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### The evolution of animal societies

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# THE EVOLUTION OF ANIMAL SOCIETIES

An exploration of the effects of population structure, life-history and behavioural plasticity



rijksuniversiteit  
 groningen

Andres Eduardo Quiñones

The evolution of animal societies: An exploration of the effects of population structure, life-history and behavioural plasticity.

The research reported in this thesis was carried at the Theoretical Research in Evolutionary Life Sciences (TRÉS), which is part of the Groningen Institute for Evolutionary Life Sciences (GELIFES) of the University of Groningen (the Netherlands), according to the requirements of the graduate school of science (Faculty of Mathematics and Natural Sciences, University of Groningen).

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# The evolution of animal societies

An exploration of the effects of population structure, life-history and behavioural plasticity

## PhD thesis

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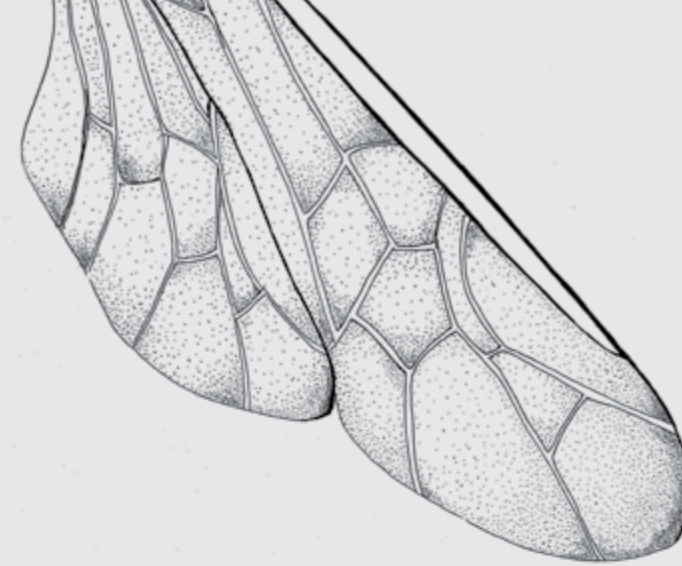
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# CONTENT

	Introduction and Outline of the thesis	9			
CHAPTER 1	Cultural evolution of cooperation: the interplay between forms of social learning and group selection <i>Evolution and Human Behavior</i> 34:342–349. <a href="https://doi.org/10.1016/j.evolhumbehav.2013.06.001">10.1016/j.evolhumbehav.2013.06.001</a>	33	CHAPTER 5	Negotiation and appeasement can be more effective drivers of sociality than kin selection <i>Phil. Trans. R. Soc. B</i> 371:20150089. <a href="https://doi.org/10.1098/rstb.2015.0089">DOI: 10.1098/rstb.2015.0089</a>	145
CHAPTER 2	A unified model of preadaptations that trigger the evolutionary transition to eusociality <i>Under review at: Nature Communications</i>	53	CHAPTER 6	A general model of negotiation in asymmetric evolutionary games	179
CHAPTER 3	Worker ovicide can drive the evolution of social polymorphism and split sex ratios	91	CHAPTER 7	Afterthoughts: The evolutionary transition to eusociality	209
CHAPTER 4	Cryptic extended brood care in the facultatively eusocial sweat bee <i>Megalopta genalis</i> (Hymenoptera: Halictidae) <i>Insectes Sociaux</i> (2015) 62: 307. <a href="https://doi.org/10.1007/s00040-015-0409-3">doi:10.1007/s00040-015-0409-3</a>	129		CITED LITERATURE	227
				ENGLISH SUMMARY	251
				SAMENVATTING	259
				ACKNOWLEDGEMENTS	267
				CURRICULUM VITAE	273



INTRODUCTION AND OUTLINE OF  
THE THESIS



One of the cornerstones of human dominant position on the planet is our social nature. Many, if not all, facets of our lives develop in a social context. Some of those facets are by definition social. Others, despite not being inherently social, have become intertwined with our social nature such that we find it difficult to imagine them outside a social context. Science, just as an example, has developed as a social construct; to such extent, that some of its defining features require the interaction between peers. It is, therefore, not surprising that in the study of the natural world social behaviours are also the ones that, most prominently, catch our attention and curiosity. From the communications songs of humpback whales to the incessant laborious worker ant, social behaviours appeal to our own social nature and magnify our thirst for answers. The study of social evolution is an attempt to use the Darwinian framework to have a deeper understanding of nature's social dimension, and along with it, our own.

It was Darwin himself who first addressed some key issues of social behaviour from an evolutionary perspective. The most famous segment of the *origin of species* dealing with social behaviour is probably in chapter 7 where he discusses the worker castes of social insects. Darwin refers to the existence of sterile worker caste in social insects as “*one special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory*” (Darwin 1859). The problem that Darwin saw on the existence of a sterile caste was twofold (Ratnieks et al. 2010). First, and according to him the less important difficulty, the sterility of individuals; how can natural selection drive individuals to completely cease their reproductive effort, when it is precisely reproduction which is the currency in which individuals are measured in the struggle for existence? Secondly, the contrastingly different morphological and behavioural features of workers and queens; how can workers pass on the traits that characterize them if they don't reproduce? The answer Darwin provides for this special difficulty is quite likely the predecessor of two fundamental theories of social evolution: kin selection and group selection theory. However, Darwin himself did not explicitly mention either of these two phrases; hence, he obviously did not make a distinction between them. His answer is that natural selection does not only act at the level of the individual but also at the level of the family and/or the ‘community’; although, he did not specify what community actually is.

Darwin's views on the evolution of the sterile castes of social insects, and other social behaviours, implicitly point towards one element that is prevalent in all theories of social behaviour: conflict. Darwin's solution to the worker caste problem is framed in terms of the conflict between different levels of organization. In the case of the worker caste, it may be in the interest of the individual worker to reproduce; however, the interest of the colony is that some of its individuals refrain from reproduction to boost colony productivity. According to Darwin's logic, if natural selection at the level of the family is strong enough, we expect evolution to lead some members of the colony to be sterile. This conflict can also be framed as one between two classes of individuals: the offspring (worker) and the mother (queen). In such conflict, the offspring interest may lie with its own reproduction, and the mother's interest in having a worker do the work for her. However, taking into account that both share genes, their evolutionary interest is in line with the reproduction of either one. It is interesting to see that both of these perspectives highlight different faces of the conflict that underlie social behaviour. The first highlights the hierarchical aspects of sociality. While the later one, highlights the necessary constraint to ameliorate conflict, the degree of kinship between individuals.

Social evolution theory has been mainly focused on finding processes and conditions that ameliorate conflict, and mechanisms that allow individuals find a solution to their conflicts, in order to understand evolutionary origins of social behaviour. Group selection theory is concerned with the conflicts between an individual and its social group; and under what conditions these conflicts are diminished (Frank 1986). Kin selection theory (Hamilton 1964a) is about how genotypic correlations between individuals align the evolutionary interest of individuals. The theory of reciprocal altruism (Trivers 1971) is about how individual's response rules allow them to find different solutions to their conflicting interests. These are the three most prominent frameworks to understand the evolution of social behaviours.

This thesis is about the evolutionary origins of social behaviours and about the conflicts of interests inherent to social interactions. In the tradition of kin selection theory, we derived conditions under which genetic correlations and life-history structures ameliorate the conflict between individuals, hence, allowing natural selection to drive the evolution of the worker caste (Chapters 2 and 3). In the philosophy of the theory

of reciprocal altruism, we investigated behavioural strategies with which individuals can respond to each other and find a solution to their conflicting interests (Chapters 5 and 6). There are, nonetheless, two elements of novelty that are worth mentioning. First, the models presented in the thesis include the simultaneous evolution of multiple traits. For example in chapter two, we allow the coevolution of sex ratios and worker behaviour; behaviours whose evolution had been modelled before separately. The coevolutionary perspective we used provided new insights into the evolutionary transition to eusociality. Secondly, our models include the interaction between genetic correlations, which align conflicting interests, and response rules, which allow compromises in the conflicts; namely, integrating elements from the two leading frameworks to understand the evolution of social behaviours. Finally, this thesis is not a comprehensive study of a particular social behaviour, but rather, it comprises a set of research papers inspired by specific biological systems. Chapter one is inspired by the early evolution of human societies. Chapters 2 – 4 are inspired by primitively social insects, such as paper wasps and sweat bees. Chapters 5 and 6 are inspired by the cooperatively breeding cichlid fish *Neolamprologus pulcher*, although chapter 6 presents an analysis of much more general scope. The connection between these different systems appears to be no other than the fact that they sparked mine and my collaborators' curiosity. However, I leave it up to the reader to find any deeper link.

In this introduction I will first describe quite generally three theoretical and conceptual frameworks under which the chapters of the thesis are circumscribed. Secondly, I will introduce the two main biological systems I studied, outlining the questions that were addressed.

## Theories on the evolution of cooperation

Social evolution is concerned in general with the evolution of traits that affect the fitness of an individual as well as that of her interacting partners. However, there has been a disproportionate amount of research, both theoretically and empirically, on traits that have a negative effect on an actor, and a positive effect on the partners. Despite much controversy about the semantics of the field (West et al. 2007a, 2007b; Wilson 2007), we can collect these traits under the umbrella of costly cooperation. The evolution of cooperation has become a field of study on its own; it now attracts

researchers from diverse backgrounds such as: biology, psychology, computer sciences, economics, physics, mathematics, sociology and political sciences. There is a multitude of reasons of why the study of cooperation has grown to such extent, and why it has such multidisciplinary character. Some have to do with human interests to understand our own nature; some authors believe humans to be the champions of cooperation (Molleman, 2014; van den Berg 2015). Other reasons have to do with the fact that many of the political, social and economic issues faced by societies nowadays can be framed as a cooperation problem (e.g.: environmental degradation and global warming) (Hardin 1968; Ehrlich and Ehrlich 2013).

The three theoretical frameworks I will discuss in this introduction have been mainly used for the study of cooperation. They are, however, not the only frameworks used to study the evolution of cooperation nor are their applicability restricted to the study of cooperation. I chose to elaborate on these, due to their direct relevance to the research chapters of this thesis.

### *Group selection theory*

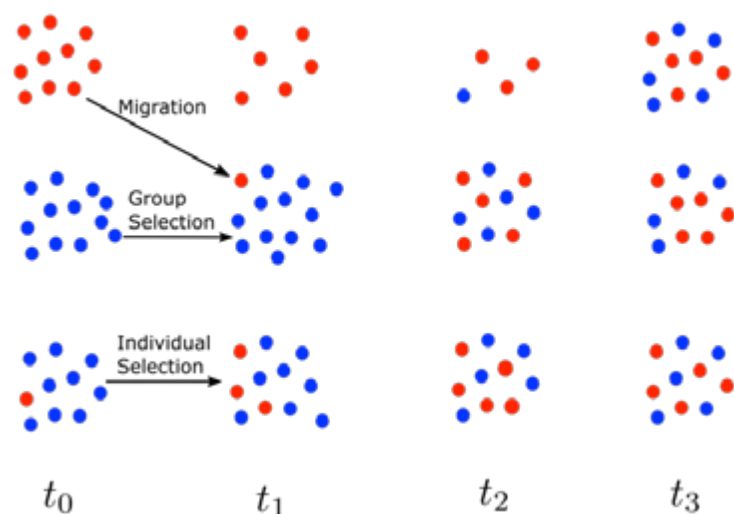
*“It must not be forgotten that although a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe . . . an increase in the number of well-endowed men and an advancement in the standard of morality will certainly give an immense advantage to one tribe over another.”*

Charles Darwin, The descent of man (1871)

Cooperative acts often involve conflicts between an individual and its group. When behaviours of individuals inside a group favour the overall performance of group, but come with a detriment on individual's reproduction, there is a conflict between the two levels of organization. Behaviours where individuals seem to follow their own interest are often called selfish; while behaviours that seem to favour the interests of the group are referred to as cooperative or altruistic.

It was Darwin who first extended the logic of natural selection to explain social behaviours that seem to harm the reproduction of individuals (Darwin 1859, 1871).





**Figure 1. The problem with group selection.** Here I represent the change in frequency of cooperative strategies in a meta-population composed of three sub-populations. Blue and red dots symbolize co-operators and defectors, respectively. At  $t_0$  a best case scenario for group selection, there are big differences in the frequency of co-operators between the groups. These differences lead groups with more co-operators to grow more than groups with defectors ( $t_1$ ). However, defectors can migrate into cooperative groups; and, they reproduce faster inside those groups. Thus, despite the advantage that group selection might confer to cooperative groups, individual level processes diminish the variation between the groups; and, with time, group level process are rendered weak.

Just as in a population of individuals, the idea is: if there is a meta-population of groups where there is variation in traits that characterize the groups, those groups that bear traits favouring survival and/or reproduction will be selected; and the meta-population will be in time composed mostly of groups with those traits. In our social evolution context, the traits that characterize populations can be thought of as the frequency of a social behaviour individuals express inside the group. Thus, in such group structured populations a cooperative or altruistic act will be selected for through the effect it has at the group level, and the population will be mostly composed of individuals with the social trait.

There is, however, an important caveat to this argument: the process of natural selection is fuelled by the existence of variation, in the trait under selection, between the entities being selected (Fisher 1930); and processes working at the level of the individual, such as migration and selection, will typically reduce the variation between groups. If the trait reduces the survival and reproduction of individuals

within their group, selection inside all groups will select individuals that do not express the trait, reducing the variation between them. Moreover, the flux of individuals between the different groups, migration, will also tend to homogenize the frequency of traits in the overall meta-population. Hence, if these individual level processes, migration and selection, act faster than the group level process, natural selection will not favour cooperative traits (Figure 1). Altogether, the potential of group selection to favour social traits will depend on how variation is split among the two levels, individual and groups (Okasha 2006). Due to this tension between the different levels of organization, the process has been renamed by some authors as multilevel selection (Okasha 2006).

Multilevel selection theory, or group selection theory, has been a controversial topic in evolutionary biology. After Darwin's initial ideas on the topic, it was Wynne-Edwards in his book *Animal dispersion in relation to social behaviour* (1962) who more prominently brought the subject to attention. Wynne-Edwards argued that animals have the capacity to regulate their reproduction, and restrain the consumption of resources when these are lacking. He claimed this to be an adaptation at the group level, driven by group selection. Wynne-Edwards views on group selection sparked controversy, and brought opposition from prominent evolutionary biologists such as George Williams in his book *Adaptation and natural selection* (1966). Earlier formal models of group selection suggested that group selection is indeed a theoretical possibility; however, those models also suggested the conditions for such process to work to be very restrictive (Maynard Smith 1964, 1976). Around the same time of the first group selection controversy, W.C. Hamilton published the two seminal papers that originated kin selection theory (see below (Hamilton 1964a, 1964b)). The foundations of kin selection theory provided a competing hypothesis for the explanation of social behaviours; one that gathered a lot more support among evolutionary biologists (Maynard Smith 1964). Later on, the work of George Price formally linked group and kin selection theories, showing there is an underlying process common to both (Price 1970, 1972; Queller 1992; Frank 1998; Gardner 2008). Price derived a general equation that expressed evolutionary change in terms of covariance (Price 1970), and used to have a hierarchical theory of selection, formalizing group selection reasoning (Price 1972). The same covariance equation can be used to derive Hamilton's rule in a more general way than originally done

by Hamilton (Gardner 2008). From a conceptual point of view, this link makes sense when one keeps in mind that kin-selection's coefficient of relatedness is a statistical measure of how structured a population is; and in the context of group structured populations, such measure also quantifies how variation is split among the two hierarchical levels (groups and individuals). Nevertheless, the group selection controversy seems to come back every other decade. In the last few years, several papers have demanded a revision of social evolution theory, claiming that group selection must have a more prominent role (Wilson and Hölldobler 2005; Traulsen and Nowak 2006; Wilson 2007; Wilson and Wilson 2007). These demands have faced the expected negative response from other members of the evolutionary biology community (Lehmann and Keller 2006; Lehmann et al. 2007a; West et al. 2007a, 2007b).

Since the rise of cultural evolution theory (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985), group selection theory has had a new surge in popularity with the development of its cultural analogue: cultural group selection. As mentioned before, the main criticism to group selection is that individual level processes, which tend to be faster, exhaust the required variation for group selection to favour social behaviours. However, this criticism implicitly assumes that behavioural traits are inherited vertically (i.e.: from parents to offspring). When traits are transmitted by any form of social learning, transmission can happen horizontally as well as vertically; that is, between genetically unrelated individuals from the same generation. Horizontal transmission of cultural variants has the potential, in some cases, to homogenize groups and prevent the spread of less cooperative variants. Specifically, the social learning rules: conformism, when individual tend to learn the most common cultural trait, and leader-following, when individuals tend to learn from leaders, reduce variation inside groups and increase variation between groups. For instance, if two groups differ in the most common trait, individuals in those groups will tend to adopt different traits; thus, conformism will enlarge these differences and facilitate the action of group selection. In a cooperation context, in groups that start with cooperation as the most common trait conformism will prevent the spread of defectors. Due to this homogenizing effect, cultural group selection has been proposed to favour cooperative behaviours (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1982, 1985). Although, several models have formalized

this verbal argument, controversy still remains on the effect that homogenizing rules have on the cultural evolution of cooperation (Henrich and Boyd 2001; Lehmann and Feldman 2008; Lehmann et al. 2008; Boyd et al. 2011). Such disagreements seem to come from different modelling assumptions. In an attempt to settle this controversy, in chapter 1, we develop a series of individual-based simulation models. We contrasted combinations of different forms of social leaning, and different mechanisms of group selection, assessing in which cases cooperative behaviours are favoured.

### ***Kin selection theory***

*“Would I jump in a lake  
To save my drowning cousin?  
It's not a risk I'd take  
For him plus half a dozen.  
But if you raise the stake  
And make the prize my brother?  
Now that's a deal I'll make. . .  
If you'll just toss in another...”*

D. C. Queller (2001)

W. D. Hamilton laid the foundations for what later would be referred to as kin selection theory in two papers published in 1964. Hamilton formalized mathematically previous ideas that high degree of kinship promotes the evolution of social behaviours. In order to make such formalization, he came up with the concept of inclusive fitness, as an extension of the concept of fitness already used at the time among evolutionary biologists. Inclusive fitness is a conceptual and mathematical tool to analyse and understand the evolution of social behaviours. But, Hamilton's insight, that interactions between genetically related individuals promotes the evolution of social behaviours, is independent of the mathematical tool of inclusive fitness. Hamilton himself acknowledged this, and called the alternative neighbour-modulated fitness. Later theoretical work using such alternative mathematical approach have confirmed this important conceptual insight (Uyenoyama and Feldman 1980; Taylor and

Frank 1996). A key point in the popularization of Hamilton's work is the simplicity with which he captured his ideas in an inequality, that later came to be known as Hamilton's rule (Charnov 1977). The inequality states that social behaviours, which provide fitness benefits ( $b$ ) to the partner at a cost ( $c$ ) to the actor, will be selected by natural selection whenever the benefits weighted by the coefficient of relatedness ( $r$ ) are larger than the costs, or mathematically

$$b \cdot r > c. \quad (1)$$

In the context of a social behaviour, when individuals interact with relatives they are interacting with partners that share, to certain degree, the tendency to express the same behaviour as themselves. Thus, the consequences of the social behaviour they express are restricted also to those behaviourally similar individuals. So, if the social behaviour we are interested in is cooperation -which provides fitness benefits to the partner- the benefits of cooperative acts will be focused on individuals that also cooperate. Conversely, uncooperative individuals –cheaters- will tend to interact among themselves. Under this interaction structure, the benefits of cooperation will increase the relative fitness of co-operators; hence, natural selection will lead to a higher frequency of cooperative acts in the population.

Interaction with relatives favours cooperative acts because the assortment of genotypes in the interaction structure targets the benefits of cooperation towards co-operators. The assortment of genotypes, however, is not restricted to family structures. Instead, genetic relatedness is a statistical measure of assortment; and assortment can occur due to processes such as limited dispersal. In such cases, even if social partners are not direct family members, they have a high chance to share a genetic background, hence, to behave similarly. Genetic relatedness is, therefore, a measure of how structured interactions are between individuals in a population. Technically, relatedness is the regression coefficient between the phenotypic trait of the actor and genotypic trait of the receiver, determining the behaviour of interest (Michod and Hamilton 1980; Gardner et al. 2011). If such coefficient is positive, the trait of the focal individual is a good predictor of the trait of the interacting partner. In other words, co-operators tend to interact with co-operators, and defectors tend to interact with defectors.

Since Hamilton's seminal work a lot of attention has been paid to the genetic component of the inequality; however, later developments of the theoretical framework have allowed a closer interaction with the ecology and life-history of social organisms. Beyond the technical definition, relatedness allows an intuitive understanding in the context of family relationships. It is not necessary to compute a regression coefficient to understand that brothers are more related than cousins. Moreover, with the development of molecular biology techniques, relatedness became quite easy to quantify both in the laboratory and in the field. Therefore, kin selection and relatedness reached the centre stage in field of behavioural biology; and became the leading explanation for social behaviours. Kin selection theory, however, is not a theory of only genetic relatedness. The benefits and costs in Hamilton's inequality must implicitly include ecological and life-history considerations. Hamilton's rule, in its simplest form, is a conceptualization of selective pressures, rather than a full account of those pressures. Later theoretical developments have allowed to make the connections between kin selection and ecology more explicit, and to derive clear-cut predictions that can potentially be tested in biological systems (Pen and Weissing 2000a, 2000b; Wild and Taylor 2006; McLeod and Wild 2013a, 2013b, 2014). These connections are achieved by using class-structured models which can capture the ecology and life-history relevant for the biological system in mind (Taylor 1990; Taylor and Frank 1996; Taylor et al. 2007). In this thesis, in chapters 2 and 3, we use such an approach to model the evolution of eusociality. We develop class-structured models inspired by the life-histories of primitively social insects to investigate the conditions that favour the transition from solitary to eusocial life.

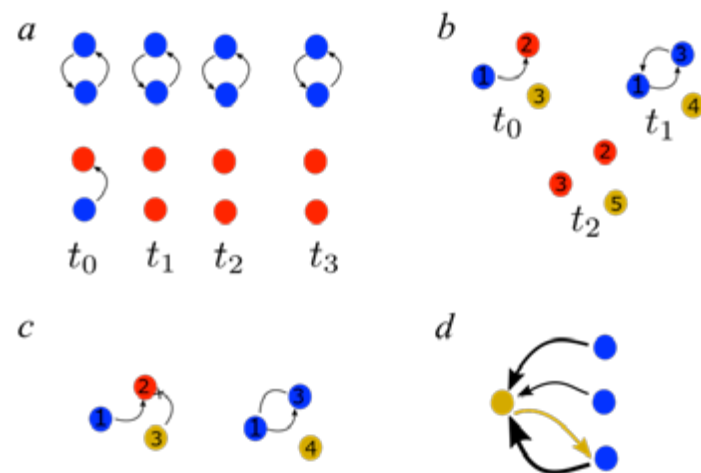
### ***The theory of reciprocal altruism and other responsive strategies***

*“Who are the fittest: those who are continually at war with each other, or those who support one another?”*

Petr A. Kropotkin (1902)

Robert Trivers formalized in a mathematical argument the idea that when individuals reciprocate each other's actions cooperative behaviours have a chance to be selected for (Trivers 1971). Trivers explained the idea of reciprocal altruism using the example of a man drowning due to a muscle cramp; whose chances of surviving

would be considerably increased if he were to receive help from another person. This potential altruist, on the other side, would only incur the cost of a small probability of drowning himself, given that he is not physically impaired as the drowning man is. There is nothing in saving his peer for the potential altruist, unless individuals in that population often found themselves in such situation. In that case, individuals might want to have a good standing with their peers, in case they were to need saving at a later point. In general the idea is: if individuals are willing to help only other individuals that help, it pays off to help because in the long run the costs paid will be more than compensated by help from fellow reciprocators. There are, of course, conditions that are necessary or that favour reciprocal behaviour. Individuals must have the chance to interact repeatedly, and they must be able to discriminate between cooperators and non-cooperators (Figure 2a).



**Figure 2. The evolution of cooperation through responsive strategies.** In a co-operators (blue circles) respond to their partners with the same behaviour they received. This leads to co-operators enjoying the benefits of cooperation more often than defectors (red). Information regarding a partner's behaviour can come not only from direct interaction; but also, from observing previous encounters of that partner. In b individual 1 cooperates while individual 2 defects in an interaction that individual 3 observes. At a later time points, individual 3 uses the information gathered and cooperates with individual 1, and defects with individual 2. Individuals 4 and 5 observe these interactions, and can potentially use this information. This has been referred to as indirect reciprocity. In c individual cooperates while individual 2 defects; individual 3 observes the interaction and punished individual 2. In contrast in an interaction between two co-operators (individuals 1 and 3), individual 4 does not punish. Thus, cooperation can also be stable when defection is punished by other individuals. In d two types of individuals (blue and yellow) can potentially interact. Blue individuals offer a certain level of cooperation (width of the arrows represent the size of the offer); yellow individual chooses to cooperate with the blue individual that offers the highest contribution. Through this partner choice higher levels of cooperation can be selected for.

Reciprocity achieves, through the response of individuals, the benefits of cooperation to be given primarily to other cooperators. Since Triver's seminal paper, theoretical models on reciprocity have flourished, mostly using the framework of the prisoner's dilemma. It is known now that reciprocal interactions do not need to be established only by the response of an individual to its interacting partner behaviour; instead, individuals can base their decisions on the reputation in cooperativeness of their partners (Boyd and Richerson 1989; Nowak and Sigmund 1998). Under certain conditions, individuals do not need to respond to a specific partner but rather they can respond to their encounter with any other individual from a small group, and still establish cooperation (Pfeiffer et al. 2005; van Doorn and Taborsky 2012). In all these forms of reciprocity, the benefits of cooperation are restricted to other cooperators by a combination of the interaction structure and the way individuals use the acts of their partners to decide whether to cooperate or not.

Alternative mechanisms that explain the evolution of cooperation among unrelated individuals also involve response rules that either punish defectors, or reward co-operators. Punishment, or strong reciprocity, is a mechanism proposed to favour the evolution of cooperation (Clutton-Brock and Parker 1995; Gintis 2000). Punishment occurs when individuals impose fitness costs on partners that don't cooperate. So instead of responding to defectors with lack of cooperation, punishers respond with extra fitness costs (Figure 2c). The fitness costs assure that even though the benefits of cooperation are obtained by defectors, their fitness is lower than co-operators; that is if there are enough individuals punishing. Punishment has been shown to stabilize cooperation in certain contexts. However, when individuals do not directly obtain benefits from punishment, punishment itself is not evolutionarily stable (Lehmann and Keller 2006; Lehmann et al. 2007b) unless there are particular conditions, such as population structure, favouring it (Gintis 2000; Boyd et al. 2003). Yet another mechanism that allows the evolution of cooperation among unrelated individuals is biological markets. Under the market mechanism, cooperation evolves through the choice of partners that individuals make in an interaction (Noë and Hammerstein 1994). The theory envisions two or more classes of individuals that exchange different goods. These classes can be either different species or types of individuals in a single species. It is in the interest of each individual to provide less of the good to the partner; however, if the partner can choose she will choose the individual that

provides a better deal (Figure 2d). Thus, it is the response of individuals to the offers of the potential partners what drives the goods to be exchanged between the partners.

All the different mechanisms described so far that allow the evolution of social behaviours do not necessarily act independently. On the contrary, when studying a specific biological system it seems plausible to find more than one. In chapter 5 of this thesis, we use models to capture the evolution of cooperative breeding in a cichlid fish. Our model involves the evolution of responsive strategies, which conceptually resemble the mechanisms described in this section, such as reciprocity, punishment, and partner choice. Moreover, we compare situations with and without kin interaction to understand the interplay of the different mechanisms that allow the evolution of cooperation. In chapter 6 we use analytical techniques to get a deeper understanding of the evolution of these responsive strategies.

### ***Evolutionary transitions: the evolution of eusociality***

*“What is this ‘spirit of the hive’—where does it reside?... It disposes pitilessly of the wealth and the happiness, the liberty and life of all these winged people; and yet with discretion, as though governed itself by some great duty.”*

Maurice Maeterlinck (1901)

Eusociality is the social structure where some offspring stay at their natal nest and devote their life to cooperate with their parents in caring for their sibling. Dispersing and phylopatric offspring come to belong to two distinct castes characterized by different behavioural, physiological and reproductive patterns; individuals define their caste at an early point of their development, and rarely switch later on in their life-time (Crespi and Yanega 1995). Even though the castes are defined by a multitude of factors, the most important characteristic defining them is their contribution to the reproduction of the social group. The reproductive caste, ‘queens’, monopolize reproduction within their social group, while ‘workers’ are mainly in charge of brood caring, and nest maintenance. The clear discrimination in tasks between these castes leads the social group to present a strict reproductive division of labour.



**Figure 3. Difference between primitively and advanced eusociality.** *a* shows queen and workers from leaf-cutter ants (*Atta texana*), an advanced eusocial species. Queen and workers can be clearly distinguished; their size difference can span up to two orders of magnitude. In contrast, *b* shows two females from eusocial paper wasp species (*Mischocyttarus* sp.) there is no morphological distinction between the castes in primitively social species. Images © Alex Wild, used by permission.

Within this definition there is still a wide variety of social structures that fall under the umbrella of eusociality. A rough classification divides eusocial species into ‘primitively eusocial’ and ‘highly eusocial’ (Crespi and Yanega 1995). The distinction between these two types of eusocial species is mainly whether the reproductive caste can potentially take on the tasks of the ‘worker’ caste in some situations. For example, in social sweat bees and *Polistes* wasps queens can produce a brood of reproductive males and females if their workers die. In contrast, in highly advanced eusocial species, such as leaf-cutter ants and honey-bees, the queen cannot produce viable reproductive offspring without the presence of worker in the colony (Hölldobler and Wilson 2010). As a matter of fact, leaf-cutter queens cannot do much without their workers, they die pretty soon if they are without a worker force. This classification highlights the degree, and variation, of dependency that individuals reach in eusocial species. Nevertheless, dependency and reproductive roles are not the only characteristics that vary among eusocial nests. This classification also reflects the degree of differentiation between the two castes in morphological, physiological and life-history traits. A queen and a worker leaf-cutter ant can differ in size by two orders of magnitude; a queen can live up to 20 years, while a worker can die within a couple of weeks. In some primitively eusocial species, there is no way to physically distinguish between a queen and a worker (Figure 3).

Advanced eusocial insects are the emblematic image of eusociality. Each colony is a complex system of individuals working together towards the common goal of

production of reproductive individuals. Colonies in some cases reach the astonishing number of 30 million individuals, where most of these individuals are full and half-sisters that belong to up to 5 different castes. All these castes are adapted to divide the different tasks of the colony to such extent that their morphology is radically different from each other. Advanced social insects are known to have complex communication systems that include visual (Frisch 1953) and chemical cues (Oystaeyen et al. 2014). These communication systems allow them to produce self-organized patterns of behaviour (Bonabeau et al. 1997; Camazine et al. 2003), which lead to: astonishing foraging patterns (Deneubourg et al. 1989, 1990; Camazine and Sneyd 1991; Perna et al. 2012; Reid et al. 2015) and construction of complex structures (Bonabeau et al. 1998; Johnson 2009; Khuong et al. 2016). Even before all these patterns were described and explained in the detail known today, advanced social insect colonies were referred to as ‘super-organisms’ (Wheeler 1922). In a way, the idea of ‘super-organism’ foresaw the classification of the evolution of eusociality as a major evolutionary transition in individuality (Maynard Smith and Szathmary 1998; West et al. 2015).

Major transitions are events in the history of life that radically increased the level of complexity that biological entities could achieve. Despite the difficulties in defining and measuring complexity, major transitions encompass a list of changes that unequivocally open radically new paths for evolution. For example, multicellular organisms are more complex than unicellular organisms because they have the added complexity of regulating cell-to-cell interactions in their development; thus, the evolution of multicellularity is a major transition. Many of the major transitions consist of the formation of a new level of organization from the collective action of entities of the lower level. Another feature linked to the previous one is division of labour, when entities in the lower level divide the tasks necessary for the maintenance of the higher level. Finally, major transitions involve changes in the way that information is collected, stored and transmitted. The evolution of eusociality was classified as one out of the eight major evolutionary transitions in the history of life (Maynard Smith and Szathmary 1998). In line with the idea of a ‘super-organism’, eusocial colonies form a new level of organization; individuals that are part of the eusocial colony cannot reproduce outside the context of the colony. They certainly divide labour by splitting up the nest tasks among different types of individuals (castes). And, in order

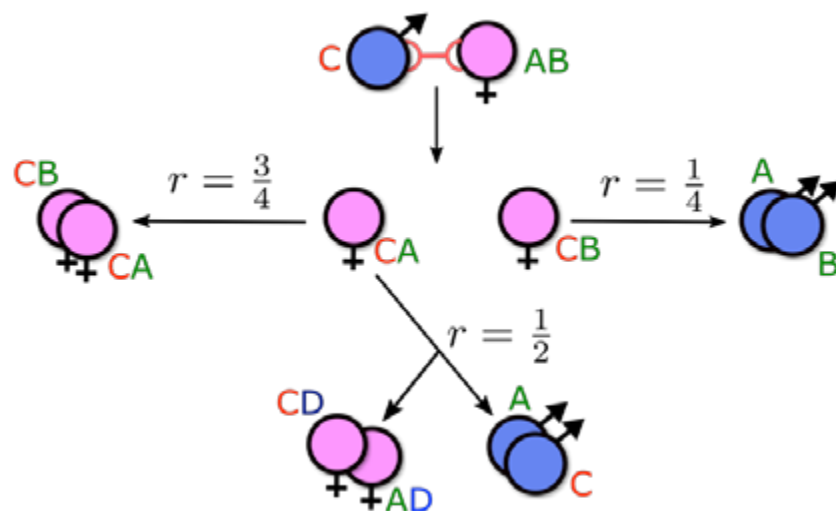
to coordinate the functioning of the whole colony that has evolved complex forms of communication. The level of complexity reached by eusocial taxa is incomparable to that of any of their cousins.

Since the major transitions were originally proposed, the evolution of cooperation has been regarded as the cornerstone in the major transitions (Maynard Smith and Szathmary 1998; West et al. 2015). Evidently, cooperation plays a major role in the formation of a new level of organization. However, cooperation is not the defining feature of major transitions: there are many examples of cooperation that have not led to a major transition; and it takes more than one behavioral trait to form a new level of organization (West et al. 2015). Likewise, in explanations on the evolution of eusociality, altruism has had a predominant role (Hamilton 1964a; Foster et al. 2006; Ratnieks and Helantera 2009; Nowak et al. 2010). It is true that altruism, defined as a behaviour that reduces the life-time reproduction of an actor while increasing that of a receiver, is a cornerstone of eusociality. However, altruism alone does not bring about the structural changes necessary to complete a major transition. In order to have mutual dependency among members of a social group, evolutionary changes must accrue both in the altruistic individuals (workers) and in the reproductive individuals (queens). Moreover, several features of a species, such as behaviour, ecology and life-history, will adjust along the way. Generally, our theories on major evolutionary transition transitions must include the co-evolution of multiple traits, and the feedback between them (Crespi 2004), rather than conditions for the evolution of a single behavioural trait.

In that spirit, in chapters 2 and 3 we develop models on the co-evolution of multiple traits that influence key features of the evolution of eusociality, with special reference to eusociality in primitively social insects. Primitively social insects fulfil some, but not all, the characteristics of the major transition to eusociality (West et al. 2015). Moreover, they present a wide diversity in social structures (Schwarz et al. 2007). Primitively social insects, therefore, provide the opportunity to phylogenetically test hypotheses about the initial stages of the major transition to eusociality. In the models presented in chapters 2 and 3, we assess whether certain life-histories found in primitively social insects favour the initial evolution of eusociality. More specifically, we start with Hamilton’s original haplodiploidy hypothesis (see

Figure 4), and analyse how combinations of pre-adaptations influence selection for eusociality

In chapter 4, I present some data that evidences the presence of extended maternal care in a primitively social bee, which shows polymorphism in social behaviour. Maternal care has been hypothesized to be another preadaptation to eusociality (Plateaux-Quénu 2008). However, sweat bees were assumed not to have extended maternal care, due to the presence of mass provisioning and closed brood cells. Mass provisioning is when females gather all the food necessary for the growth of one offspring before laying the egg. And brood cells are a physical barrier between the growing brood and their mother. The data of chapter 4 shows that, despite this physical barrier, female sweat bees can assess the state of their brood, and open the brood cells to care for their offspring. These events, however, occur seldom and only when females sense the need for their care. Our data adds up to recent evidence that primitively social bees present extended maternal care (Plateaux-Quénu 2008).



**Figure 4. The haplodiploidy hypothesis (Hamilton 1964b).** Under haplodiploid sex-determination there is a relatedness asymmetry between the sexes. Females arise from a fertilized egg, while males from an unfertilized egg. Thus, if the mother is singly mated, sisters will be related to each other by  $\frac{3}{4}$ . In contrast, females are only related to their daughters by  $\frac{1}{2}$ . All else being equal, a female would prefer to have an extra sister than an extra daughter. Hamilton argued that this asymmetry will make haplodiploid species to evolve eusociality more often. Trivers and Hare (1976) correctly pointed out that this argument ignored the male side of the brood. Sisters are less related to their brothers than to their sons. Hence, under even sex ratios siblings and offspring are equally valuable. However, if the sex ratio of the siblings is female bias, there is a chance that haplodiploidy favours eusociality.

## The evolution of cooperative breeding

*“The universal basis of co-operation is the proportioning of benefits received to services rendered.”*

Herbert Spencer (1897)

Cooperative brood care, when individuals help raise the offspring of other individuals, is a key component of eusociality; however, it is a much more general phenomena that is present in many species that do not fit the definition of eusociality. Cooperatively breeding societies are present in a wide range of taxa (e.g.: insects, arachnids, mammals, birds and fish), and have very diverse characteristics when it comes to composition, degree of dependency and size. Moreover, these characteristics of the social groups are not phylogenetically correlated; in other words, the diversity of characteristics can be found within each of the big taxa that present cooperative breeding. Thus, it is much more challenging, if not impossible, to find a general explanation for cooperative breeding.

Under the Darwinian paradigm, the most interesting part of cooperative breeding is its apparently selfless nature. Why would an individual invest her own resources into raising offspring that are not her own? Such behaviour would surely be selected against. Kin selection theory (see section above) provided the first formal explanation for cooperative behaviours, including cooperative breeding. Natural selection will favour individuals who invest in raising offspring of other individuals, if those helped individuals are relatives. By helping relatives reproduce individuals are, to a certain extent, indirectly promoting the spread of their own genes. Kin selection became the leading explanation for cooperative breeding, and gathered a lot of empirical support (Komdeur 1994; Cockburn 1998; Russell and Hatchwell 2001; Hatchwell 2009; Cornwallis et al. 2010).

Kin selection theory, in its more basic form, presents an evolutionary mechanism of how social behaviours can be selected for. However, the basic kin selection model is a conceptual model that is hard to translate into a clear-cut hypothesis of when to expect cooperative breeding to evolve. In contrast, several verbal hypotheses stress the importance of ecology and life-history in the evolution of delayed dispersal and

cooperative breeding (Gaston 1978; Emlen 1982; Stacey and Ligon 1987; Hatchwell and Komdeur 2000), and attempt to make predictions on the scenarios where we expect the evolution of such social groups. In that same line, modern kin selection models integrate the life-history and ecological hypotheses and make more clear predictions of the presence of cooperative breeding (Pen and Weissing 2000a; McLeod and Wild 2013a, 2014). These models are quantifying the benefits and costs involved inside Hamilton's rule (Wild and Taylor 2006).

In recent years, the more detailed study of many more cooperative breeding systems has shown the prevalence of social groups where help is not uniquely directed to related individuals, and in some cases they are not directed to relatives at all (Clutton-Brock and Parker 1995; Clutton-Brock 2002, 2009; Riehl 2013). These findings have called for theoretical explanations for the evolution of cooperative breeding in a framework different from kin selection theory. Moreover, they show that kin selection alone cannot explain the distribution of cooperative breeding in the tree of life. Therefore, several evolutionary explanations for cooperative breeding among unrelated individuals have been explored in the last few years, both theoretically empirically, including the pay-to-stay mechanism (Gaston 1978; Kokko et al. 2002; Bergmüller and Taborsky 2005; Hamilton and Taborsky 2005) and group augmentation (Kokko et al. 2001; Kingma et al. 2014). However, given the prevalence of interaction among relatives in cooperative breeding groups, all these potential mechanisms for the evolution of cooperation could interact with kin selection processes. Disentangling the consequences of the interaction of different process is a fundamental step towards an evolutionary explanation of cooperative breeding.

In chapter 5 we present an evolutionary model of the pay-to-stay mechanism, one of the hypotheses for the evolution of cooperative breeding that has gather support in the last few years. We model the pay-to-stay mechanisms as a negotiation between two responsive partners that interact repeatedly; hence, integrating elements of the theory of reciprocal altruism (see above). Furthermore, we evaluate how the mechanism responsible for the pay-to-stay scenario interacts with the presence of genetic relatedness between the interaction partners. Inspired in the pay-to-stay model, in chapter 6, we develop a general model for situations where individual negotiate outcomes to their conflicts on interests.

## Outline of the Thesis

This thesis consists of three parts. The first part consists of one chapter about the evolution of cooperation in human groups. The second part, encompassing three chapters, is about the evolution of eusociality. And, the last part is about negotiation games and their role in the evolution of cooperative breeding.

In chapter 1, I contribute to the discussion of whether cultural group selection can drive the evolution of cooperation. Using an individual based simulation model I contrast two different forms of group selection and three different social learning rules. Group selection is implemented as a “replacement” mechanism, where groups completely replace each other's cultural traits; or as a “contagion” mechanism, where cultural traits invade groups when individuals copy the cultural traits of individuals in other groups. As for the learning rules, we first use pay-off based learning as an analogue to natural selection where individuals assess the pay-off of other individuals, and copy their traits with a probability that is proportional to the difference in pay-off. Secondly, we use frequency-dependent social learning in the form of conformism, that is, when individuals preferentially copy the most common trait in their social environment. The systematic comparison of the six scenarios (combination of two group selection processes and three social learning rules), provide a challenge to the idea that conformism greatly favours the evolution of cooperation through cultural group selection.

In chapter 2, I present a series of models of the evolution of eusociality inspired by the life-history of primitively social insects. By contrasting models that assume different genetics (haplodiploidy and diploidy), life cycles (female hibernation and larval diapause) and forms of sex determination (flexible or fixed), we assess the effect of conditions that have been proposed as important preadaptations for the evolution of eusociality. Moreover, we show that when these preadaptations act in concert the transition to eusociality is accompanied by a change in life-history; and, the life cycle that emerges from evolution resembles that of advanced social insects. The models we present in chapter 2 ignore the conflict of interests that arises over the sex allocation of the colony between workers and queens. In chapter 3 we extend one of the models presented in chapter 2, and include worker fratricide as a mechanism for workers to take control over the sex ratio of the colony. We find that such



mechanism for worker control facilitates in some circumstances the initial evolution of worker behaviour. However, it also favours intermediate levels in the tendency to become a worker. Thus, populations end up showing polyphenism in their social behaviour; that is, when some nests are eusocial and some are solitary. We argue that the presence of such polyphenism in many species should not be immediately assumed to be a transitional state to eusociality; but rather, alternative explanations must be taken into account. We provide one here. Finally, our model shows that the costs of fratricide split the production of the sexes. In cases with social polyphenisms, the split is between social and solitary nests. In fully eusocial populations, the split is triggered by evolutionary branching. Overall, the model presents hypotheses for the diversity of life cycles in primitively social insects.

In chapter 4, I present evidence of extended maternal care in a primitively social sweat bee. Sweat bees are the taxon with most variation in social behaviour, and where eusociality has evolved most times. Sweat bees were thought to lack extended maternal care because of their provisioning strategy. Sweat bees have mass provisioning: females collect all the food necessary for the development of an egg before they lay the egg. After they have collected all the food they lay the egg and seal the brood cell that contains all the food and the egg. The sealing of the cell was seen as the end of brood care for these bees. This is in contrast to progressive provisioning, found in advanced social insects, where females provide food throughout the development of the larvae. Using a set of artificial nests we found that nest foundresses do care for the brood after the brood cell is closed. They are apparently aware of the state of their offspring and, if necessary, open the brood cell and care for the brood. This evidence of cryptic extended maternal care in a primitively eusocial bees supports the idea that maternal care is a preadaptation to eusociality.

In chapter 5, we present a model of the pay-to-stay hypotheses for the evolution of cooperative breeding. The model is inspired by the natural history of the cooperatively breeding cichlid *N. pulcher*, a system where the pay-to-stay hypothesis has received much support in the last few years. We model the pay-to-stay scenario as a negotiation between two partners, a breeder and a subordinate. We assume their negotiation proceeds as a series of repeated interactions where the partners

use behavioural reaction norms to determine their actions. We assess the evolution of those reaction norms under different levels of genetic relatedness. We find two different evolutionary equilibria: one driven by the negotiation dynamics, and another one driven by kin selection processes. Moreover, genetic relatedness favours the evolution of kin selected help, but harms the achievement of the negotiated equilibria. Given that the negotiated equilibria yields a higher level of help, higher levels of genetic relatedness produce on average lower levels of help.

Building upon the model of chapter 5, in chapter 6, we present a general model of the evolution of reaction norms in the context of negotiation games. We first outline some general features of the negotiation, such as the line of neutral equilibria. Furthermore, we show that the evolutionary stability of that set of equilibrium points depends on the slope and curvature of the reaction norms of the two partners. We illustrate these results by using the specific example of the interaction of a breeder and a subordinate (chapter 5).