate controls to find out if wasps from distant localities are less likely to be accepted on a nest than wasps from nearby nests. I also want to make some homing experiments to find out the flight range. [...] I am also thinking of the possibility of a biometrical study which would use some sort of intraclass correlation coefficient to try to show how the average genetical relationship falls off with distance - from a nest to a neighbor nest, and from the local group to others” (Hamilton to West-Eberhard; 5 October 1967; Z1X83/1/10).

In a letter to Zucchi, Hamilton explicitly expressed his intention to test the flight range of wasps so as to support his conjectures about the connection between low dispersal, inbreeding and the evolution of multi-queen colonies. He wrote: “One of my intentions in coming to Brazil this time is to try to find out more about how far sexual wasps disperse from their nests in *Polistes* and *Polybiinae*” (Hamilton to Zucchi; 10 December 1967; Z1X89). Or in slightly different terms: “As regards social insects, I have the idea that lack of incentives to migration and long distance dispersal of the sexual adults may lead to greater viscosity of population, and this viscosity may help to account or the relative commonness of pleometrosis (perhaps you call it polygyny) in tropical social insects” (Hamilton to Zucchi; 10 December 1967; Z1X89).

Following up on his reflections on the role of viscosity and inbreeding, Hamilton focused on trying to find out by observing wasps’ social behaviour if population viscosity and inbreeding have played a role in the evolution of self-sacrificing behaviours in

Hymenoptera. Yet, the number of things that Hamilton wanted to research seemed, again, rather unrealistic to pursue given the short amount of time that he could spend traveling. Hamilton was aware of this issue and, to West-Eberhard, he expressed his doubts and said: “Altogether then it is fairly obvious that I will fritter away my time as I did before, trying to cover far too much and doing nothing properly” (Hamilton to West-Eberhard; 5 October 1967; Z1X83/1/10).

2.6.2 ‘Maldita k’. Is relatedness the whole story?

Most of the conversations between Hamilton and West-Eberhard revolved around how to balance the importance of factors related to relatedness (r) and ecological factors (c and b). Following up on her research on the evolution of social dominance in *Polistes* wasps (West 1967; West-Eberhard 1969), in the late 1960s and early 1970s, West-Eberhard was trying to figure out how the cost/benefit side of Hamilton’s formula (k) would work in different biological situations.

In a letter to Hamilton, she asked for clarifications about how to actually use the k beyond the case of *Polistes*. She wrote: “Dear Bill, I have been in a quandary for three days over your maldita $k > 1/r$. Since I am trying to write a discussion of extreme variations in k that affect the evolution of altruism, I have had to look very closely at how this expression (condition) applies to different kinds of social organization and from different points of view within a society” (West-Eberhard to Hamilton; 16 March 1972; Z2X34/1/1).

Hamilton replied to West-Eberhard by encouraging her to work on k , expressing his opinion about the timeliness of this kind of work. He also expressed his disappointment

for the usual “confusion and carelessness” showed by most scientists in the treatment of the cost/benefit side of the formula after the publication of “The Genetical Theory of Social Behavior” (Hamilton to West-Eberhard; 18 March 1973; Z2X34/1/1). Yet, Hamilton would still focus mostly on the coefficient of relatedness rather than on the ecological factors in the theory (West-Eberhard 1975, 2009).

However, in several passages and conversations, also because he was pushed in this direction by several colleagues and collaborators, Hamilton expressed doubts about the role, or at least the omnipotency of relatedness in the explanation of the evolution of social life, above all in relation to the haplodiploidy hypothesis. For instance, in his “Altruism and Related Phenomena” (Hamilton 1972), while talking about termite societies, which do not have a haplodiploid sex-determination system, and whose evolution can thus not be explained by appealing to the kind of arguments that apply to Hymenoptera, Hamilton admitted the importance of taking into account factors that are not reducible to relatedness and that rather speak to the importance of the costs and benefits of social life, the k in Hamilton’s formula. He wrote: “In such circumstances it is easy to see advantages of division of labor once the termites began to extend their burrows, to build, and to achieve homeostasis of their dark environment. These particular factors have no connection with genetical relatedness, but, of course, insisting on the necessity of relatedness in no way precludes other factors as necessary or contributory” (Hamilton 1972, p. 275).

In a conversation with West-Eberhard from the late 1970s, Hamilton seemed even more open to acknowledging the importance of other factors, beside haplodiploidy, in explanations of why social life evolved. Yet he also admitted to be still skeptical about

whether or not these other factors might outage the importance of the skewed relatedness ratios due to haplodiploid sex determination. He wrote to West-Eberhard: “[...] you and Alexander and others may be right that my original papers overstated the role of special relatedness and understated that of specially high available benefit/cost ratios. About this I am not sure yet” (Hamilton to West-Eberhard; 26 February 1979; Z1BOX66).

Finally, reflecting on his work in the early 1970s while assembling the collected volume of *Narrow Roads to Gene Land*, Hamilton seemed to be more open to the possibility of other factors playing an important role in the evolution of sterile castes at least in Hymenoptera. Though he admitted that “biases of relatedness are clearly not the whole story” (Hamilton, 1996a, p. 266), he still thought that: “Whether other factors that must also apply to the evolution of sterility may be more potent forces, however, so that the special pattern imposed by haplodiploidy is swamped by them and therefore hardly detectable, is much less clear” (Hamilton 1996a, pp. 265-266).

2.6.3 Working on a book on wasps

In the early 1970s, after returning from his second trip to Brazil, Hamilton and West-Eberhard started working on the project of a co-authored book on wasps. After years of long and detailed correspondence, West-Eberhard and Hamilton met in person during Hamilton’s visit at Harvard in May 1969 (Hamilton 1971; West-Eberhard 2009). At Harvard, the idea of writing a book on wasps came up for the first time. Hamilton’s and West-Eberhard’s joint effort to write a book on wasp never came to the point of being published. Yet, looking into the thought process that went into it helps show Hamilton’s continuous commitment to the empirical study of wasp social life as well as his interests

in specific features of wasps' social life that relevant to his understanding of social evolution.

In a letter from 1970, Hamilton reported to West-Eberhard that the famous scholar of wasps Philip Stradberry was about to publish a book on wasps. Rather than sharing with West-Eberhard a scientific evaluation of Stradberry's work, Hamilton shared with the American evolutionary biologist his personal impressions about Stradberry's affection towards wasps as an object of investigation: "Philip is certainly quite an expert on wasps and is very hard working and has actually published work on wasps (which I haven't), but somehow I never detected the affection for wasps that seems to animate you and me and this implies one respect in which our book should be different and perhaps better" (Hamilton to West-Eberhard; 21 June 1970; Z1X83/1/10).

In a letter dated a few months after their first meeting, West-Eberhard reported to Hamilton that an inspiring example for their book was Wilson's *The Insect Societies*, published in 1971 by Harvard University Press (West-Eberhard to Hamilton; 28 December 1971; Z2X34/1/1). According to West-Eberhard: "One vision I have of the book is as a handbook on the social wasps" that, similarly to what Wilson did with social insects in general, would summarize everything that is known on them and that would be appealing both to a lay audience and to specialists (West-Eberhard to Hamilton; 1-6 March 1972; Z2X34/1/1). West-Eberhard and Hamilton decided to get in touch with Harvard University Press and provide a tentative index as well as the main topics that the book would cover (West-Eberhard to Hamilton; 1 March 1972; Z2X34/1/1).

The agreed, tentative order of the chapters for the book is reported in Table 1 from a letter of West-Eberhard to Hamilton. While figuring out who should be in charge of the

single chapters, the two scientists decided to each rank the chapters that they were most interested in writing (West-Eberhard to Hamilton; 12 June 1972; Z2X34/1/1). Not surprisingly to them, their rankings turned out to be mostly complementary. Hamilton was mostly interested in working on building behaviors and nest forms, which he had closely observed, photographed and drawn during his trips in Brazil as well as during his numerous observations in the British countryside (Seegerstrale 2013). He also expressed high interest in working on the chapter about the geographic distribution of wasps, which was one of his main interests since the first trip to South America. Both West-Eberhard and Hamilton were interested in working on the evolution of wasp sociality. West-Eberhard suggested that: "... it would be interesting for us to write essays on this topic independently, then discuss and synthesize them" (West-Eberhard to Hamilton; 19 June 1972; Z2X34/1/1).

Table 1. Tentative order of chapters for the planned book on wasps

Chapters	MJ	H	Who should write the chapter
Biology of genera	1	8	MJ
Nature of wasp societies	2	15	MJ
Evolution of social life in wasps	3	3	Both
Activities of workers	4	14	MJ
Nature and determination of castes	5	13	MJ
Behavior of males	6	9	MJ
Autumn and winter behavior	7	10	MJ
Communication orientation ecc	8	11	MJ
Relations with other animals	9	7	Bill

Biology of social parasite	10	17	Bill
Non-social biology	11	17	MJ
Introduction	12	5	Bill
Geography and phylogeny	13	2	Bill
Key to the genera	14	6	Bill

Though exciting, the project of writing a book seemed in those years overwhelming to Hamilton. He finally decided to give up on co-authoring the book and to devote more time to pressing theoretical issues that his theory had raised demanding attention from many sides. To West-Eberhard, he admitted: “Your mention of homework for our book makes me nervous. ... My theoretical work continues to chase me ... Hence, further hopelessness about getting near the wasps. I really feel that you must treat it just as your book and only bring me in again if I do in fact manage to work up some suitable offerings in time. The way things are going at present it looks like becoming the hobby of my retirement!” (Hamilton to West-Eberhard; 18 March 1973; Z2X34/1/1).

In the letter to West-Eberhard from 1973, where he announced that he would give up on writing a book on wasps, Hamilton made clear that he would try to focus on his theoretical work. He said: “... I do feel that my theoretical work has some originality... and if people seem interested in it, it is wrong for me to refuse to explain or defend it” (Hamilton to West-Eberhard; 18 march 1973; Z2X34/1/1).

2.6.4 Balancing evidence, theory and hypotheses

Upon return from his second trip to Brazil, Hamilton was asked to work on a paper where he could explain and revise his 1964 arguments and ideas about “how relatedness affects

the evolution of social insects” (Hamilton, 1996a, p. 255). The paper, originally written for a volume in German (Hamilton, 1996), came out first in English in the *Annual Review of Ecology and Systematics* with the title “Altruism and Related Phenomena, mainly in Social Insects” (Hamilton, 1972). This article represents an update on the ideas Hamilton had presented in 1964. In “Altruism and Related Phenomena, mainly in Social Insects”, Hamilton tried to connect his empirical observations and his ideas about inbreeding and viscosity to a new mathematical formulation of inclusive fitness theory and to the haplodiploidy hypothesis.

Hamilton had addressed again the problem of the evolution of self-sacrificing behaviors, though not focusing on the specific case of social insects, also in his 1970 paper in *Nature*, “Selfish and Spiteful Behavior in an Evolutionary Model” (Hamilton 1970). Both in “Selfish and Spiteful Behavior” and in “Altruism and Related Phenomena”, Hamilton included inbreeding into the mathematical formulation of inclusive fitness theory. He admitted that this reformulation had been made possible by the re-derivation of his formula developed during the collaboration with George Price (Hamilton 1996a, 256). Importantly, in both papers, Hamilton presented his ideas about the connection between viscosity and inbreeding for the first time in published form. He explicitly connected viscosity (or low dispersion) and inbreeding, with the degree of sociability and multiple mating (polygyny) and argued that: “Highly dispersive species will show little positive sociability although they may be gregarious. They are more likely than indispersive species to be polygamous” (Hamilton 1970, p. 214).

Yet, in the same article, Hamilton also acknowledged problems related to the connection between viscosity and sociability, due to the competition emerging among

relatives in populations with high viscosity and low dispersal. In fact, in later years he commented that: "... low dispersal by itself (population 'viscosity') as a way of reaching high relatedness has snags. The point is that, to be effective, altruism must put offspring into competition with no altruists, not bunch them in a wasteful competition with their own kind" (Hamilton 1996a, p. 188).

In "Altruism and Related Phenomena", Hamilton also went back to deal with the challenges posed by social insects to the explanation of the evolution of social behavior. In presenting empirical evidence, he warned the reader that, in order to test inclusive fitness theory, it would have been necessary to possess quantitative measurements of fitness as well as of relatedness. However, at the time, such measurement did not exist and it was thus necessary to rely mostly on qualitative data. Hamilton wrote: "Although the argument is potentially quantitative, social biology is still very far from providing the multiple measurements of fitness and coefficients of relatedness that would permit exact tests of the theory. So, instead, relevant evidence is sought in the mass of mainly qualitative observations that are already stored in the literature" (Hamilton 1972, p. 272).

Similarly to Part II of "The Genetical Evolution of Social Behavior", in "Altruism and Related Phenomena, mainly in Social Insects", Hamilton presented a great variety of examples drawing mostly on existing literature, but also filtered through his first-hand knowledge of wasp and other social systems, both inside and outside the order Hymenoptera. Beside presenting the case of the non-haplodiploid termites, Hamilton detailed the behaviors of haploid males, laying workers and rival queens, as well as toleration and cooperation in the absence of kinship, from intra to interspecific cases (Hamilton, 1972). Yet, the bulk of the empirical discussion in the paper still focused on

social wasps. Although Hamilton used here a new formulation of inclusive fitness theory that included inbreeding, the polygyny puzzle that had accompanied Hamilton since his first trip to South America still remained. As Hamilton openly admitted: “In my opinion, the polygyny in *Polybiini*, [...] provides the most testing difficulty for the interpretation of the social insect pattern which is offered in this review” (Hamilton 1972, p. 216).

Differently from the doubts he had expressed to colleagues and friends about the value of the haplodiploidy hypotheses, in the section “Association, Polygyny and Parasitism” of the 1972 paper, Hamilton strongly reasserted his trust in the power of the haplodiploidy hypothesis. Here, he did so particularly through a step-by-step critique of hypotheses relying on the so-called semi-social route (e.g. Lin and Michener, 1972), according to which aggregations of adults (semi-social aggregations), rather than families made out of a mother and their offspring (sub-social families) lead to the production of groups that are sub-social and contain self-sacrificing individuals.

Hamilton’s position with respect to hypotheses relying on the semi-social route had not been very consistent over the years. At times, he seemed to support such hypotheses. For instance, while expressing his tentative ideas about the role that inbreeding might play in raising relatedness, he wrote to West-Eberhard: “As is also evident from what I mentioned above about inbreeding I have become more favorably inclined towards Michener’s view about the evolution of social insects, providing one can assume that the nest aggregation stage involves a high degree of local inbreeding and also some tendency for workers to work for their mothers rather than to give their services indiscriminately” (Hamilton to West-Eberhard; 5 October 1967; Z1X83/1/10).

In the 1972 paper, Hamilton reasserted strongly his ideas in favor of the haplodiploidy hypothesis and against hypotheses relying on the semi-social route. He attacked the core of the semi-social route and used most of the ideas he had developed till that moment to reassess the importance of haplodiploidy and close kinship in understanding the evolution of social behaviors. Summing up his ideas about these different hypothetical explanations of why self-sacrificing behaviors evolved, Hamilton wrote: “It is certainly not impossible for worker-like behavior to evolve in a group of sisters if the advantage to the colony is high enough. On the other hand, high advantage is unnecessary to arrive at the matrifilial colony: male haploid animals gravitate naturally towards this condition provided that the sex ratio or some ability to discriminate enables the worker to work mainly in rearing sisters. Therefore it seems likely that the worker-like attributes involved in association—submission, ovary inhibition, etc.—arise during a matrifilial phase and that these attributes subsequently permit association between foundresses when certain additional conditions are satisfied” (Hamilton 1972, pp. 290-291).

2.7 Conclusions

This article has dealt with Hamilton’s empirical work in the 1960s mostly focusing on his attempts to deal with the puzzling social behaviors of wasp societies. Hamilton’s empirical work was rather unsystematic. As he often admitted, he was trying to do too much in too little time. In looking for empirical evidence, Hamilton could not rely on quantitative measurements of fitness, relatedness or of the cost/benefit characterizing social behaviors. Thus, he had to look for relevant evidence both “in the mass of mainly

qualitative observations that are already stored in the literature” (Hamilton 1972, p. 272) and by directly engaging in empirical work. Hamilton started exploring the biological processes underpinning the coefficient of relatedness and tried to bind and connect those phenomena within the framework of his theory. He started producing evidence on many factors that could influence the degree of relatedness in the colony, from flight range to possible number of queen matings and dispersal capabilities of different wasps.

Hamilton carefully explored the correlation between viscosity, inbreeding, and relatedness. He thought that, due to the high viscosity observed in wasp colonies, increases in inbreeding could affect the overall relatedness in the population. He tried to find correlations between viscosity and inbreeding and relatedness also in order to make sense of polygynous associations in wasps. Nonetheless, the wasp puzzle remained and Hamilton was not actually able to solve it. Because of the results of his exploration of actual biological systems, Hamilton questioned several times whether or not his focus on relatedness in his interpretation of how the theory of inclusive fitness could apply to existing biological systems. He also questioned the validity of his haplodiploidy hypothesis. At times, he accepted its limitations. Other times, he tried to defend it against alternative hypotheses about the evolution of social behaviors in insects.

Hamilton’s work encouraged a reassessment and rethinking of ideas and hypotheses about the natural history of the evolution of social life, mostly in social insects. In subsequent years, also thanks to the emergence of techniques to measure and calculate the main variables in Hamilton’s formula, empirical work on social wasps and their evolution abounded. Some works aimed mostly to prove or disprove Hamilton’s ideas on the evolutionary factors driving social evolution (e.g. Strassmann 1979, 1981a);

some others leaned more towards a reconceptualization of the theory or to test whether the theory could help explain main settings, steps and mechanisms leading to the evolution of social behaviors (e.g. West-Eberhard 1975, 1978a).

Hamilton's work in the 1960s suggests the importance of combining different experimental, observational, conceptual and theoretical approaches in understanding the main features of social evolution. As a whole, and not only because of the importance of his theoretical achievements, Hamilton's approach can still inspire and support future research projects and attempts to explain why self-sacrificing behaviors and social life evolved.

CHAPTER 3

AN INVESTIGATIVE FRAMEWORK FOR THEORY EVALUATION

INCLUSIVE FITNESS THEORY AND THE STUDY OF WASP SOCIETIES (1960S-1970S)

“But testing that generalization, and confronting the predictions and confusions it has raised, has led researchers through labyrinthine paths of hypothesis and observation.”

(M.J. West-Eberhard, 1991)

3.1 Introduction

William Donald Hamilton’s *inclusive fitness theory* has dominated the study of the evolution of social life since its publication in “The Genetical Evolution of Social Behavior” in 1964 (Hamilton 1964a, 1964b). Philosophical conversations about our understanding of social evolution have often revolved around the theory, its shortcomings and its developments (e.g. Wilson and Sober 1994). Less attention has been paid to how scientists attempted to evaluate the theory against empirical evidence and what this implies for our understanding of social evolution and social life more generally. This paper asks: How have scientists evaluated inclusive fitness theory against empirical evidence? More generally, it asks: What are the main epistemological features of theory evaluation in the research practice of social evolution?

Two important alternatives characterize philosophical accounts of the relationship between theories/models and empirical data. The first are *theory/model-first* accounts.

They understand theory evaluation as a *top-down* process that starts with the derivation of hypotheses from the theory or models and ends with the *confirmation* or *falsification* of such hypotheses through empirical data (e.g. Earman 1983; Hempel 1965; Giere 2004, 2010). The second are *experiment-first* accounts. They explain how experiments produce knowledge about phenomena, mainly as a *bottom-up* process (e.g. Bogen and Woodward 1988; Hacking 1983; Rheinberger 1997; Woodward 1989, 2011). Both kinds of accounts keep a hierarchical distinction between inferences from the data and inferences from theories or models.

Drawing on an analysis of actual attempts to evaluate inclusive fitness theory in the 1960s and 1970s (Hamilton 1964b, 1972; West 1967; West-Eberhard 1969, 1973, 1975; Strassmann, 1989, 1981a, 1981c), this paper shows that neither theory/model-first nor experiment-first accounts accommodate theory evaluation in social evolution. It criticizes the strong hierarchical distinction between top-down inferences from the theory and bottom-up inferences from empirical data that both theory/model-first and experiment-first accounts rely on. It argues that accounts of theory evaluation that aim to accommodate scientific practice have to articulate how inferences from the theory (top-down) and inferences from the data (bottom-up) mutually inform one another in the generation of hypotheses and statements about phenomena.

These epistemological conclusions rely on the analysis of the works of three important evolutionary biologists, who attempted to evaluate inclusive fitness theory: W.D. Hamilton (Hamilton 1964a, 1964b, 1972), M.J. West-Eberhard (West, 1967; West-Eberhard 1969, 1973, 1975), and J.E. Strassmann (Strassmann 1979, 1981a, 1981c; Strassmann and Orgren, 1983; Strassmann et al. 1984a, 1984b). These three scientists used

social wasps, especially *Polistes*, in the study of why social life evolved. Their works from the 1960s and 1970s show the wide variety of practices and inferences scientists actually used in the evaluation of inclusive fitness theory. In those years, the study of social biology was still: "... very far from providing the multiple measurements ... that would permit exact tests of the theory" (Hamilton 1972, 272). Thus, researchers had to "... go through labyrinthine paths of hypotheses and observations" (West-Eberhard 1991) in order to evaluate inclusive fitness theory against empirical evidence.

The *investigative framework for theory evaluation* presented in this paper articulates how, in social evolution, bottom-up and top-down inferences inform one another and support the generation of hypotheses and statements about phenomena. It shows how these kinds of inferences animate both the *interpretation* of parameters in abstract models with biological mechanisms or quantities (i.e. costs, benefits and relatedness) and the *coordination* of elements of abstract models with elements of a real bio-social system (e.g. wasp societies). In this way, the investigative framework provides an alternative to theory/model-first and experiment-first accounts of scientific inquiry and lays the ground for further accounts that aim to accommodate actual research practice.

This paper first presents some main features of theory/model-first and experiment-first accounts of scientific inquiry. Second, it introduces inclusive fitness theory and elaborates on the reasons that have made *Polistes* a model system for the investigation of the evolution of social life. Third, it delves into the details of Hamilton's, West-Eberhard's and Strassmann's empirical work on wasps from the 1960s and 1970s. Finally, relying on the works of these three scientists, it fleshes out the *investigative*

framework for theory evaluation and elaborates on its main epistemological features as an alternative to both theory-first and experiment-first accounts of scientific inquiry.

3.2 Theory-first versus Experiment-first Accounts

Philosophical accounts of the relationship between theories/models and empirical data come in two main forms. The first are *theory/models-first* accounts, which understand theory testing as a *top-down* inferential process of inferences from theories and models. The second are *experiment-first* accounts, which explain how experiments produce knowledge about phenomena, mainly as a *bottom-up* inferential process from the data. The following presentation of the two alternatives focuses on Giere's hierarchical schema as an examples of theory/model-first account (e.g. Giere 1988, 2004, 2010) and on Bogen and Woodward's three-level schema as an example of experiment-first account (e.g. Bogen and Woodward 1988; Woodward 1989, 2011).

3.2.1 *Theory/model-first accounts*

Theory-first accounts of scientific inquiry have explained in different ways how hypotheses are derived top-down from theories and then tested against empirical claims. The so-called Hypothetico-deductive (H-D) model presents the typical image of theory testing as a top-down process. The H-D model conceives of theories and observation reports as linguistic entities. It looks at theory testing as a semantic relationship between these two kinds of sentences and relies on the ideas of confirmation or falsification (e.g. Hempel 1965).

According to the H-D model, a theory is confirmed if we can derive from it true statements about events or phenomena we can detect in the world. Briefly, theory testing

is the process in which scientists derive hypotheses from the theory and then deduce observational predictions from those hypotheses. If the predictions are in accordance with what the theory says, the theory is confirmed. If the predictions do not come out as the theory says, the theory is not supported and, at least parts of it should be rejected (Godfrey-Smith 2003). If we add Popper's idea of falsification to this characterization of theory testing, according to the hypothetico-deductive model of theory testing, observational evidence argues for the truth of theories whose deductive consequences it verifies, and against those whose consequences it falsifies (Popper 1959).

Away from linguistic accounts of theories and hypotheses, philosophers have focused on models and the mediating role they play between theories and empirical evidence (e.g. Giere 2004, 2010; Morgan and Morrison 1999). Giere for instance wrote: "There is ... no direct relationship between sets of statements and the real world. The relationship is indirect through the intermediary of a theoretical model" (Giere 1988, 82). Seminal works in the account of theory testing through the use of models are, for instance, Suppes' semantic view (Suppes 1960; Lloyd 1994), Morgan and Morrison's characterization of theoretical models as partially autonomous mediators between theories and the world (Morgan and Morrison 1999), and Giere's hierarchical approach to models (Giere 1979, 1988, 2004, 2010). We refer here to Giere's *hierarchical model* to exemplify important features of this model-first approach relevant to our understanding of theory evaluation.

According to Giere's hierarchical model (Figure 5), theories and empirical data are mediated through a hierarchy of models, some of which are *representational* and

some of which are *experimental*. According to Giere, representational models are derived from principles and higher-level theories (i.e. principled models) via *specification*; experimental models emerge from observations via *generalization* (Giere 2004, 2010). Giere keeps a strong distinction between experimental models and representational models. Specification from theory and generalization from empirical data independently generate hypotheses or predictions about the phenomena under investigation.

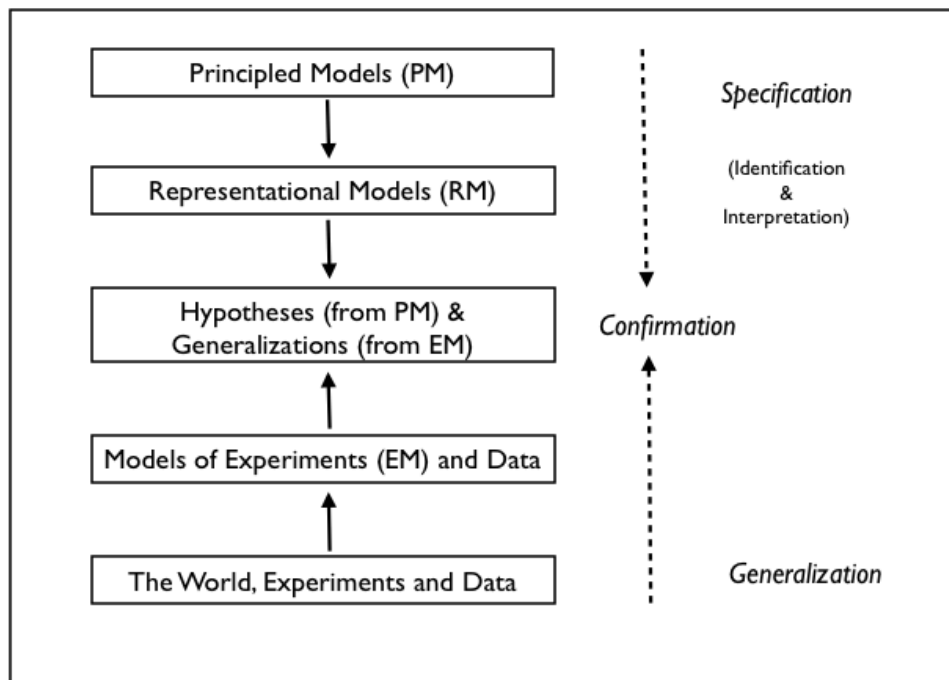


Figure 5. An example of theory/model-first account (adapted from Giere 2010, 270)

Giere does not pay much attention to the bottom-up component of generalization and focuses mostly on the process of specification of representational models (Giere 2010). In Giere's hierarchical model, principled models are what is usually referred to as theories (e.g. Newton's law of motion) and characterize a specific perspective on the world (e.g. Newton's mechanical perspective on the world). It is not possible to use

principled models by themselves to make any direct claim about the world. They do not represent anything. The process of *specification* allows scientists to refer theories to the world. According to Giere, specification comes in three main steps. First, *adding conditions and constraints* allows for the generation of families of *representational models* (e.g. from the laws of motion to models of two body interaction in a gravitational space). Second, elements of the representational model are *interpreted* with processes and entities (e.g. physical notions of mass, position and velocity). Third, through *identification*, elements of a representational model are identified (or coordinated) with elements of a real system (e.g. the moon and earth gravitational interaction).

Along the lines of previous accounts of theory testing, Giere proposes that the relationship between representational models and experimental models is one of *confirmation*. Representational models—which are derived from theories independently from empirical investigations—are tested by comparison with models of data, not directly with data—which are generated independently from theories or representational models (Giere 2010). The relationship between representational models and the world is then a relationship of similarity, or fit, that is supposed to be “short of a perfect fit” (Giere, 2010, p. 274).

Mitchell and Gronenborn, contra Giere, have recently argued that *confirmation* is not the only way of framing how experimental models relate to representational and principled models. Instead, they claim, it is important to extend “the set of model-theory relationships beyond confirmation”, because, for instance, “while experimental models of protein structure can and are used to test principled models, they also are used more directly in the construction of predictive hypotheses” (Mitchell and Gronenborn,

forthcoming). Mitchell and Gronenborn acknowledge here the constructive and generative role of experimental models and refuse to reduce their role to the confirmation and testing of hypotheses derived through *specification* from principled models.

According to Mitchell and Gronenborn, “even when there are well-established principles, there are still constructive relationships that require the use of data models to derive hypotheses” (Mitchell and Gronenborn, forthcoming).

Both linguistic accounts such as the H-D model and accounts of theory testing in terms of models share a *confirmational* approach. They see theories and models as providing some kind of representation of reality. The role of *observational statements* in the H-D model as well as, for instance, the role of *experimental models* in Giere’s hierarchical account is to *confirm* or *falsify* existing theoretical statements or principled and representational models. Yet, along the lines of Mitchell and Gronenborn’s critique, this paper shows that *confirmation* is not the only way of understanding, for instance, the relationship between theoretical statements and observational statements (in the H-D language) or between experimental models and representational or principled models (in Giere’s language). Relying on the description of theory evaluation in the research practice of evolutionary biologists in the 1960s and 1970s, it argues that it is important to account for more generative and constructive roles of empirical investigations.

3.2.2 *Experiment-first accounts*

Differently from theory/model-first accounts, experiment-first accounts of scientific inquiry privilege the role of bottom-up inferences from empirical data in the generation of claims about phenomena. Starting in the early 1980s, so-called neo-experimentalists

emerged around Hacking's slogan (Hacking 1983) that "Experiment has a life of its own". As Rheinberger claimed, these approaches tried to escape a 'theory first' type of philosophy of science perspective (Rheinberger 1994, p. 26). Thus, they focused on the practices of experimentation in their material and practical aspects.

Neo-experimentalists argued that experiments, or entire experimental systems, often develop and work independently from high level theories (e.g. Hacking 1983; Rheinberger 1994). This means, first, that experimental techniques, modes of experimental design as well as instruments for experimentation and experimental protocols are independent from theoretical commitments (Rheinberger 1994). Also, it means that experiments are not usually performed with the purpose of testing theories. It is very common that experiments are more exploratory, uncover new features of the natural world (phenomena) and produce data that are not clearly connected to any theory or hypothesis (Rheinberger 1994; Hacking 1983).

Bogen and Woodward extended similar thoughts beyond the realm of purely experimental sciences. They applied them to: "areas of scientific investigation that did not involve experimentation (understood as active manipulation of nature) but instead involved the generation of data by more passive forms of observation" (Woodward 2011). In fields as diverse as economics and chemistry, they found a variety of assumptions and techniques for data, production, data analysis and data interpretation that seemed to have a "life on their own". Examples are, statistical techniques used to analyze data, data mining procedures or even ideas about how to measure or operationalize quantities of interest that are not necessarily provided by the theory (Woodward 2011).

According to Bogen and Woodward, scientific phenomena are in the world. They are the *explananda* of scientific theories and models; they are what our theories and models are about. Therefore, phenomena are the center of scientific work, theories aim to explain phenomena, and data are evidence for the phenomena and do not speak directly to the test or refutation of theories (Figure 6). Phenomena are detected and measured through the use of data. Data, in turn, constitute the evidence scientists use to find out about phenomena. According to Bogen and Woodward: “We are justified in believing claims about phenomena as long as data are available which constitute reliable evidence for such claims” (Bogen & Woodward 1988, 350).

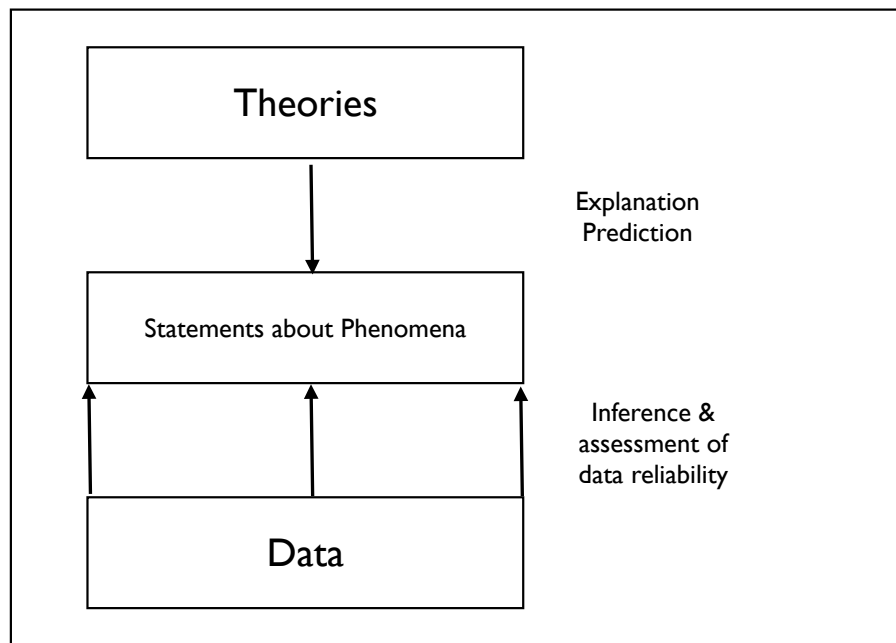


Figure 6. An example of experiment first account (from, Bogen and Woodward 1988)

Bogen and Woodward concentrate on phenomena such as the melting point of lead and the behavior of the reticular formation of the brain during the sleep. On the one

hand, according to Bogen and Woodward, data are idiosyncratic to particular experimental contexts, since they cannot occur outside of those contexts. They are the result of complex interactions—among large number of disparate causal factors. Data are the product of complex procedures. On the other hand, the detection of phenomena results from the assessment of the reliability of experimental data. For instance, data serving as evidence for the value of the melting point of lead might take the form of a record of temperature readings taken from a thermometer of some particular design.

It is by assessing the reliability of data, Bogen and Woodward claim, that we can identify, detect and stabilize the phenomena that we want to explain. If a reliable way is found to gather data in support of the existence of a phenomenon, the phenomenon can be inferred and its relevant features detected. Considerations that are relevant for the assessment of reliability are: control of possible confounding factors; replicability of experiments; problems of data reduction; empirical investigations of equipment (Woodward, 1989). Independent experimental access to phenomena also provides evidence of their existence and the properties attributed to them (Woodward 1989, 395).

Experiment-first accounts, such as Bogen and Woodward's model, move away from a confirmation-based understanding of the relationship between theory and empirical evidence. They show that empirical practices do not only serve to falsify or confirm theoretical statements. Experiments, for instance, play more creative and exploratory roles in the generation of statements and hypotheses about phenomena. Also, experiment-first accounts try to adhere to the description of actual scientific practice in different disciplinary settings. Yet, they often fail to recognize, and account for, the

influential role of theoretical commitments and assumptions in investigations of social evolution in scientific practice.

3.2.3 *Beyond theory/model-first and experiment-first accounts*

Both theory/model-first accounts and experiment-first accounts keep a strong hierarchical distinction between bottom-up (from the data) and top-down inferences (from theories or models). The next sections deal with the practices involved in theory evaluation in social evolution. They show that in research practice, this strong hierarchical distinction between the two does not hold. Rather, inferences from the data inform inferences from theories or models and, vice versa, inferences from theories or models inform inferences from the data. Therefore, they argue that a practice-oriented account of theory evaluation ought to be able to account for how inferences from theories and models as well as inferences from the data inform one another in the generation of predictions, hypotheses and explanations

3.3 Inclusive Fitness Theory and *Polistes* Wasps

Inclusive fitness theory applied a neo-Darwinian approach based on population genetics to the investigation of social evolution (Hamilton 1964a, 1964b). It directed the attention of evolutionary biologists towards ecological (i.e. costs and benefits) and genetic (i.e. relatedness) factors underpinning the evolution of social behaviors (Hamilton 1963; Wilson 1971). This theory seemed to provide an explanation of why self-sacrificing behaviors, so-called altruistic behaviors, have evolved (Hamilton 1964b). Such behaviors increase the fitness of the individual receiving them but decrease the fitness of the

individuals performing them. Therefore, they have raised important challenges to Darwinian explanations in terms of individual fitness (Darwin 1959; Williams 1966).

Insects of the order Hymenoptera, wasps, ants and bees, display the most varied and exaggerated examples of altruistic behaviors, as workers in these societies are mostly sterile but help rear the offspring of the reproductive individual, the queen (Hamilton 1964b; Wilson 1971). The variety and exaggeration of social traits among insects offered an ample testing ground for general theories of social behavior (e.g. Hamilton 1964a; West-Eberhard 1975; Strassmann 1979). This section reports the core ideas characterizing inclusive fitness theory and presents the reasons why scientists studied social wasps, especially *Polistes*, in order to evaluate whether the theory could help explain the evolution of social life in actual biological systems.

3.3.1 *Inclusive fitness theory and Hamilton's Rule*

In its popular formulations, classical evolutionary theory shows how most organismal features result from reproductive competition among individuals (Williams 1966). Reproductive costs and benefits are measured in terms of fitness, the number of adult offspring an individual leaves in the following generations (Williams 1966). Altruistic behaviors, say those behaviors that lower the fitness of the individuals performing them while benefiting other individuals, have provided important challenges to evolutionary explanations in terms of fitness (Dugatkin 2006; Williams 1966). In “The Genetical Evolution of Social Behavior I & II”, Hamilton introduced the idea of *inclusive fitness* and provided a new account of why altruistic behaviors evolve (Hamilton 1964a, 1964b).

According to the classical theory of evolution by natural selection, alleles change in frequency in a population due to their effects on the personal reproduction of that individual. Usually, the effect of an allele is on the individual organism that carries it. Yet, an allele can also leave more copies of itself by increasing the fitness of other individuals that carry copy of the same gene, due to common descent. According to Hamilton's idea of *inclusive fitness*, the overall fitness of an individual consists of two parts: first, its personal fitness; second, the sum of all the effects it causes to the fitness of its relatives (Hamilton 1963). In other words, the individual's effect on the gene pool of succeeding generations is composed of (1) the individual's own offspring and (2) the effects of the individual on the reproduction of other individuals.

The mechanism of *kin selection*, relying on the idea of inclusive fitness, claims that natural selection favors social behaviors, if it increases the inclusive fitness of the performer, not just its individual fitness. For any genotype, in order for an altruistic trait to evolve, an increase in fitness in some group of relatives by a factor greater than the reciprocal of the *coefficient of relatedness* for that group has to compensate for the sacrifice of fitness of the performer of the altruistic action. The coefficient of relationship is a measure of the probability that a given gene that is present in the altruistic actor (let's say a worker wasp) will be present in the recipient of the action (let's say, the brood of the queen wasp they help to raise) due to common descent (Wilson 1971, p. 328).

So-called *Hamilton's rule* roughly summarizes the conditions favoring the evolution of altruistic traits (Hamilton 1963; Charnov 1977). It specified genetic and ecological conditions favoring the increase in frequency of a gene with altruistic effects in a population (Hamilton 1964a). According to the rule, altruistic traits can evolve if:

$br > c$, where r is the coefficient of relatedness; b and c are respectively the loss (costs to the actor) and gain in fitness (benefits to the recipient) of the altruistic action. If we write k as the ratio of gains to loss in fitness, then the equation can be rewritten as $k > 1/r$ (Hamilton 1963). In order for altruistic behaviors to evolve, the ratio of gains in fitness to loss in fitness must exceed the reciprocal of the coefficient of relatedness. Therefore, the formula points out the importance of quantifying and measuring both relatedness (r) and social, ecological, demographic factors (b and c) if we want to explain how, for instance, reproductive division of labor in Hymenoptera evolved (Hamilton 1964b).

3.3.2 *Polistes and Social Evolution*

Among the social insects, studies of wasps have played an important role in attempts to evaluate and test theories about why social behaviors evolve (e.g. Burian 1994; West-Eberhard, 1996). Beside the easy accessibility of their nests and the practical opportunities that *Polistes* offered to observation and experimentation (Burian 1994; Pardi 1994), wasps of the genus *Polistes* became important organisms to study why social behaviors evolved for two main reasons. First, *Polistes* are primitively eusocial (e.g. West 1967; West-Eberhard 1969). Second, they are cosmopolitan and show a wide variety of adaptations to different environments (e.g. Richards 1971, 1978a).

Polistes is a primitively eusocial genus and differs from highly eusocial insects such as most ants and bees (Wilson 1971). Highly eusocial insects are characterized by distinct morphological castes. In highly eusocial species, it is possible to distinguish queens and workers, say reproductive and non-reproductive castes, just by looking at their morphology. In *Polistes* societies the only differences between the castes are

behavioral and all females are potential breeders (e.g. Marchal 1896; Rouboud 1916).

Non-differentiated castes are almost surely the primitive condition in the evolution of social behavior and anatomically differentiated castes are instead highly derived.

Therefore, primitively eusocial species have served as proxies for the understanding of factors and settings leading to the evolution of social life (Burian 1991).

Polistes societies are organized in a linear social hierarchy (Pardi 1946b). In this genus, social dominance relies on reproductive dominance and on the physiological and developmental mechanisms that regulate it, i.e. on the status of ovarian development of single wasps (Pardi 1946a). In a *Polistes* society, every wasp on the nest could actually become the most dominant one, the alpha-wasp. So, each wasp could potentially abandon the nest and found another one. The mechanisms that prevent potential queens from abandoning the colony and becoming solitary, dominant egg-layers in a different nest are likely to represent important features of primitively stages of social evolution (Evans 1958).

In *Polistes*, fights and control mechanisms characterize both the establishment of the social hierarchy and its maintenance during the yearly life cycle. Over the course of the year, each colony goes through a series of stages that constitute its life cycle. Fertilized queens overwinter in crevices or under bark (e.g. Pardi 1942). In temperate climates in early spring, they start building a new colony either singly or jointly with other auxiliary foundresses. When several females participate in the foundation of a new colony, scientists talk of polygynic foundation. Out of the founding females, one becomes the leader and the others become auxiliaries or leave. The founding females are very aggressive when interacting with each other: bites, antennal clashing, clasping the

other wasps are some of the behaviors characterizing colony foundation (Rau 1939). From these fights and aggressive interactions, a social hierarchy emerges (Pardi 1942, 1946a).

After the foundation, in late spring or early summer, the first larvae hatch giving rise to sterile workers. This phase is usually referred to as the workers phase. At a later time, reproductive females emerge. The new adults are either haploid males or females that will become the new potential foundresses (e.g. Heldmann 1936; Pardi 1942). The reproductive phase lasts until late summer or mid fall when the wasps disperse from their natal nest. Between colony decline and their entry into the hibernacula, the sites where *Polistes* hibernate, males and non-worker potential gynes mate. The fertilized females re-emerge after hibernation in the spring and start founding a new nest. During the founding and worker phase, individuals differentiate into reproductive castes (Heldmann 1936; Pardi 1942).

Though it is possible to generalize some important patterns in the life cycle of this genus, *Polistes* societies come in very different forms in both temperate and tropical regions and “ [...] show a seemingly inexhaustible variety of social behaviors” (West-Eberhard 1996, 62), including solitary and social nest founding, nest usurpation, surreptitious oviposition, worker behavior, idleness, high levels of aggressiveness that take the form of ritualized displays or mortal battles. Thanks to the wide variety of species and to the numerous adaptations to different environments, comparative studies in *Polistes* have been extremely useful to investigate mechanisms of adaptation (West-Eberhard 1990). Also, they can support generalization about the evolution of social behavior. As specific features are present in some individuals and not in others,

comparing different behaviors within species of the same genus has supported the development of hypotheses about the transition from solitary to social life (e.g. West-Eberhard 1978a). It also made it possible to produce generalizations about the pathways followed in other insect genera in the evolution of social behaviors (West-Eberhard 1978a).

Importantly, after *Polistes*, wasp scholars have investigated other species of wasps belonging to different genera, families and subfamilies of wasps in both temperate and tropical environments in order to shed light on the evolution of social life, from *Polibinii* to *Belonogaster*, *Stenogastrinae* and *Ropalidia* (e.g. Gadagkar 2009; Turillazzi 2014; Turillazzi and West-Eberhard, 1996). The growing understanding of these different social systems has encouraged a more contextual perspective on the place that *Polistes* occupy within the *Vespinae* and has provided the opportunity to develop important comparative analysis in the explanation of the evolution of social life (e.g. Turillazzi, 1996).

3.4 Evaluating Inclusive Fitness Theory and Studying Wasps

With its focus on both ecological (i.e. costs and benefits) and genetic (i.e. relatedness) factors, inclusive fitness theory raised new challenges, and opened new lines of empirical research in the study of social evolution. In the 1960s and 1970s, inclusive fitness theory was new and it was unclear whether it was applicable to the evolution of actual biological systems, such as the evolution of social life and reproductive division of labor in wasp societies. The following sections present three important bodies of work from the 1960s and 1970s that have investigated *Polistes* wasps in the evaluation of inclusive fitness theory:

- Hamilton's attempts to evaluate the theory of inclusive fitness by investigating mostly tropical *Polistes* wasps (Hamilton 1964b).
- M.J. West-Eberhard's work on the evolution of social dominance in *Polistes* and polygyny in swarm founding wasps, mostly in the Polibinii (West-Eberhard 1967, 1969, 1973, 1975, 1978a).
- J.E. Strassman's early experimental tests of inclusive fitness in *Polistes exclamans* (Strassmann 1979, 1981a, 1981c; Strassmann and Orgren 1983).

Table 1 summarizes some important features of Hamilton's, West-Eberhard's, and Strassmann's attempts to evaluate inclusive fitness theory. It highlights the importance of *interpretation* and *identification/coordination* in the generation of statements and hypotheses about the evolution of social life. It points out how: (1) The three scientists *interpreted* the parameters in the abstract model referring to different biological and ecological factors (i.e. costs, benefits and relatedness) (Column I); (2) The three scientists *identified*, or coordinated, such parameters with different elements and features of wasp social systems (Column II); (3) A wide variety of empirical investigations informed the *identification* and *interpretation* of Hamilton's formula in the three examples of theory evaluation from the 1960s and 1970s(Column III).

Table 2. Main features of the three case studies

Theory evaluation	I. <i>Interpretation of parameters in the theory</i>	II. <i>Identification of aspects of wasp social biology</i>	III. <i>Empirical practices used</i>
W.D. Hamilton (1964a, 1964b, 1972)	Genetical factors (relatedness)	Dominance, polygyny and polyandry in both <i>Polistes</i> and non- <i>Polistes</i> wasps	(1) Observations of nests in the wild (2) Attempts of comparative analyses (3) Observations of behavioral and physiological characters
		Viscosity and inbreeding	
M.J. West-Eberhard (1967, 1969, 1973, 1975, 1978)	Ecological factors (costs and benefits)	Dominance and polygyny in both <i>Polistes</i> and non- <i>Polistes</i> wasps	(1) Observation of colonies in the wild (2) Comparative analyses of behavioral, anatomical, and physiological characters
		Costs and benefits in fitness due to dominance relations	
J.E. Strassmann (1979; 1981a, 1981b; 1983)	Ecological and genetic factors (Relatedness, costs and benefits)	Dominance and polygyny mostly in <i>Polistes</i>	(1) Natural and manipulative experiments using satellite nests (2) Observation of behavioral, anatomical and physiological features of wasp colonies
		Population structure and relatedness	

3.5 W.D. Hamilton's Evaluation of Inclusive Fitness Theory

Mostly during some trips to the Amazons in the early 1960s, Hamilton engaged in empirical research and attempted to evaluate his theory of inclusive fitness (Hughes, 2004; Segerstrale, 2013). Wasps of the genus *Polistes* played a central role in his attempts

(Hamilton, 1964b). Hamilton's observations focused mostly on relatedness and kinship. The numerous observations and data he collected in his empirical explorations contributed to the further development of the mathematical formulation of the theory (Hamilton, 1972)

3.5.1 Polistes and the polygyny puzzle

Two were the main biological features of wasp social life that puzzled Hamilton: polygyny, say the presence at nest foundation of multiple egg-laying and potentially unrelated females (Hamilton 1964b); and polyandry or multiple mating, say the fact that the reproductive individuals mate multiple times (Hamilton 1964b). Both polyandry and polygyny lower the degree of relatedness in colonies. Therefore, they posed important challenges to Hamilton's explanations of the evolution of social life in terms of inclusive fitness.

By mating with multiple males, the queen's progeny become very genetically diverse. Thus, multiple mating decreases the degree of relatedness among self-sacrificing workers and the queen or her brood. This makes it difficult to explain why the workers would perform altruistic behaviors in such colonies. According to Hamilton, this clearly raised the problem of how self-sacrificing behaviors in wasps were even possible, when the colonies are made out of workers with different genetic origins.

In polygynous colonies, the workers attend a brood produced by more than one female, which means that they are not attending a brood composed only by full sisters. Also polygyny lowers the degree of relatedness in the colony. According to Hamilton, rather than favoring altruistic behavior, polygyny seems to be favorable to the spreading

of genes causing selfish behaviors, which would lower the efficiency of social life. Yet, according to Hamilton: “ (...) it does not seem to do the colonies much harm and the species concerned are highly successful in many cases” (Hamilton 1964b, p. 36).

Polistes are partially polygynous and partially monogynous, as wasps of this genus show different modes of nest foundation and life cycles depending on the climate and on the latitude (Richards and Richards, 1951). Hamilton wrote: “The geographic distribution of the association phenomenon in *Polistes* is striking” (Hamilton 1964b, 37). *Polistes* have different modes of colony foundation that go from mostly monogynous in colder regions to polygynous in the tropics. In temperate regions, usually, several wasps contribute to the foundation of the nest, a phenomenon usually referred to as pleometrosis, but one of them becomes the only egg-laying and dominant one (Pardi 1942, 1948). The rest of the wasps, the auxiliaries or subordinates cannot reproduce and, if any, they succeed in laying only a few eggs. Hamilton focused on the coefficient of relatedness and had difficulties explaining the ready acceptance of non-reproductive roles by auxiliaries in *Polistes* co-foundresses using inclusive fitness theory. Although the foundation happens among siblings, Hamilton found it hard to explain why non-reproductive females rear the offspring of their sisters that are less closely related to them ($r=3/8$) than their own offspring ($r=1/2$).

3.5.2 Observations, dissections and hasty field experiments

Hamilton addressed the challenges raised by polygyny and polyandry by looking into the behavioral, biological and social mechanisms that would increase the degree of relatedness in the colony, the r in his formula. Already in the 1964 paper, he surmised

that one way to increase the degree of relatedness in the case of polygynic or pleometrotic colonies was inbreeding and that inbreeding depended on the high viscosity of wasp population structure (Hamilton 1964b, p. 65).

In several trips to Brazil in the 1960s, Hamilton wanted to figure out how viscosity could lead to inbreeding and, in doing so, contribute to make the degree of relatedness higher. Before the discovery of genetic markers and techniques to assess the genetic relationship of individuals in a colony, finding out about kinship and relatedness was not an easy task. Still, Hamilton tried to find indirect clues in the behaviors of the wasps that hint at the level of relatedness in colonies and how that affected individuals' behaviors.

In some homing experiments, Hamilton looked for a correlation between relatedness and the distribution of the population in a certain area. In this way, Hamilton wanted to see whether average relatedness could correlate with geographic proximity (Hamilton, Notebook I; ZIX55/1/3). He looked into the viscosity of wasp populations trying to figure out whether or not the offspring would disperse slowly from their site of origin or if they would tend to stay close to the nest. In some of these experiments he tried to test the flight range of the wasps so as to see if there were differences between the capacity to fly far away and the level of altruistic behaviors in the colonies (Hamilton, Notebook I; ZIX55/1/3).

Also, Hamilton performed some transference experiments where he would introduce wasps unrelated to the rest of the colony (or related as a control) to see the different reactions. In these experiments he tried to find out if wasps from distant

localities are less likely to be accepted on a nest than wasps from nearby nests (Hamilton, Notebook II; ZIX55/1/3).

Yet, Hamilton did not limit his observations and experiments to the behavior of the wasps. Right upon arrival Kerr's lab in Rio Claro, Hamilton learned new techniques about how to carefully dissect wasps in order to find out about the physiological status of their internal organs. On the third day he was in Rio Claro, he performed his first wasp dissections and started a very accurate Index Card system to collect physiological observations about the wasps he had collected (Hamilton; Z1XUN/15).

Hamilton focused mostly on *Polistes*, but not only, as he observed several species of social and solitary wasps. He looked at the polygyny puzzle in two groups of the Vespidae family: the subfamily Polybiinae and the genus *Polistes* belonging to the subfamily Polistinae (Richards and Richards 1951). He closely observed and reported behaviors and experimental observations about 8 genera of wasps, 8 genera of bees and 2 genera of ants (Hughes 2002). He collected and observed wasp nests of *Polistes fuscatus*, *Polistes canadiensis*, *Mischocyttarus cassanunga*, *Mischocyttarus dormans*, *Polistes cinerascens*, *Apoica pallida*, *Protopolybia minutissima* and others (Hamilton, Index Cards; Z1XUN/15).

3.5.3 Adjusting the theory

In the late 1960s, after his second trip to Brazil, Hamilton was asked to work on a paper where he could explain and revise his 1964 arguments and ideas about “how relatedness affects the evolution of social insects” (Hamilton 1996a, p. 255). Beside other modifications, in the 1972 paper “Altruism and Related Phenomena, mainly in Social

Insects”, Hamilton included inbreeding into his formulation of the mathematical model of inclusive fitness and newly discussed the situation of Polygynous wasp colonies (Hamilton 1972). He was able to incorporate inbreeding into the model thanks to the re-derivation of his formula developed during his collaboration with George Price (Hamilton 1996a, 256). Although the model was improved, it was still not able to address the puzzle that, mostly Polygyny, posed to the haplodiploidy hypothesis.

According to Hamilton, inbreeding might be a good way to explain the puzzle, as it raises the degree of relatedness in the colony. Hamilton wrote: “Unless there is a very high degree of inbreeding, why does not intracolony selection for queen-like behavior break down the system? Why do workers work so willingly and by what device are the fierce struggles for dominance that occur, for example, in queenless *Apis* and *Vespa* colonies prevented?” (Hamilton 1972, p. 216). But Hamilton admitted as well that: “If inbreeding is the answer, would we not expect more genetic diversity between colonies, relative to uniformity within colonies, than we actually observe?” and added “But these questions cannot be answered yet.” (Hamilton 1972, p. 216).

So, adding inbreeding to the model did not actually help to solve the puzzle. In fact, Hamilton in the 1972 review still claimed that: “In my opinion, the polygyny in Polybiini, [...] provides the most testing difficulty for the interpretation of the social insect pattern which is offered in this review” (Hamilton 1972, p. 216). Hamilton, in the late 1960s, was thinking about including other factors and processes in the explanation of how altruistic behaviors might have emerged in evolutionary history. Still, such factors would have had to contribute, according to Hamilton, to raising the relatedness in the colony (Hamilton 1972).

3.5.4 Summing up: top-down and bottom-up components of theory evaluation

In his attempts to see how inclusive fitness theory could help make sense of the evolution of social life in actual biological situations, Hamilton interpreted the theory focusing mainly on the role of relatedness. He wanted to see if the theory could help explain why auxiliaries in *Polistes* wasps give up their reproductive capacities and what made polygyny possible.

Rather than trying to test well-formulated hypotheses, Hamilton explored first the demographic (e.g. dispersal and migrations) and biological (e.g. ovarian development) mechanisms underpinning the coefficient of relatedness. These open explorations allowed Hamilton to identify features of wasp social systems that were relevant for an understanding of the evolution of social life, such as viscosity and inbreeding.

As a result of his empirical explorations, Hamilton modified the theory of inclusive fitness including inbreeding and viscosity of population structure as important factors for the understanding of social evolution. In order to have the theory fit the genetically heterogeneous foundress groups of tropical *Polistes*, he looked for ways to include genetic factors that could increase relatedness in the theory, such as viscosity and its connection to inbreeding.

3.6. M.J. West-Eberhard's Evaluation of Inclusive Fitness Theory

Mary Jane West-Eberhard is one of the most important evolutionary biologists of the post-war era. Over the course of the last decades, West-Eberhard's work on wasp societies has provided a great variety of empirical data and information about wasp social life (e.g. West-Eberhard 1987). At the same time, West-Eberhard's work hugely

contributed to the theoretical development of theories of social evolution (e.g. West-Eberhard 1975, 2003). In later years, her work provided groundbreaking contributions to the understanding of phenotypic evolution at the intersection of developmental biology and evolutionary biology (West-Eberhard 1985, 1987, 2003).

Since the early years of her career, inclusive fitness theory was West-Eberhard's theoretical framework of reference. Yet, according to West-Eberhard, an exclusive focus on genetic factors—the coefficient of relatedness, the r in the formula—was not enough to explain why self-sacrificing behaviors evolved. Differently from Hamilton, she stressed the importance of looking into the ecological factors underpinning social life, the costs and benefits in fitness (i.e. the k in the formula). Along the lines of the natural history and ethological tradition, West-Eberhard relied mostly on observations of wasps in their natural environment as well as on comparative analysis of different species and genera both from literature and from direct observations.

3.6.1 Dominance in Polistes and polygyny in Metapolybia

West-Eberhard graduated under the supervision of D. Alexander with a dissertation from the title *The Social Biology of Polistes Wasps*, published in the Miscellaneous Publications of the Museum of Zoology, University of Michigan (West-Eberhard 1969). Here, West-Eberhard attempted to understand why social dominance in *Polistes* wasps evolved (e.g. West 1967; West-Eberhard 1969). She published a short article in *Science* in 1967 with the title “Foundress Association in Polistine Wasps. Dominance Hierarchies and the Evolution of Social Behavior”, which presented her main evolutionary arguments (West 1967).

In her dissertation, West-Eberhard reported the results of field observations of marked wasps on non-manipulated nests at their natural sites. She studied colonies of *Polistes fuscatus* (an inhabitant of temperate climates, near Ann Arbor in southeastern Michigan) and *Polistes canadensis* (an inhabitant of tropical environments, near Cali in west central Colombia). West-Eberhard observed that, both in temperate and tropical *Polistes* species, nest mates cofounded new nests. In both species, a single female could be the exclusive egg-layer for a period of time long enough to make all of the workers her daughters.

West-Eberhard used her observations in order to address the problem Hamilton had faced in evaluating whether inclusive fitness could help explain the behavior of subordinate individuals in *Polistes* societies (Hamilton 1964b). Hamilton found it difficult to explain the ready acceptance of non-reproductive roles by auxiliaries in *Polistes* foundress association. Here, even if the foundation happens among siblings, it is hard to explain why non-reproductive females rear the offspring of their sisters that are less closely related to them than their own offspring ($r=3/8$). This problem does not occur when thinking about the sterility of daughter workers on a parental nest. In this case, due to haplodiploidy and under the assumption that the female mates only once (no multiple mating), the daughters are more closely related to those of their sisters ($r=3/4$) than to those of their own daughters ($r=1/2$).

In order to assess the degree of relatedness among the founding females, West-Eberhard had to rely on purely behavioral evidence (see, West-Eberhard 2009, pp. 22-23). Observing their behaviors, West-Eberhard concluded that associated foundresses, in polygynous *Polistes* colonies are likely to be siblings and that females known to have

emerged from the same parental nest associate in colony founding.

West-Eberhard relied on estimations of relatedness based on behavioral evidence. Yet, she mostly focused on trying to understand how to measure and assess costs and benefits in fitness of subordinate behaviors. In fact, she wrote: “The likelihood of association depends not only on the closeness of relationship among co-foundresses, but also on the difference in independent reproductive capacity between associates and the degree to which the presence of the joiner augments the reproduction of the joined female” (West 1967, p. 1585). The differences in reproductive capacity of the joiners as well as the degree to which, by joining the nest, some individuals increase the reproduction of the other females are not genetical factors. Rather, they both count for factors pertaining to the k (i.e. the ration of costs and benefits in fitness) in Hamilton’s formula.

By looking into factors affecting costs and benefits, and therefore by using a different interpretation of inclusive fitness theory from Hamilton, West-Eberhard was able to provide a different explanation of why subordinates wasps give up their reproductive capacities in polygynous wasp societies. She concluded that dominance relationships, the fact that some individuals give up their reproductive capacities in favor of the dominant wasps, maximize k for each individual and not only for the dominant wasp. They do so by enhancing the likelihood that the relatively inferior reproductives become workers on nests of superior reproductive, which are thus free to specialize in egg laying. This is why, West-Eberhard concluded: “The dominance hierarchy in wasps, and perhaps other social animals, may thus play an important role in the assignment of different functions (roles) to closely related individuals having different reproductive

capacities in such a way that both dominant and subordinate individuals derive reproductive benefits” (West 1967, p. 1585)

In the work for her doctoral dissertation, West-Eberhard had shed new light on the evolution of social dominance in *Polistes* colonies. Yet, Hamilton had also pointed out that: “... the polygyny in Polibiini, [...] provides the most testing difficulty for the interpretation of the social insect pattern which is offered in this review” (Hamilton 1972, p. 216). In Colombia, West-Eberhard was able to observe a colony of a *Metapolybia* (West-Eberhard 2009), a genus of the Polibiini family. In a paper with the title “The Establishment of Reproductive Dominance in Social Wasp Colonies” in 1977, West-Eberhard detailed the swarming cycle, dominance system, and queen determination mechanisms of a swarm-founding, polygynous tropical social wasp (West-Eberhard 1977).

According to West-Eberhard, *Metapolybia* showed how to reconcile the polygyny, swarm-founding tropical species with inclusive fitness theory, one of Hamilton’s main puzzles (Hamilton 1972). West-Eberhard found out a mechanism in this genus of swarm founding tropical wasps that allowed them to keep the genetic relatedness high. This mechanism consisted in the cyclic reduction of queen number to one, with the effect of cyclic restoration of relatedness to the level of a mother and daughter workers before reproductive swarms were produced (West-Eberhard 1977, p. 2009). In colonies of *Metapolybia*, West-Eberhard also observed that females co-founding nests would alternate different phases of cooperation and conflict. They cooperate while the group supporting their capacity to reproduce was small. Then they would compete when the colony became large and the weakest individuals would lose

their capacity to reproduce, although they had contributed to the success of the females that won the competition by laying eggs and producing workers. These mechanisms met the predictions of inclusive fitness theory.

From her important 1967 article on *Polistes* social dominance to her work on the evolution of polygyny in neo-tropical *Metapolybia*, West-Eberhard showed how, when r is relatively low, the other factors contributing to inclusive fitness (c and b) are relatively high. West-Eberhard interpreted the formula in a way that was different from Hamilton's own interpretation. She used it as a "behavioral and developmental decision rule" (West-Eberhard 2009, p. 28). This meant that, whereas Hamilton would look for mechanisms increasing the r , West-Eberhard would instead look for "individual phenotypic differences, such as those in ovarian development, size or aggressiveness – indicators of differences in reproductive capacity that could be environmentally influenced and would affect the benefit/cost side of Hamilton's Rule" (West-Eberhard 2009, p. 29).

Relying on her observations of *Metapolybia* and other species of wasps, West-Eberhard did not simply suggest revisions to inclusive fitness, as Hamilton did (Hamilton 1972). Rather, she tried to see how different theoretical frameworks, focusing on different aspects of social evolution, could help explain why social life evolved. For instance, she claimed: "The examples to be cited are intended to illustrate the use of kin selection theory in conjunction with other ideas that are not intended to 'prove' the existence of kin selection nor to show that it is the only possible explanation of the examples given" (West-Eberhard 1975).

3.6.2 *Natural history and comparative analyses*

West-Eberhard's hypotheses about the evolution of social life were supported by numerous observations and by the knowledge of naturalistic literature on wasps. In later years, she presented her way of conducting empirical work in a long passage of her autobiography. This passage shows the importance West-Eberhard attributed to bottom-up, exploratory inferences in the process of evaluation of theory of social evolution. West-Eberhard pushed forward the importance of open and exploratory, empirical work on the bio-social systems under investigation in the process of theory evaluation. She rejected the utility of manipulative experiments, as manipulations can actually hinder the understanding of how colonies of wasps actually function and evolve.

West-Eberhard wrote: "In fieldwork on wasps I never set out to test a particular evolutionary hypothesis. Rather, my intention has always been to learn everything I can about behavior and natural history of un-manipulated individuals in the circumstances where they are found, with simple experiments (such as removals of dominant individuals) that mimic natural events and therefore can illuminate their consequences" (West-Eberhard 2009, p. 39).

In West-Eberhard's work, together with naturalistic observations, comparative analyses also represented an essential source of data for the understanding of the evolution of social life. Comparative studies involve comparison of a diverse range of characters (anatomical, physiological, behavioral etc). They examine the correlates, or conditions, of presence and absence of the trait. "They start with a character state, and then undertake comparisons designed to reveal the evolutionary/historical manipulations (conditions) that have produced that result under natural selection" (West-Eberhard

1990). Under the assumption that differences in behaviors among different taxa are due to the action of natural selection, comparative analyses can provide information about the main factors (the evolutionary and historical manipulations) causing the evolution of certain features.

3.6.3 Summing up: top-down and bottom-up components in theory evaluation

In her works from the 1960s and early 1970s, West-Eberhard interpreted Hamilton's formula as a behavioral and developmental decision rule. She engaged in extensive observations of wasp behaviors with a focus on the costs and benefits in Hamilton's rule. Detailed observations and comparative analysis of wasp behaviors constituted the main tools she had to interpret the theory and coordinate it to the actual biology of social wasps and understand the adaptive responses social organisms developed to different environments in terms of inclusive fitness. West-Eberhard's empirical observations and comparative analysis informed the interpretation of Hamilton's rule and allowed her to generate numerous hypotheses about why social life has evolved (West 1967; West-Eberhard 1973).

In her more recent works, M.J. West-Eberhard added to her comparative and observational approach, a focus on the developmental mechanisms underpinning evolutionary change. She wrote: "Although much can be deduced from dissections and comparative studies of natural history, a developmental approach to the evolution of sociality invites a combination of such research with laboratory and experimental studies of regulatory mechanisms, especially hormones" (West-Eberhard 1996, p. 208). This approach also had consequences for the understanding of social evolution in wasps that

integrated West-Eberhard's comparative approach with results from developmental biology and genetic (e.g. West-Eberhard 1987, 2003).

3.7 J.E. Strassmann's Evaluation of Inclusive Fitness Theory

In the opening paragraph of her dissertation *Kin Selection and the Population Biology of the Social Wasp, *Polistes exclamans** at Rice University, Strassmann admitted: "Daniel Otte first introduced me to Texas wasps, and encouraged me to work on insects. Discussions with him in June 1976, helped me to make the jump from natural history to hypothesis testing" (Strassmann 1979, p. iv). Starting with her dissertation, Joan Strassman published an impressive number of works on wasps, where she investigated multiple aspects related to the evolution of social life in wasps. From her early works, Strassmann aimed to test hypotheses and predictions from inclusive fitness theory.

Strassmann's organism of choice was *Polistes*. Although she admitted that "Quantification of kin selection [...] is very difficult. [...]" (Strassmann 1979, p. 45), she attempted to understand if predictions from the theory could help explain why certain features of *Polistes* wasps evolved. She wanted to measure and quantify both the ecological (b/c) and genetic (r) parameters in Hamilton's rule and thereby draw implications about the evolution of social life (Hamilton, 1964).

3.7.1 *Polistes exclamans*

Strassmann explained that the reason why she decided to focus on *Polistes* was their primitively eusocial nature. She even proposed to enlarge the category of *primitive eusociality* to some mammals and birds (Strassmann 1979, p. 6). Therefore, Strassmann motivated her focus on *Polistes* by claiming that using her proposed extended

definition: “ Results of investigations on Polistinae wasps may be generally applicable to the expanded roster of primitively eusocial organisms” (Strassmann 1979, p. 6).

Polistes exclamans and *Polistes annularis* were Strassman’s organisms of choice. These species have two unique features in their yearly life cycle. First, they produce more males earlier in the spring, contrary to most wasps in temperate climates, which tend to produce males in the fall. Second, some colonies produce satellite nests. The satellites are located near the original nest and can be initiated both by a worker and by a queen. Strassmann in her dissertation reported the results of years of observations and experimentation on *Polistes exclamans*, starting in February 1976 until the end in February 1979. The results from these observations provided material for some major papers that came out in the late 1970s and early 1980s.

Above all in the 1970s, the main challenge for any test of kin selection consisted, according to Strassmann, in the possibility to actually measure the degree of relatedness in a colony, as no tools were available in order to perform such measurements. Therefore, she had to use indirect methods in order to get an idea of the degree of relatedness among individuals in a colony: “Individual members of a group are marked and observed exhaustively as they mate, rear young, and perish. Then their offspring are observed. In this way, genetic relationships between individuals and reproductive success of various group members, data vital to testing kin selection, are obtained”(Strassmann 1979, p. 5).

Important for the possibility to provide an experimental test of kin selection was also the knowledge of the exact life cycle and population biology of *Polistes exclamans*. Chapter 2 of Strassmann’ dissertation deals exactly with such features of wasp societies: “Population biology of *Polistes exclamans*” (Chapter 2). In this chapter Strassmann

described the life cycle of the wasp nests and provided details about the demographics and main features of these nests: “Knowledge of the colony cycle of a given species is critical in testing predictions generated by genetical theories on the evolution of social behavior such as kin selection because only with this information can the following be determined: 1. The number of tenures of egg layers; 2. The relation of less fertile females (workers) to the brood they raise and defend; 3. The alternatives workers have, if any, to raising this brood” (Strassmann 1979, p. 55).

3.7.2 *Experimental tests of kin selection*

Strassman made use of the peculiar situation offered by *Polistes exclamans* satellite nests in order to test kin selection. According to Strassmann: “Three criteria must be met to test kin selection: 1. Knowledge of genetic relatedness, 2. Individuals that follow alternative behavioral choices, and 3. Individuals that initially possess identical potential reproductive success” (Strassmann 1981a, p. 87). She thought that *Polistes exclamans* largely met these criteria as relatedness can be assessed through the maternal line, in case multiple mating is not a complicating factor.

A satellite nest is a nest started by a worker, or by queen of a nest, near the main nest. These satellites provided a natural experimental setting in order to measure the parameters specified by kin selection theory in natural situations allowing in this way to test hypotheses derived from kin selection theory. The reason of this opportunity offered by satellite nests is that: “When a satellite nest is initiated, workers on the main nest have a choice between raising larvae on the satellite, and raising larvae on the main nest. The alternative that workers choose was investigated to determine if they choose in a way that

maximizes their inclusive fitness or that of their mothers.” (Strassmann 1981a, p. 61)

Inclusive fitness is measured here as Nr , with N being the number of larvae that can be raised by a worker at a give nest; r is the individual’s relatedness to those larvae.

Strassmann defined the experimental practices that she used in order to test inclusive fitness theory as natural manipulations. She wrote: “The experimental manipulations reported here are similar to natural occurrences to which the wasps may be expected to have evolved an adaptive response. Workers commonly die foraging, and with the small numbers involved, it is not impossible that a satellite could be deprived of all its workers. Nests were knocked down at dawn, the time birds most often knock down so this also represents a natural manipulation” (Strassmann 1979, p. 82)

So, what kind of hypotheses can be derived from kin selection theory that can be tested by way of natural manipulations? Strassmann wrote: “According to kin selection theory, workers should prefer to raise close relatives over distant relatives or non-relatives. Worker females are more closely related to larvae on a queen-initiated satellite, which are their sisters, than they are to larvae on a worker-initiated satellite, which are their nieces. Therefore, according to kin selection, workers are predicted to be more likely to join a satellite initiated by a queen than they are to join a satellite initiated by a worker” (Strassmann 1979, p. 3). In other words: “If satellite initiators and joiners are maximizing their inclusive fitness and satellites do not normally produce more than twice as many larvae per worker as can be produced on the main nest, we can predict the following under the hypothesis of kin selection: 1. When the queen is alive, she will initiate most satellites; 2. When the queen is dead as many satellites will be initiated by workers as were previously begun by queens; 3. All other things being equal, more

workers will join a queen satellite than will join a worker satellite while the queen is alive. After her death, workers will join worker satellites.” (Strassmann `1981a, p. 64)

Strassmann tested these predictions by observing circumstances of natural satellite formations and by performing experiments of worker choice between the main nest and the satellite nest when all workers on satellite were removed. She removed all workers from the queen-initiated satellites as well as from worker initiated satellites. She then observed the satellites and took note of the patterns followed by workers from the original nest. These are the three main sets of experiments Strassmann performed, in order to test hypotheses derived from kin selection theory:

- Experiment 1
 - Workers have to choose between (1) queen satellites, and (2) worker satellites with (a) living and (b) dead queens.
 - Results: “Workers are more likely to join a queen satellite than they are to join a worker satellite while the queen is alive, though they will join a worker satellite after the queen is dead.” (Strassmann 1981a, p.77).
- Experiment 2
 - Then main nests were knocked down to determine if all workers then go to satellites. Finally all workers and queens were collected and dissected to affirm the identity of the queen as only ovipositor, and to determine if workers joining satellites were different in age or ovarian condition from workers not joining satellites” (Strassmann 1981a, p. 65).

- Results: “After a main nest is knocked down, wasps do not always join a satellite” (Strassmann 1981a, p. 77).
- Experiment 3
 - “From nests without queens, workers initiated satellites in greater numbers than workers initiated satellites while original queens were alive. Workers were less likely to join worker-initiated satellites while original queens were still alive. The behavior of workers and queens maximized the inclusive fitness of both workers and queens. It is clear that worker behavior follows the predictions of a genetical theory of sociality” (Strassmann 1981a, p. 81).

Strassmann’s conclusions of her experimental manipulations seemed pretty clear: “More workers joined queen initiated satellites than joined worker initiated satellites, fulfilling the prediction of kin selection” (Strassmann 1979, p. 3).

3.7.3 From experimental tests to evolutionary hypotheses

According to Strassman, it was possible to explain the results obtained in these three sets of experiments by referring both to ecological and genetic factors. The behaviors observed are likely adaptations to the long Texas summers. “Early male production allows nests to continue even after original queens have died, because workers mate and oviposit. These mated workers also initiate satellite nests. Satellite nests probably represent a complex adaptation to the ill effects of nest permanence. Bird predation on

nests and infestation of nests by *E. polistes* both probably make satellite nest formation advantageous.” (Strassmann, 1981a, 59).

Observations of *Polistes exclamans* in two different areas of Texas allowed Strassmann to produce adaptive explanations of differences in behaviors and population structure in different populations of the same species. She observed that wasps of the same species had a viscous structure with lower dispersion rates in west Texas and a panmictic structure in east Texas. According to Strassmann, wasps in colonies with lower dispersion rates have higher levels of inbreeding and tend to cooperate more, whereas wasps in panmictic populations tend to show higher levels of competition. Therefore, she hypothetically connected costs and benefits in fitness and the population structure that certain populations have evolved to different climates. Strassmann hypothesized that viscosity is connected to polygyny, on the one hand, and panmictic population structure to monogyny, on the other hand (Strassmann and Orgren, 1983).

3.7.4 Summing up: top-down and bottom-up components of theory evaluation

In her works in the late 1970s, Strassmann wanted to test kin selection theory with a rigorous experimental process of hypothesis testing. She chose the opportunities offered by the natural occurrence of satellite nests in *Polistes exclamans* and tried to measure the factors expressed in Hamilton’s rule. Yet, in order to generate hypotheses and predictions Strassmann had to closely investigate the wasp societies she was dealing with. She focused on detailing their life cycles and population structure. Detailed observations and comparative analysis both of populations of the same species and of populations of

different species informed the generation of Strassmann's evolutionary hypotheses, rather than a strict attempt to confirm predictions from inclusive fitness theory.

Strassmann's later works, mostly in collaboration with her husband, the evolutionary biologist David C. Queller, unveiled numerous other aspects of wasp social life and its evolution. Among others, one major contribution to the field of social evolution consisted in the use the two scientists made of microsatellite, or single tandem repeats, as genetic markers for the measurement and quantification of kinship and relatedness. Thanks to microsatellites, it was possible to identify relatives and quantify population structure. This method allowed for more rigorous testing and measurements of the predictions of kin selection theory (e.g. Queller and Goodnight 1989). Through the use of microsatellites, Strassmann and Queller were even able to show that in polygynous colonies with many queens relatedness was kept at levels consistent with kin selection (Queller et al. 1988; Queller and Goodnight 1989).

3.8 An Investigative Framework for Theory Evaluation

The analysis of Hamilton's, West-Eberhard's and Strassmann's works shows the wide array of investigative practices involved in the evaluation of inclusive fitness theory in the 1960s and 1970s. Figure 8 abstracts from the differences of the three cases and visualizes the common features of theory evaluation in the form of an *investigative framework*. The three examples presented above represent different ways of working within this framework.

The *investigative framework for theory evaluation* is organized around three sets of products (the boxes in Figure 7): 1. Empirical data (lower box); 2. Hypotheses about

phenomena (middle box); 3. Theories and models (upper box). The arrows in the figure represent the practices that scientists use in theory evaluation. The bigger and dotted arrows departing from the lower (i.e. Data) and upper boxes (i.e. Theories and Models) represent the two processes contributing to the generation of hypotheses: top-down inferences from the theory and bottom-up inferences from empirical data.

The arrowed and dotted margins of the middle box (i.e. Hypotheses about Phenomena) visualize how both inferences from the theory and inferences from the data contribute to the generation of hypotheses. Both kinds of inferences inform the coordination of abstract models to real biological systems (see: dotted margins of middle box) as well as the interpretation of such models through biological mechanisms (see: dotted margins of middle box).

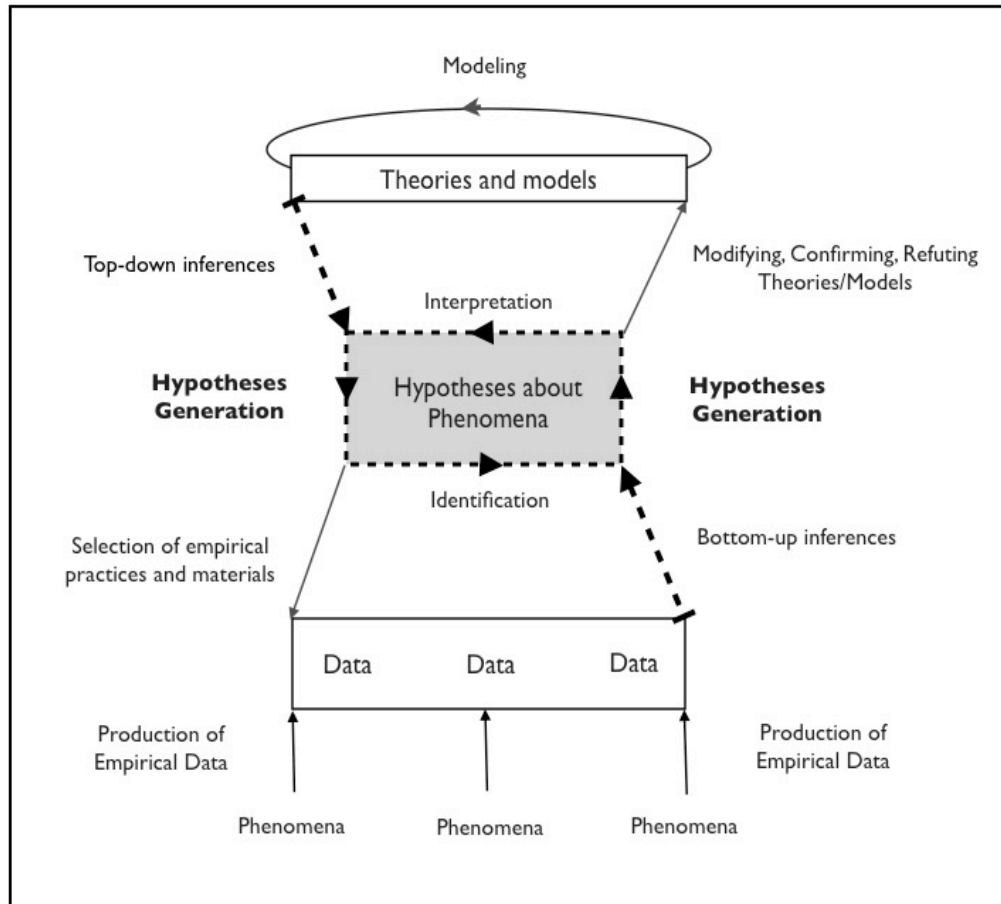


Figure 7. An investigative framework for theory evaluation

The idea of investigative framework represents a development of Bogen and Woodward's three level model of scientific inquiry (Figure 6; e.g. Bogen and Woodward 1988, 1989). Hypotheses and predictions about why social life has evolved correspond to the statements or claims about phenomena that Bogen and Woodward talk about in their model. Similarly to Bogen and Woodward's model, the investigative framework retains that, instead of testing theoretical claims by direct comparison to raw data, scientists use data to infer facts about phenomena, and not to confirm or falsify theories.

Also, again similarly to Bogen and Woodward's model, in the investigative framework, bottom-up, inferential, exploratory practices play a fundamental role in the generation of hypotheses and predictions about phenomena of social evolution. Yet, differently from Bogen and Woodward's model, in the *investigative framework*, hypotheses and statements about phenomena of social evolution emerge from a process that is both top-down—*inferences* from theories and models—and bottom-up—*inferences* from empirical data. Inferences from the theory as well as inferences from empirical data inform one another in the generation of hypotheses and statements about the evolution of social life.

The following discussion of the *investigative framework* highlights the role of both *top-down* derivations from theories and *bottom-up* inferences from empirical data in the generation of hypotheses and statements about phenomena in social evolution. Giere's treatment of *interpretation* and *identification* provides a starting point for an account of the main steps of theory evaluation. Yet, both contra Giere and contra Bogen and Woodward, the *investigative framework* articulates how bottom-up and top-down inferences inform one another in the generation of hypotheses in theory evaluation.

3.8.1 Identification and interpretation in the practice of theory evaluation

The formal theory Hamilton presented in "The Genetical Evolution of Social Behavior" (Hamilton 1964a) is a complex mathematical construct that applies the principles of population genetics to the understanding of the evolution of social life (Grafen 2004). Similarly to the principled models Giere talks about, inclusive fitness theory characterizes a specific perspective on the world. The theory gives expression to a neo-Darwinian

approach to the understanding of the evolution of social behavior (Wilson 1971). In Giere's terms, inclusive fitness theory represents a kind of principled model. It is the formal extension of population genetics models and does not make any direct claim about the world.

Hamilton's rule expressed the conditions under which an altruistic character can be selected. The rule sets the conditions of diffusion of altruistic genes and pointed out the role of ecological (benefits and costs in fitness) as well as of genetic factors (relatedness) (Hamilton 1963). Hamilton's formula, in Giere's terms, offers a kind of representational model. The formula, in its more or less complex formulations, is the abstract model that scientists attempted to evaluate in their empirical works in the 1960s and 1970s (Hamilton 1963; West-Eberhard 1975)s.

In order to generate hypotheses and statements about phenomena of social evolution, scientists such as Hamilton, West-Eberhard and Strassmann had to anchor the parameters in the formula to features of biological systems in the real world. They had to *interpret* the formula by looking into specific biological features of social systems (roughly, the costs, benefits and relatedness in certain societies). Also, they had to *coordinate (identify)* real bio-social systems whose evolution could be described using the rule. In this way, they made use of the formula and generated hypotheses (statements about phenomena) about why social behaviors evolved.

Hamilton, West-Eberhard and Strassmann struggled to understand: (1) how to interpret and balance the different parameters in Hamilton's formula against one another (West-Eberhard, 1975, 1978a) as well as (2) how to interpret and measure parameters in the formula (Strassmann, 1979, 1981a). The interpretation of the formula in their works

was not just a top-down process. Rather, it emerged from top-down and bottom-up inferences that informed one another in the generation of statements and hypotheses about phenomena of social evolution.

An example of how inferences from the data and inferences from theories or models were involved in the interpretation of Hamilton's formula becomes apparent if we consider the differences between Hamilton's and West-Eberhard's works. Hamilton stressed the importance of genetic factors and the coefficient of relatedness (Hamilton 1964a, 1964b). West-Eberhard focused on costs and benefits (West-Eberhard 1975, 1978a). Both attempts to interpret the formula led to the generation of hypotheses about why social life evolved making use of empirical data.

In the evaluation of inclusive fitness theory, West-Eberhard generated hypotheses, first, about the evolution of social dominance in *Polistes* (West 1967) and, second, about the adaptive value of Polygyny in *Polibinii* (West-Eberhard 1973). Such hypotheses did not emerge as derivations from the theory. Instead, they emerged from the empirical study (observations and comparative analysis) of what might count as costs and benefits in fitness or of how ecological and genetic factors play out in explaining why certain behaviors evolved. A similar process of interpretation characterized Hamilton's work on social wasps in the 1960s. In this case, Hamilton's focus on genetic factors led him to interpret the formula in a different way and to perform empirical investigations focusing on population structure and viscosity. His hypotheses about why social life evolved in wasps revolved around genetic factors and relatedness and how these features showed in certain kinds of population structure.

The attempts to actually measure the parameters in Hamilton's formula were also part of the process of interpretation of the formula. Strassmann's work from the very beginning attempted to measure the different parameters in the formula and to understand how the different factors played out in the biology of actual wasp societies. This work aimed to provide quantitative arguments that could show whether or not inclusive fitness theory actually applied to the evolution of actual biological systems.

The *identification*, or coordination, of the elements in the formula with features of actual biological systems also involved a wide range of conceptual and empirical practices. Such practices importantly involved the use of wasp societies as important systems for the evaluation of inclusive fitness. Rheinberger pointed out the importance played by specific systems in the investigation of biological phenomena: "... we have, at the basis of biological research, the choice of a system, and a range of maneuvers that it allows us to perform" (Rheinberger 1997, p. 25). Besides the easy accessibility of their nests and the practical opportunities that they offered to observation and experimentation, *Polistes* also allowed scientists to look into a wide range of primitively eusocial behaviors in a wide variety of environments.

Wasp societies in their different forms, such as swarm founding wasps or wasps with polygynous foundation and social hierarchy became important systems for the study of social evolution. These systems came already packaged with a series of experimental, methodological and conceptual tools or procedures (Rheinberger 1997). In the investigation of wasp societies, scientists engaged in three main sets of empirical practices: (1) Empirical observations and experiments about behavioral and physiological features of wasp colonies; (2) Natural and manipulative experiments on wasp colonies;

(3) Comparative analyses. Empirical observations and experiments have provided information about behavioral, physiological and anatomical mechanisms governing social life in wasp societies. Natural and manipulative experiments of wasp nests have provided information about the main *factors* (e.g. relatedness, costs and benefits in fitness) contributing to the evolution of social life. Under the assumption that the correlation of certain traits and certain situations is maintained by natural selection, comparative analyses provided information about the main steps leading to the emergence of social behaviors (West-Eberhard 1990).

Empirical investigations contributed to coordinating the parameters in the formula with main features of wasp societies in order to explain why social life evolved in those systems. Hypotheses and statements about why social life evolved have been the product of these exploratory, empirical works as much as of inferences from Hamilton's formula. For instance, although the hypotheses Strassmann's tested were derived from the theory of inclusive fitness, they also relied on the detailed knowledge of *Polistes exclamans*, their behaviors and life cycles in different regions and climates (Strassmann 1979, 1981a). Also, West-Eberhard observations of numerous nests, first, of different *Polistes* species and, then, of several swarm founding Polibinii both with naturalistic observations and with comparative analysis informed the production of hypotheses about why certain social features might have evolved.

In order to better understand the role of empirical work in the interpretation and coordination of Hamilton's formula to actual biological systems, it would be important to account for how multiple lines of evidence (i.e. from naturalistic observations, experiments and comparative analysis) were integrated in the formulation of evolutionary

hypotheses. In theory evaluation in social evolution, each set of empirical practices has provided distinct information about why social life evolved. Therefore, along the lines of recent works on integration in scientific practice (e.g. Mitchell and Gronenborn, forthcoming; Mitchell 2003) it would be important to account for how multiple lines of evidence have been integrated in the production of statements about phenomena as part of the process of interpretation and identification of abstract models and theories when data were scarce and hard to obtain in the 1960s and 1970s.

3.8.2 The investigative framework in epistemological context

The analysis of Hamilton's, West-Eberhard's and Strassmann's attempts to evaluate inclusive fitness theory shows that the interpretation of the theory as well as its coordination to actual biological mechanisms took place at the interface of inferences from theories and inferences from empirical data. In the evaluation of inclusive fitness theory, empirical practices—from the experimental and observational exploration of wasp societies to the integration of different sets of data—have informed both identification and interpretation of Hamilton's formula. They both have contributed to the generation of hypotheses and statements about why social life evolved.

The account of theory evaluation presented in the investigative framework with a focus on identification and interpretation represents an alternative to both theory/model-first and to experiment-first accounts of scientific inquiry. It questions the hierarchical distinction between bottom-up inferences from the data and top-down inferences from abstract models. It argues that both bottom-up and top-down inferences inform one

another in the generation of hypotheses in the evaluation of theories about the evolution of social life.

Differently from experiment-first accounts, such as Bogen and Woodward's model, the investigative framework for theory evaluation shows that statements about phenomena in the form of hypotheses are not the product only of inferences from the data. Responding to some criticism about the original formulation of the three-level model (data/phenomena/theory) (Schindler 2007), Woodward admitted that theories also play a role in the inferential processes from data to statements about phenomena (Woodward 2011). He admitted that explanatory theories actually play a role in the process of inference from data to phenomena, in the formulation of statements about phenomena, though not an explanatory role. Woodward suggested that theories can *motivate* scientists to look into specific quantities and variables or can even *provide a vocabulary* for scientists for characterizing the results of measurements and assessment of a given phenomenon (Woodward 2011).

Woodward's acknowledgement of the way explanatory theories influence bottom-up inferences and practices leading to the formulation of statements about phenomena gets closer to the reality of scientific practice. Yet, it does not accommodate the recursive interaction of top-down and bottom-up components in the generation of statements about phenomena emerging from the examples of theory evaluation presented in this paper. It does not account for how theory evaluation, in the identification and interpretation of abstract models, recursively involves both forms of derivations from the theory and forms of inferences from the data.

Theory-first accounts, such as Giere's hierarchical model, also keep a strong distinction between the bottom-up generation of experimental models and hypotheses and the top-down specification of theories and representational models. It ends up with two kinds of hypotheses, one derived from the models through specification, and one inferred from the data through generalization. The latter is supposed to help confirm or falsify the former. Also this model-first account does not pay justice to the constant and recursive interaction of bottom-up and top-down processes involved in the generation of statements and hypotheses about phenomena. It does not account for how empirical explorations and investigations made possible the interpretation and identification of abstract models in scientific practice.

The contribution of empirical work to the process of evaluation of Hamilton's formula is therefore not confined to the confirmation of hypotheses derived top-down from the model, as argued in Giere's model. Neither, it is the only way to account for the generation of hypotheses about phenomena of social evolution, as argued in Bogen and Woodward's model. Rather, a constant interplay of top-down derivations and bottom-up inferences contribute to the generation of hypotheses and statements about phenomena in theory evaluation in social evolution.

3.9 Conclusions

A focus on theories and models has traditionally monopolized debates and conversations about our understanding of social evolution (e.g. Wilson and Sober 1994). In more recent years, investigations of the molecular and genomic underpinnings of evolutionary processes have shifted this focus and stressed the importance of big data in the study of

the evolution of social life (e.g. Fischman et al. 2011; Patalano et al. 2015). This paper focuses on a time when theoretical models about the evolution of social life were new, hypotheses contentious and empirical data scarce. It shows how scientists have creatively struggled to produce evidence about how and why social life evolves. It also shows how theory evaluation happens through a recursive process that always involves both theoretical and empirical work.

The idea of *investigative framework for theory evaluation* with its recursive features points out the importance of keeping a strong connection between empirical and theoretical work. Both are always necessary to advance our knowledge of complex evolutionary phenomena. They inform one another in the study of why social life evolved. Hypotheses in these exploratory investigations are not mere devices to confirm theories, but rather creative tools to give shape to empirical data in order to get a better understanding of phenomena of social evolution. If we want to understand how knowledge has been produced and if we want to advance scientific efforts in the investigation of the evolution of complex evolutionary phenomena even today, it is important to be aware of how different experimental, observational, conceptual and theoretical practices recursively act together.

CONCLUSION

Philosopher of science William C. Wimsatt once argued: “Our normative claims should more often be rooted in heuristics of effective and efficient problem solving and scientific practice, or demands of the situation, than any general logical or deontological claim” (Wimsatt 2007, p. 320). This dissertation has followed Wimsatt’s invitation to (1) detail and describe scientific practices as they unfold in specific situations and (2) root epistemological and normative claims in the understanding of scientific practices.

The question that informed the three chapters above is: How have scientists *generated* and *evaluated* new concepts and theories about social life and its evolution by *investigating* wasp societies? Two interrelated theses emerged in the process of answering this question. The first is historical and descriptive. It argues that scientists have generated and evaluated new concepts and theories about social life and its evolution by constantly interweaving empirical, conceptual and theoretical investigations. The second is epistemological and normative. It argues that, if we want to advance our knowledge of how social life works and why it evolves, it is important to foster the synergistic and recursive use of experimental, observational, conceptual and theoretical practices.

In order to account for how scientists have generated and evaluated new ideas against empirical evidence, both historical and epistemological arguments have relied on a broad notion of scientific practice. This notion encompasses empirical, conceptual and theoretical aspects of scientific work (Soler et al. 2104). The narratives have captured the generation and evaluation of scientific ideas in their temporal unfolding within the life of individual scientists. The reconstruction of Leo Pardi’s and William D. Hamilton’s

investigative pathways recorded how empirical and conceptual/theoretical practices informed one another in the evaluation of new concepts and theories (Chapter 1 & 2). Drawing upon the narratives, the *investigative framework* provided an integrated and holistic account of theory evaluation (Chapter 3). First, this account has articulated the interrelation of different practices in the investigation of phenomena of social evolution. Second, it has shown how inferences from the data and inferences from the theories inform one another in the generation of hypotheses and statements about phenomena of social evolution.

Chapter 1 has detailed how, between 1937 and 1952, Pardi generated and evaluated the concepts of *social* and *reproductive dominance* to explain the mechanisms governing *Polistes* wasp societies. Over the course of more than ten years, Pardi's research recursively transitioned between empirical observations and the further articulation of the concepts of social and reproductive dominance: from early histological and physiological works (1937-1941) to the first development of the idea of social dominance (1941-1942); and from the articulation of the relationship between social and reproductive dominance (1942-1950) to the design of experiments that could prove the existence of such relationship after E.P. Deleurance's attack (1950-1952).

The reconstruction of Pardi's investigative pathway has shown how the Italian scientist developed a peculiar etho-physiological approach in the study of animal behavior that brought together the observational approach of natural history, the comparative style of morphology, and experimental methods from embryology and physiology (Pardi 1972). It has also shown that Pardi's etho-physiological investigations in the 1940s constantly interwove empirical investigations with the (re-)conceptualization

of ideas and conceptual frameworks—e.g. social hierarchy, social dominance, and reproductive dominance—in the attempt to explain the mechanisms underpinning social life in *Polistes* wasps.

Chapter 2 has reconstructed how, between 1964 and 1972, Hamilton attempted to evaluate whether the theory of inclusive fitness could help explain why social life evolved in actual bio-social systems. The detailed account of Hamilton's empirical investigations in those years shows how the British evolutionary biologist progressively articulated his ideas on social evolution transitioning back and forth between empirical explorations and theory development. Hamilton engaged in the evaluation of his own theory of inclusive fitness by: doing empirical work in the first trip to Brazil (1964-1965), questioning the haplodiploidy hypothesis and rethinking the theory after the trip (1965-1968), attempting to do more empirical work in the second trip to Brazil (1968-1969), and eventually revising the theory (1969-1972).

Hamilton's investigative pathway has shown how inferences from empirical data as well as inferences from the theory mutually informed one another in Hamilton's way of evaluating inclusive fitness theory against biological evidence. Hamilton attempted to evaluate inclusive fitness theory by constantly transitioning between empirical explorations, experimental manipulations and theoretical elaborations. The process of theory evaluation in Hamilton's scientific practice led him to question whether or not his focus on relatedness in the theory of inclusive fitness was the most appropriate; the validity of his haplodiploidy hypothesis to explain the origins of self-sacrificing behaviors in Hymenoptera; and the correctness of his theoretical achievements.

In Chapter 3, Hamilton's empirical investigations, West-Eberhard's work on the evolution of social dominance and polygyny, and Strassmann's experimental manipulations of *Polistes* colonies have inspired a normative account of theory evaluation in the form of an *investigative framework*. The *investigative framework for theory evaluation* presented here abstracts from the details of single efforts to evaluate inclusive fitness theory. It captures the common denominator of scientists' creative struggles to generate evolutionary hypotheses about why social life has evolved and to support them with empirical evidence.

The framework has articulated a holistic and integrated perspective on theory evaluation. It has captured the recursive nature of theory evaluation that emerges from the narrative of scientists' investigative pathways and has shown how theory evaluation involves the synergistic use of multiple practices. In particular, it has focused, first, on the challenges of *coordinating* mathematical models (i.e. Hamilton's formula) to actual bio-social systems (e.g. wasp societies). Second, it has fleshed out how scientists have attempted to *interpret* mathematical models and tried to recognize the biological mechanisms underpinning the functioning of such systems. It has pointed out how empirical investigations, from comparative analysis to naturalistic observations and experimental manipulations, have not only been used to test existing hypotheses derived from the theories, but have rather informed the generation of hypotheses and predictions in theory evaluation.

This account of theory evaluation has provided an alternative to both *theory/model-first* accounts of theory testing (e.g. Gierie 2010) and *experiment-first* accounts of scientific inquiry (e.g. Bogen and Woodward 1988; Rheinberger 1997). The

former have argued that hypotheses are first derived from theories and then tested against empirical evidence. The latter have pointed out the generative roles of empirical work in discovering features of phenomena, which are not necessarily predicted by any existing theory. The investigative framework for theory evaluation has acknowledged the importance of both accounts, but has also argued that none of them suffice to recount how scientists have advanced our knowledge of the evolution of complex bio-social systems.

Both the narrative and the epistemological lines of inquiry in this dissertation have focused on the evaluation of a single conceptual—i.e. Pardi’ ideas of social dominance—or theoretical framework—i.e. Hamilton’s inclusive fitness theory. This focus has supported the elaboration of a holistic and integrated understanding of theory evaluation in specific historical and cultural contexts. Yet, in many instances, concepts as well as theories need to be compared with other concepts and theories. Often, choices have to be made among alternative conceptual or theoretical frameworks. This realization points out directions for further research that would complement the focus on single theories and concepts in this dissertation with the account of how to choose among alternative theories and concepts. This is true both for the narrative reconstructions and for the epistemological reflections.

For instance, in the reconstruction of Hamilton’s attempts to evaluate inclusive fitness theory, it is important to complement the analysis presented in Chapter 2 with a more thorough reconstruction of how Hamilton confronted alternative hypotheses and approaches in social evolution prominent in those years, such as Alexander’s mutualism (Alexander 1974) and Michener’s sub-social route (e.g. Lin and Michener 1972). It is

important to answer questions such as: How did these alternative hypotheses and approaches actually influence Hamilton's way of thinking about and evaluating social evolution? And how did Hamilton address the challenges that such alternative approaches raised to his own theory?

On the epistemological side of things, the focus on the evaluation of one theory also invites reconsideration of theory choice how theory happens in scientific practice. Often the problem of confirmation and evaluation of scientific theories has been framed in terms of theory choice (e.g. Laudan, 1978). In this case, the problem is not how we evaluate a single theory, but rather how we can choose between competing theories dealing with the same phenomena. By focusing on the evaluation of a single theory, the investigative framework for theory evaluation presented in Chapter 3 has provided a starting point for the reassessment of questions related to theory choice. By encouraging a more thorough analysis of the interrelation of multiple scientific practices as well as of how different practices mutually inform one another, the framework also invites to reconsider also the way we can choose among different theories and concepts.

This dissertation narrated the work of different scientists struggling with how to produce evidence that could bear on the evaluation of important concepts and theories. All these works suggest the importance of combining different experimental, observational, conceptual and theoretical approaches in understanding the main features of social life. As a whole, the reconstruction of the works of these scientists will hopefully inspire and support future research projects and attempts to explain how and why social life evolved.

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