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Evolution of acquiescence to manipulation

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To the Graduate Council:

I am submitting herewith a dissertation written by Mauricio González-Forero entitled "Evolution of acquiescence to manipulation." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

Sergey Gavrilets, Major Professor

We have read this dissertation and recommend its acceptance:

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(Original signatures are on file with official student records.)

Evolution of acquiescence to manipulation

A Dissertation
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Manipulation by parents undoubtedly is a factor in the case and I have to admit that enthusiasm for the ’altruistic’ factor has led me to underemphasize the mother’s position of power. Yet I am certain that an ’altruistic’ willingness to be manipulated is also a factor and I still see hymenopteran daughters as natural masochists in this respect.

W. D. Hamilton (1975a)

Abstract

A productive framework to study phenotypic evolution is based on the notion of "inclusive fitness", which considers how an individual's phenotype affects the fitness of other individuals. A promising extension of the notion of inclusive fitness is that of the "extended phenotype", which considers how an individual's phenotype affects its environment, including the phenotype of other individuals. Affecting another individual's phenotype is sometimes referred to as manipulation (which introduces indirect genetic effects). However, manipulated individuals may evolve resistance to manipulation, possibly reducing or eliminating the manipulated behavior (and the indirect genetic effects). In this dissertation I use mathematical modeling to identify different ways in which acquiescence (i.e., no resistance) to manipulation evolves. In Chapter 1, I show how costs of resistance may cause the evolution of acquiescence. In Chapter 2, I find that manipulation may cause the evolution of social efficiency, which can eliminate selection for resistance. In Chapter 3, I obtain that manipulation causes the evolution of maternal exploitation, which can also eliminate selection for resistance. In Appendices I-III, I present population genetics models of maternal manipulation that prompted the general models of chapters 1-3. Together, the results presented in this dissertation suggest that manipulation may be a particularly powerful promoter of stable social behavior.

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Introduction

The problem of acquiescence

During the 1910's to the 1930's, Fisher, Haldane, and Wright showed how phenotypes or behaviors with a genetic basis evolve when they are subject to natural selection. Their work focused mostly on phenotypes that affect the fitness of the individuals that express the phenotype. Hamilton (1964a) extended this theory by focusing on phenotypes that also affect the fitness of other individuals. He referred to such phenotypes as social.

In an attempt to further extend evolutionary theory, Dawkins (1982) introduced the idea of phenotypes that affect the environment, including the phenotypes of other individuals. Dawkins (1982) referred to such phenotypes as extended phenotypes. In contrast to Fisher, Haldane, Wright, and Hamilton, Dawkins (1982) did not study mathematically the evolutionary dynamics of extended phenotypes. Extended phenotypes that alter the abiotic environment are often identified under the rubric of niche construction (Odling-Smee, 1988). On the other hand, extended phenotypes that have an effect on the phenotype of other individuals are sometimes referred to as involving manipulation (Dawkins and Krebs, 1978; Dawkins, 1982; Krebs and Dawkins, 1984) and therefore as involving indirect genetic effects (IGE's; i.e., the genotypes of extended phenotypes correlate with phenotypes of other individuals) (Kirkpatrick and Lande, 1989; Moore et al., 1997). Mathematical study of the evolution of niche-constructing phenotypes or of phenotypes that are subject to indirect genetic effects has shown that the evolutionary dynamics may be substantially different to what happens when such factors are not considered.

Niche constructing phenotypes modify the environment and thus the selection pressures they are subject to. This effect can change the speed and direction of selection relative to the dynamics when niche construction does not occur (Laland et al., 1996; Odling-Smee et al., 2003). Similarly, phenotypes that are subject to indirect genetic effects display peculiar evolutionary dynamics. Since in this case another trait partially or completely controls (statistically, not necessarily causally) a focal trait, there is no need for genetic variation in the focal trait for it to evolve (Kirkpatrick and Lande, 1989; Moore et al., 1997; McGlothlin et al., 2010). The direction of selection for the focal trait may be opposite to the direction of its evolution (Kirkpatrick and Lande, 1989; Moore et al., 1997; McGlothlin et al., 2010). The evolutionary change can be dramatically fast (Kirkpatrick and Lande, 1989; Moore et al., 1997; McGlothlin et al., 2010). Even relatedness is not necessary for altruism to be favored if the altruism of focal individuals is controlled by non-focal individuals (McGlothlin et al., 2010).

The biological importance of extended phenotypes does not come from their unusual evolutionary dynamics. Instead, their importance stems from their presumable ubiquity. Phenotypes often influence their abiotic environment in sustained ways, with important effects such as the production of oxygen, ecological succession, and nutrient cycling (Odling-Smee et al., 2003). In addition, individuals constantly adjust their phenotypes or behaviors according to those of other individuals, which is an essential component of social interactions (Dawkins, 1982; Moore et al., 1997; Maestripieri and Mateo, 2009). However, studies of the evolutionary dynamics of the extended phenotypes that alter other individuals' phenotype typically assume that individuals allow others to partially or completely control their traits (Kirkpatrick and Lande, 1989; Moore et al., 1997; McGlothlin et al., 2010). Such manipulation may often go against the fitness interests of the manipulated individuals. In such a case, manipulated individuals would be selected to resist manipulation, possibly reducing or eliminating the IGE's.

In this dissertation I use mathematical modeling to study how acquiescence (i.e., no resistance) to manipulation can evolve. I define manipulation as the partial or complete control of another individual's behavior or phenotype. Previous mathematical models addressing problems relevant to th evolution of acquiescence to manipulation are listed in Tables 1-3. These approaches have either focused on specific traits and systems, or have not addressed the evolution of acquiescence in general. To attack the problem in an effective way, in the initially stages of this dissertation I also focused on eusociality as possible acquiescence to manipulation (appendices I-III). Thus, in the following section I discuss the problem of acquiescence regarding eusociality.

The problem of acquiescence in eusociality

Alexander (1974), as others before him had in mind, suggested that the evolution of eusociality may not involve altruism as indicated by Hamilton (1963, 1964b), but parental manipulation instead. That is, worker behavior may be a result of parental influence on the offspring's behavior. This suggestion attracted some attention, but fell out of favor for various reasons.

It attracted attention because queens appear to somehow inhibit the development of nest mates into reproductives (Michener and Brothers, 1974). In addition, parental manipulation is particularly easily selected for as it requires smaller benefit-cost ratios than altruism (Alexander, 1974; Trivers, 1974; Charlesworth, 1978; Charnov, 1978). However, parental manipulation immediately raises the question of why manipulated offspring would not evolve resistance to manipulation. Alexander (1974) argued that resistance to parental manipulation would be necessarily disfavored. His reasoning was that resisting offspring would have lowered fitness because their own offspring would resist their manipulation. The fallacy of this reasoning was exhibited by Dawkins (1976, p. 145-148) who, by exchanging inversely related words in Alexander's argument, showed that it would also imply that manipulating parents would have lowered fitness

Table 1: Selected previous modeling approaches to the evolution of manipulated behavior. M: manipulation. R: resistance. Re: retaliation. E: eusociality. SR: sex ratio. PI: parental investment. QG: quantitative genetics. GT: game theory. PG: population genetics. PGS: population genetics simulation. IF: inclusive fitness reasoning/modeling. A: arbitrary form of manipulation. P: policing. D: dispersal. m: maternal manipulation. Pu: punishment. HB: host behavior. TF: Taylor and Frank (1996) modeling approach. * rebelling through resistance is their "ignore solicitation model" while through inefficiency is their "prorata model". †Key paper.

Reference	Contribution	Approach
Griffing (1967)	M present (A)	QG
Maynard Smith and Parker (1976)	M and R can evolve (Re)	GT
Charlesworth (1978)	M can evolve (E)	PG
Charnov (1978)	M (E) and R (SR) can evolve	verbal
Stamps et al. (1978)	M and R can evolve (PI)	PG
Parker and Macnair (1978)	M can evolve (PI)	PG
Macnair and Parker (1978)	M can evolve (PI)	PG
Macnair and Parker (1979)	M can evolve (PI)	PG
Parker and Macnair (1979) †	M and R coevolve (PI) *	PG
Craig (1979)	M can evolve (E)	PGS
Emlen (1982)	M can evolve (E)	verbal
Vehrencamp (1983)	M and R can evolve (E)	IF
Parker (1985)	M can evolve (PI)	GT
Stubblefield and Charnov (1986)	M can evolve (E)	verbal
Ratnieks (1988)	M can evolve (P)	PG
Taylor (1988)	M can evolve (D)	IF
Kirkpatrick and Lande (1989)	M can evolve (m)	QG
Pamilo (1991)	M can evolve (E, SR)	IF
Boyd and Richerson (1992)	M can evolve (Pu)	GT
Yamamura and Higashi (1992)	M and R can evolve (E)	verbal
Poulin (1994)	M can evolve (HB)	verbal
Frank (1995)	M can evolve (P)	TF

Table 2: Continuation of Table 1. B: bribing. PDS: population dynamics simulation. C: concessions. Ev: eviction. Ef: reproductive efficiency. Ma: mating. Mat: maternal manipulation. AD: adaptive dynamics. MP: Markov process.

Reference	Contribution	Approach
Clutton-Brock and Parker (1995) †	M and R coevolve (Pu)	GT
Moore et al. (1997)	M present (A)	QG
Reeve and Keller (1997)	M can evolve (B, P)	IF
Pagel et al. (1998)	M and R can evolve (Re)	GT
Robert et al. (1999)	M and R coevolve (Re)	PDS
Wolf et al. (1999)	M present (A)	QG
Crespi and Ragsdale (2000)	M can evolve (E)	verbal
Johnstone (2000)	M is present (C, Ev, Ef)	IF
Gavrilets et al. (2001) †	M and R coevolve (Ma)	QG
Reuter and Keller (2001) †	M and R coevolve (SR, E)	IF
Wade (2001)	M can evolve (m)	PG
Boyd et al. (2003)	M can evolve (Pu)	S
Chapman (2003)	M can evolve (E)	IF
Reuter et al. (2004) †	M and R can evolve (SR)	IF, AD
Wenseleers et al. (2004a)	M present (P)	TF
Wenseleers et al. (2004b)	M present (P)	TF
Fowler (2005)	M can evolve (Pu)	GT
Helms et al. (2005)	M and R coevolve (SR)	S
Gavrilets and Hayashi (2006)	M and R coevolve (Ma)	QG
Lion et al. (2006)	M can evolve (HB)	S
Hauert et al. (2007)	M can evolve (Pu)	MP
Bijma and Wade (2008)	M present (A)	QG

Table 3: Continuation of Table 2. Ex: extortion.

Reference	Contribution	Approach
Gandon et al. (2009)	M can evolve (HB)	AD
McGlothlin et al. (2010)	M present (A)	QG
Shen and Reeve (2010)	M present (E)	IF
Queller (2011)	M present (A)	QG
Uller and Pen (2011)	M and R coevolve (D)	S
Press and Dyson (2012)	M and R can evolve (Ex)	GT
Doncaster et al. (2013)	M and R can evolve (Ex)	GT
Kawatsu (2013)	M and R coevolve (Ma)	AD

because their parents would have manipulated them. Alexander (1979, p. 38-39) later acknowledged the inadequacy of his reasoning.

The problem with parental manipulation is then that it creates a parent-offspring conflict (Trivers, 1974), the outcome of which is not straightforward. The biological details of the trait at hand change the nature of the conflict, and thereby its outcome. Models addressing the outcome of parent-offspring conflicts have tended to focus on conflicts other than conflict over offspring help, e.g., weaning conflict and sex-ratio conflict (see Tables 1-3). In a weaning conflict, the roles are flipped relative to a conflict due to parental manipulation of offspring help: offspring manipulate parents into providing additional parental care. Parental victory would then involve low costs of resistance to parents and high costs of manipulation to offspring, but this may not often be the case (Moreno-Rueda, 2007). For sex-ratio conflicts, early empirical studies suggested that offspring often win the conflict. In particular, Trivers and Hare (1976) showed that sex ratios in social insects followed offspring-favored outcomes rather than mother-favored outcomes. This finding has been reassessed, and the current view is that sex ratios are often partially controlled by workers and sometimes controlled by mothers (Boomsma, 1989; Chapuisat and Keller, 1999; Reuter and Keller, 2001; Reuter et al., 2004; Meunier et al., 2008). However, a conflict over sex ratio may also differ from that over offspring help. For example, one could argue that if a mother loses less fitness by letting offspring choose offspring sex ratio than what she gains by having them acquiesce for helping, then she could let them win the sex-ratio conflict while she pursues the conflict over help.

Another set of difficulties faced by parental manipulation has been conceptual. Alexander (1974) expressed parental manipulation as an alternative to nepotism, which was quickly taken to mean that parental manipulation is an alternative to kin selection. Papers were then written studying the evolution of altruism via either kin selection or parental manipulation (e.g., Charlesworth, 1978). This has had the implication that support for kin selection may be taken as evidence against parental manipulation, but researchers have sought to emphasize that this dichotomy is not correct (Bourke and Franks, 1995). As stated by Bourke and Franks (1995), parental manipulation is not an alternative to kin selection. On the contrary, parental manipulation is subject to kin selection. However, this has taken to yet another confusion according to which, since parental manipulation falls within kin selection, then parental manipulation is an unnecessary complication (e.g., Hölldobler and Wilson, 1990). The reasoning that has prompted this conclusion is that if there is a parent-offspring conflict over offspring help, for the parents to win the conflict it is necessary that offspring consent to manipulation, which will only happen as dictated by kin selection. As illustrated in this dissertation, some confusion may be cleared by considering a dichotomy, not between kin selection and parental manipulation, but between spontaneous and manipulated behavior.

This dissertation

Throughout this dissertation, I study the coevolution of manipulation and resistance to manipulation. I assume that the behavior (or phenotype) that is manipulated is entirely performed by the manipulated individual (e.g., helping) rather than being performed in concert between manipulated and manipulated individuals (e.g., mating). This contrasts with previous mathematical studies, which have taken a modeling approach that implicitly assumes that the manipulated behavior is expressed in concert between manipulated and manipulated individuals (e.g., Gavrilets et al., 2001; Reuter et al., 2004; Frank and Crespi, 2011). That is, under my assumption, the manipulated trait is not expressed if the manipulated individual resists, regardless of how hard the manipulator tries. In contrast, under the assumption of previous approaches, the manipulated trait can always be expressed if the manipulator tries hard enough. The relevance of one or the other assumption depends on the nature of the trait of interest.

Chapters 1 and 2 study the coevolution of manipulation and resistance among arbitrary social partners, not necessarily parental manipulation of offspring behavior. Chapter 3 applies primarily to maternal manipulation. In Chapter 1, I study the effect of costs of manipulation and resistance. I show that the occurrence of costs of resistance allows manipulated behavior to evolve under less stringent conditions than spontaneous behavior (i.e., behavior solely controlled by the focal individual). These results appear consistent with so-called primitive eusociality. In Chapter 2, I study the effect of the evolution of helping (or harming) efficiency. I find that the evolution of such social efficiency can eventually eliminate selection for resistance. These results appear consistent with worker specialization in so-called advanced eusociality. In Chapter 3, I study the effect of the maternal ability to influence the condition of the recipients of help. I assume that the mother can decrease the condition of recipients by not providing care to them. I obtain that such a mother can then lose her tendency to provide maternal care and become highly fertile while her manipulated offspring become selected to acquiesce to manipulation and raise their mother's offspring. These results appear consistent with queen specialization in advanced eusociality.

The methods used to derive the results of chapters 1–3 are based on techniques derived from the Price (1970) equation (Taylor and Frank, 1996; Frank, 1997, 1998). Such methods are very simple and very general, but they hide much complexity which may bring confusion (Frank, 2013). In order to avoid confusion, I devoted most of my years as a PhD student developing explicitly genetic mathematical models for the coevolution of manipulation and resistance. For those models, which I present in appendices I–III, I focused on maternal manipulation of offspring helping behavior. Appendix I develops a population genetics model for 72 different biological scenarios. I use this model to explore scenarios that are particularly favorable for manipulated helping (i.e., where manipulation and acquiescence evolve). This exploration shows that manipulated helping evolves more easily when the helping is directed only toward non-manipulated siblings (extending what was found by Charlesworth, 1978), that both conditional and constitutive costs of resistance can cause acquiescence to evolve, and that additive and dominant allelic effects yield qualitatively similar conflict outcomes. Appendix II focuses on the scenarios where recipients of help are only non-manipulated, resistance costs are conditional, and allelic effects are additive. This appendix simplifies the model of appendix I by assuming that mutation is rare and weak and that selection is weak, an approach which is often known as invasion analysis. These assumptions yield simple analytical results for the evolution of maternally manipulated helping for haploids, diploids, and haplodiploids, with the added consideration of sex-differential manipulation. I show that maternal manipulated helping is particularly likely if the mother is able to direct her manipulation effort toward the more willingly helping sex. Appendix III extends this invasion analysis to include the evolution of helping efficiency (as defined in chapter 2) and the evolution of maternal care and fertility (as defined in chapter 3). I obtain analytical expressions for the increase of each of the traits with the possibility of sex-differential manipulation for haploids, diploids, and haplodiploids. I explore this extension numerically, which yields analogous results to those presented in chapter 3.

As championed by Dawkins and Krebs, the results presented in this dissertation suggest that manipulation may be a particularly powerful force in nature for a broad range of situations including eusociality, sexual conflict, host-parasite interactions, intragenomic conflict, and cultural evolution.

Chapter 1

Evolution of manipulated behavior

The following chapter is a reprint of a paper in press in the journal American Naturalist:

González-Forero M., & Gavrilets S. Evolution of manipulated behavior. Am. Nat. In press.

The use of "we" in this part refers to my co-author and me. As the lead author of this article I was responsible for this paper. My contributions to this paper included the formulation and analysis of the model. I also wrote most of the paper.

Abstract

Many social behaviors are triggered by social partners. For example, cells in a multicellular organism often become soma via extrinsically regulated differentiation, while individuals in a eusocial colony often become helpers via extrinsic caste determination. One explanation for social triggering is that it informs when it is beneficial to express the behavior. Alternatively, social triggering can represent manipulation where social partners partially or completely control the focal individual's behavior. For instance, caste determination in primitively eusocial taxa is typically accomplished via differential feeding or dominance hierarchies, suggesting some manipulation. However, selection would favor resistance if manipulation is detrimental to manipulated parties, and the outcome of the manipulation conflict remains intricate. We analyze the coevolution of manipulation and resistance in a simple but general setting. We show that, despite possible resistance, manipulated behavior can be established under less stringent conditions than spontaneous (i.e., non-manipulated) behavior because of resistance costs. The existence of this advantage might explain why primitive eusocial behavior tends to be triggered socially and coercively. We provide a simple condition for the advantage of manipulated behavior that may help infer whether a socially triggered behavior is manipulated. We illustrate our analysis with a hypothetical example of maternal manipulation relevant to primitive eusociality.

1.1 Introduction

Behaviors that affect the reproductive success of other individuals are often referred to as social (Hamilton, 1964a). The triggers of many social behaviors frequently do not lie within the performing individual or its abiotic environment, but in the individual's social partners. For example, in social insects, differential feeding executed by nurses frequently determines whether or not individuals develop as helpers (Wheeler, 1986; Schwander et al., 2010). Similarly, in multicellular organisms, extracellular signaling performed by neighboring cells induces focal cells to differentiate into germ or soma (Extavour and Akam, 2003; Pera and Tam, 2010). Analogous socially triggered behaviors have been documented in slime molds (Gregor et al., 2010), plant-bacteria mutualisms (de Velde et al., 2010; Wang et al., 2010), biofilms (López et al., 2009), host-parasite interactions (Hughes et al., 2012; Shelley A, 2013), cooperatively breeding mammals (Rood, 1980; Wasser and Barash, 1983; Abbott, 1984; French et al., 1984; Carter et al., 1986; Russell and Lummaa, 2009), primitively and advanced eusocial taxa including mole rats (Wheeler, 1986; Sherman et al., 1991; Bennett et al., 1994; O'Donnell, 1998; Ramaswamy et al., 2004; Hanus et al., 2010; Smith et al., 2010a,b; Suryanarayanan et al., 2011; Kamakura, 2011), social trematodes (Kamiya and Poulin, 2013), and other mammals, birds, and fishes (Koyama and Kamimura, 2000; Hoover and Robinson, 2007; Kustan et al., 2012).

There are at least three general evolutionary explanations for the occurrence of socially-triggered social behavior. First, socially triggered behavior may allow for an optimal functioning at the group level (group optimality explanation) (Oster and Wilson, 1978; Schwander et al., 2010). Second, social triggering may inform the individual about when it is beneficial to express a particular social behavior (communication explanation) (Dawkins and Krebs, 1978; Bradbury and Vehrencamp, 2011). For example, social interactions can inform helpers-to-be about high benefit-cost ratios or relatedness (West Eberhard, 1975). These two explanations are closely related given a mathematical correspondence between group and individual selection (Queller, 1992b; Frank, 2012). The third explanation is that social triggering may constitute manipulation, where the social behavior is partly or completely under control of the triggering individual (Alexander, 1974; Dawkins and Krebs, 1978; Dawkins, 1982; Krebs and Dawkins, 1984). Under the first two explanations, social triggering is based on the reliability of information. When the triggering and triggered individuals conflict over the latter's social trait, there are incentives for the former to transmit unreliable information. The reception of unreliable information may cause the recipient to attend more reliable sources of information, such as intrinsic or abiotic factors. In this case, social behavior would be expected to be preferentially determined by non-social factors. In particular, the social behavior would not be expected to be preferentially determined by differential feeding, aggression, punishment, etc. Among primitively eusocial taxa, conflict is often substantial, yet these forms of determination of social behavior are typical (Alexander et al., 1991). Hence, the group optimality and communication explanation may be insufficient to account for social triggering among primitively eusocial taxa. In contrast, these forms of social determination would be preferentially expected if social triggering is manipulation. However, there are least two perceived difficulties with manipulation as a source of social behavior.

Manipulation requires that individuals have the ability to control partially or completely another individual's behavior. The power to do this has been documented for a variety of agents, ranging from internal parasites to external social partners (Dawkins, 1982; Moore, 2002; Trivers, 2011; Hughes et al., 2012; Adamo and Webster, 2013). The mechanisms by which parasites manipulate host behavior have been identified in good detail for a number of cases (Hughes et al., 2012; Adamo and Webster, 2013). In some cases, individuals (e.g., a wasp) may engage in second-order manipulation by manipulating another individual (a caterpillar) to manipulate a third (a plant) (Poelman et al., 2012). On the other end, external social partners may have the opportunity to canalize an individual's behavior (Byrne and Whitten, 1988; de Waal, 1998; Perry and Manson, 2008) for example via coercion, sensory exploitation, and deception (Clutton-Brock and Parker, 1995; Holland and Rice, 1998; Cézilly and Thomas, 2012); asymmetric interactions or control of dominants over subordinates (Maynard Smith and Parker, 1976; Vehrencamp, 1983; Johnstone, 2000; Shen and Reeve, 2010); and conformity biases of individuals in groups with particular customs (Richerson and Boyd, 2005; Whiten et al., 2005). The ability of agents to manipulate social partners has been further illustrated by an increasing number of observations of indirect genetic effects (i.e., the genetic influence on a social partner's phenotype; Wolf et al., 1998) which have been documented both in animals and non-animals (Maestripieri and Mateo, 2009; Uller et al., 2009; Genung et al., 2013).

Another key difficulty with manipulation is that it can lead to the evolution of resistance, which may limit or eliminate the expression of the manipulated behavior. The outcome of the evolutionary conflict between manipulating and manipulated parties is in general affected by a variety of factors including the costs paid by each party and life history details (Trivers, 1974; Blick, 1977; Macnair and Parker, 1978, 1979; Parker and Macnair, 1978, 1979; Stamps et al., 1978; Harpending, 1979; Parker, 1985; Yamamura and Higashi, 1992; Uller and Pen, 2011). The evolution of manipulation and/or resistance has been studied theoretically for specific types of dyadic interactions (e.g., host-parasite and male-female; Poulin, 1994; Pagel et al., 1998; Robert et al., 1999; Gavrilets et al., 2001; Wenseleers et al., 2004a; Lion et al., 2006; Gandon et al., 2009; Kawatsu, 2013). Below we study the coevolution of manipulation and resistance in a general yet simple model that allows for rather arbitrary interactions. We consider manipulated behaviors that are performed solely by manipulated parties (e.g., helping) rather than being performed in concert between manipulated and manipulating parties (e.g., mating). First, we identify conditions under which manipulated behavior is established in the population despite the possible evolution of resistance. Then, we show that manipulated behavior can be established under less stringent conditions than spontaneous (i.e., non-manipulated) behavior because of costs of resistance. This advantage of manipulated over spontaneous behavior may better explain "primitive" forms of social triggering of social behavior than common explanations in terms of spontaneous behavior. We obtain a condition that may help infer in specific cases whether a socially triggered behavior is manipulated rather than spontaneous.

1.2 Model

Fitness

We use techniques derived from the Price (1970) equation, and thus relatively few assumptions are necessary for the evolutionary analysis. We consider a population in which individuals can attempt to manipulate others to express a focal social behavior (e.g., helping or harming). In turn, manipulated individuals can resist by refraining from expressing the behavior. Individuals are, not necessarily permanently, in one of three states: in “manipulator” state (m), in “subject of manipulation” state (s), or in “target of manipulated behavior” state (t). A single individual can be a manipulator at one time and a target of manipulated behavior at another time. A manipulator m manipulates reachable subjects of manipulation s with probability p, which is assumed to be under control of the manipulator. A subject s of manipulation resists with probability q, which is assumed to be under control of the subject. We assume that an individual expresses the focal social behavior only when it is manipulated and acquiesces (i.e., it does not resist). Therefore, the probability that a subject s of manipulation expresses the focal behavior is $\varphi = P(1-q)$, where P is the average manipulation probability among the manipulators that can reach s. Thus, full resistance ($q = 1$) prevents the behavior from being expressed regardless of how large the manipulation probability P is. We study the coevolution of the population-average probabilities of manipulation p and resistance q.

When a manipulator m manipulates its subjects of manipulation, it pays a cost c_m of manipulation ($c_m \geq 0$). Letting 1 be the baseline fitness, the payoff for a manipulator is thus

$$\begin{aligned} w_m &= p(1-c_m) + (1-p) \\ &= 1 - c_m p. \end{aligned} \tag{1.1}$$

When a manipulated subject s acquiesces (which happens with probability $1-q$), it pays a cost c_a of acquiescence ($c_a \geq 0$). Alternatively, when it resists (which happens with probability q), it pays a cost c_r of resistance ($c_r \geq 0$). Hence, the payoff for a subject of manipulation is

$$\begin{aligned} w_s &= P(1-q)(1-c_a) + Pq(1-c_r) + (1-P) \\ &= 1 - c_a P(1-q) - c_r Pq. \end{aligned} \tag{1.2}$$

Finally, a target t of manipulated behavior receives a fitness effect b (either positive or negative) from its acquiescing social partners. Let Q be the average resistance probability among the subjects of manipulation with which t interacts. Let Π be the average manipulation probability among the manipulators that can reach the subjects with whom t interacts. Then, the payoff for a target of manipulated behavior is

$$\begin{aligned} w_t &= \Pi(1-Q)(1+b) + \Pi Q + (1-\Pi) \\ &= 1 + b\Pi(1-Q). \end{aligned} \tag{1.3}$$

We will make the simplifying assumption that costs of manipulation (c_m) and resistance (c_r) are constant and do not depend on the manipulation and resistance probabilities p and q.

Both manipulation and resistance are social behaviors. Evolutionary changes of social behaviors are affected by the correlation of the trait value of the actor (i.e., the individual expressing the trait) with the trait value of the actor's social partners (Hamilton, 1970; Queller, 1992a). This correlation can be measured in terms of the corresponding regression coefficient, which is customarily called relatedness. However, the correlation refers to phenomena broader than those covered by genealogical kinship (kin selection), as it can arise via other processes such as conditional response to partner's behavior which is important for reciprocity (Queller, 1985; Fletcher and Zwick, 2006; Nowak, 2006), variation among groups which is needed for group selection (Hamilton, 1975b; Grafen, 1984; Frank, 2012), and manipulation, punishment or partner choice (Queller, 2011). The techniques of Taylor and Frank (1996) and Frank (1997) allow one to easily obtain the effect of relatedness in this general sense, and hence we use them below. Using these methods, the model can also be applied to non-genetic evolution which is relevant when considering cultural manipulation. In addition, these techniques can capture rather arbitrary life-history details without making them explicit, at the cost of a lack of specificity. Because genetic or life-history details will not be made explicit, the fitness for each state ($j = m, s, t$) must be weighted by each state's reproductive value (Taylor and Frank, 1996; Frank, 1998).

The reproductive value k_j of state j $(= m, s, t)$ is the probability that individuals in the long-term future of the population descend from state-j individuals in the present ($\sum k_j = 1$). Then the fitness of a random individual is $w = \sum_j k_j w_j$ (Taylor and Frank, 1996) which in our model becomes

$$w = 1 - k_m c_m p - k_s[c_a P(1-q) + c_r P q] + k_t b \Pi(1-Q). \tag{1.4}$$

Resulting dynamic equations

We show in Appendix A that, assuming no correlation between the traits, the rates of change in manipulation and resistance can be approximated as

$$\frac{dp}{dt} = v_p k_m h_p \tag{1.5a}$$

$$\frac{dq}{dt} = v_q k_s h_q, \tag{1.5b}$$

where dx/dt denotes the derivative of x $(= p, q)$ with respect to time, v_p and v_q are the corresponding additive genetic variances, and

$$h_p = br_{tm}(1-q) - r_{sm}[c_a(1-q) + c_r q] - c_m \tag{1.6a}$$

$$h_q = -p[br_{ts} - (c_a - c_r)]. \tag{1.6b}$$

The quantities h_p and h_q represent the inclusive fitness effects (selection gradients) of manipulation and resistance. The quantities r_{ji} give the life-for-life relatedness of actor i to recipient j (Hamilton, 1972). For manipulation (eq. (1.6a)) the actors are manipulators ($i = m$), while for resistance (eq. (1.6b)) the actors are subjects ($i = s$). For both manipulation and resistance, the recipients are subjects and targets ($j = s, t$). These social interactions are described in figure 1.1. The inclusive fitness effect h of a trait gives the sum of fitness effects for recipients of the trait weighted by the corresponding relatedness of actor toward recipients. It will be important to keep in mind that relatednesses r can be negative (Hamilton, 1970). Negative relatedness occurs when actors are less related to recipients than is a random individual in the population (Gardner and West, 2004; West and Gardner, 2010). In particular, relatedness is negative when actors are less related to recipients than to bystanders that are affected by the interaction (Lehmann et al., 2006; West and Gardner, 2010), which will be relevant for a particular case below.

In the inclusive fitness effect of manipulation (eq. (1.6a)), the first term is the relatedness of manipulators toward targets (r_{tm}) times the probability of subjects' acquiescence ($1 - q$) times the fitness effect (b) on targets of manipulated behavior. The second term is the relatedness of manipulators toward subjects of manipulation (r_{sm}) times the expected fitness effect for subjects of manipulation $\{-[c_a(1-q) + c_r q]\}$. The third term is the direct fitness effect for manipulators ($-c_m$) which is weighted by the relatedness of manipulators toward themselves (i.e., 1). The inclusive fitness effect of resistance (eq. (1.6b)) can be seen as the negative of the inclusive fitness effect of acquiescence. The latter is the probability of manipulation p times a factor involving

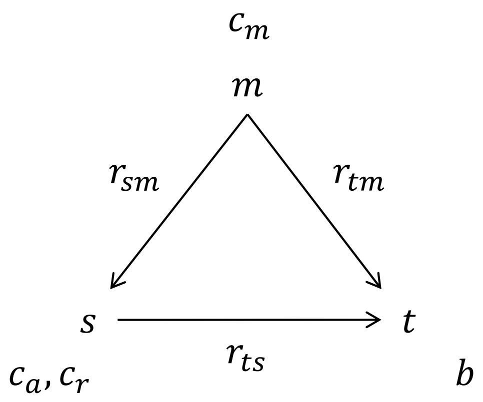

Figure 1.1: Relatednesses among social partners and their corresponding payoffs. At a given time, individuals are either manipulators (m), subjects of manipulation (s), or targets of manipulated behavior (t). Arrows correspond to the life-for-life relatedness r_{ji} of actor i to recipient j. A manipulator m can at another time be a target t of manipulated behavior, in which case $r_{tm} = 1$. Also indicated are the payoffs for each state: manipulators m pay the cost c_m of manipulation, subjects of manipulation s pay either the cost c_a of acquiescence or the cost c_r of resistance, and targets of manipulated behavior t receive a fitness effect b from acquiescing subjects.

the following terms. The first term is the relatedness of subjects of manipulation toward targets (r_{ts}) times the fitness effect (b) on targets of manipulated behavior. The second term is the direct effect of acquiescence on subjects of manipulation $[-(c_a - c_r)]$, weighted by the relatedness of subjects of manipulation toward themselves (i.e., 1). The direct effect of acquiescence can be positive despite positive costs (when $c_r > c_a$).

To analyze the coevolutionary dynamics in our model, it is helpful to write the selection gradients h_p and h_q (eqs. (1.6)) as

$$h_p = M_0 - qM \tag{1.7a}$$

$$h_q = pR. \tag{1.7b}$$

where

$$M_0 = br_{tm} - r_{sm}c_a - c_m \tag{1.8a}$$

$$M = br_{tm} - r_{sm}(c_a - c_r) \tag{1.8b}$$

$$R = -[br_{ts} - (c_a - c_r)]. \tag{1.8c}$$

M_0 is the selection gradient for manipulation when resistance is absent, M is the reduction in the selection gradient for manipulation from M_0 when resistance is full, and R is proportional to the selection gradient for resistance. It follows that manipulation is disfavored with full resistance (i.e., $M_0 - M < 0$) if manipulators' relatedness to subjects is sufficiently high (i.e., $r_{sm} > -c_m/c_r$). The direction of selection for manipulation changes at

$$q^* = \frac{M_0}{M}. \tag{1.9}$$

The model dynamics are analyzed in Appendix B.

1.3 Results

Coevolution of manipulation and resistance

Generally, the system evolves either to a state where manipulation is established and resistance disappears ($p = 1$, $q = 0$) or to a state where manipulation disappears ($p = 0$). Under certain conditions, there is also the possibility that manipulation is established but its effect is canceled by complete resistance ($p = 1$, $q = 1$).

Necessary (but not sufficient) conditions for the evolution of manipulated behavior ($p = 1$, $q = 0$) are that 1) resistance to manipulation is not favored by selection, and 2) manipulation is favored when resistance is absent. In terms of our model, the first condition translates into inequality

$$br_{ts} + c_r > c_a; \tag{1.10a}$$

that is, the indirect fitness effect to manipulated individuals (br_{ts}) and the cost of resistance (c_r) have to be sufficiently high relative to the cost of acquiescence (c_a). The second condition translates into inequality

$$br_{tm} > c_a r_{sm} + c_m. \tag{1.10b}$$

That is, the direct or indirect fitness effect to manipulators (br_{tm}) via their relatedness to the targets of manipulated behavior must be greater than the indirect cost to manipulators via their relatedness to acquiescing individuals and the direct cost of manipulation (c_m). If conditions (1.10) are not satisfied simultaneously, the population generally evolves to a state in which manipulation disappears ($p = 0$). These conditions are less likely to be satisfied if the cost of acquiescence (c_a) and manipulation (c_m) are high and/or the effect of manipulation on targets ($|b|$) and the cost of resistance (c_r) are low. It is possible that both dynamic outcomes — the evolution of manipulated behavior ($p = 1$, $q = 0$) and the disappearance of manipulation ($p = 0$) — are observed for the same sets of parameter values depending on initial conditions. Specifically, even if conditions (1.10) are satisfied, manipulation can still disappear if initial levels of resistance are high enough. The additional condition for the outcome of manipulated behavior ($p = 1$, $q = 0$) when $r_{sm} > -c_m/c_r$ is that initially

$$q < q^* + pu, \tag{1.11}$$

where $u = \sqrt{-v_q k_s R/(v_p k_m M)}$ which measures the rate of change in acquiescence relative to that of manipulation. Condition (1.11) states that for manipulated behavior to be obtained when $r_{sm} > -c_m/c_r$, resistance must be initially sufficiently small.

Figure 1.2 illustrates these dynamics. In the left column, where manipulation is not favored in the absence of resistance ($M_0 < 0$), manipulation disappears. In the right column, if resistance is favored ($R > 0$), manipulation disappears as well. Yet in the right column, if acquiescence is favored ($R < 0$), manipulated behavior is obtained if

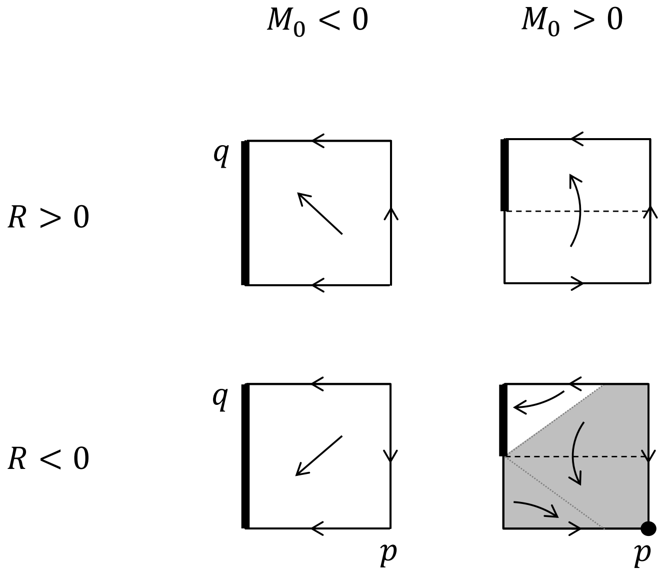

Figure 1.2: Coevolutionary dynamics of manipulation and resistance when $r_{sm} > -c_m/c_r$. Columns correspond to the sign of the selection gradient for manipulation without resistance (M_0). Rows correspond to the sign of the selection gradient for resistance (R). The direction of selection for manipulation changes at the horizontal dashed line (q^*). The arrows indicate the direction of evolutionary change for manipulation (p) and resistance (q). Stable equilibrium points and lines are in thick strokes.

resistance is initially small (gray area); if it is large, manipulation disappears. Figure 1.2 also describes the dynamics when $r_{sm} = -c_m/c_r$. In such a case, the dashed line $q^* = 1$, which makes the line $q = 1$ stable when resistance is favored ($R > 0$).

The only exception to the outcomes described above is the establishment of manipulation ($p = 1$) in spite of complete resistance ($q = 1$). This outcome can happen when resistance is favored (inequality (1.10a) is not satisfied) and

$$r_{sm} < -c_m/c_r. \tag{1.12}$$

The latter inequality requires negative relatedness of manipulators toward subjects of manipulation. Such negative relatedness can arise, for instance, when a manipulating parasite (m) is less genetically related to its manipulated host (s) than to the targets (t) of the manipulated behavior (Lehmann et al., 2006; West and Gardner, 2010). It is possible that the outcomes of full manipulation and resistance ($p = q = 1$) and of the disappearance of manipulation ($p = 0$) are observed for the same sets of parameter values depending on initial conditions. Specifically, if manipulation is disfavored when resistance is absent (i.e., condition (1.10b) is violated), manipulation increases only if the initial levels of resistance are high enough. This result may seem counterintuitive, but it arises because manipulators indirectly benefit from harming their subjects of manipulation. This indirect benefit is larger if the subject of manipulation resists and, thus, pays the costs of resistance. In this case, manipulation is favored even if the manipulated behavior is canceled by resistance. Figure 1.3 illustrates these dynamics. In the left column, manipulation is not favored in the absence of resistance ($M_0 < 0$), but it becomes favored if resistance is favored ($R > 0$) and is large enough. When acquiescence is favored ($R < 0$) manipulation disappears. In the right column, when manipulation is favored ($M_0 > 0$), sustained manipulation is canceled by resistance if resistance is favored ($R > 0$). If acquiescence is favored ($R < 0$) manipulated behavior is obtained (gray area).

Comparison to spontaneous behavior

When a social behavior is socially triggered, it is difficult to determine whether or not it is manipulated if it could also be spontaneous (e.g., due to high relatedness between actors and recipients). In this section we use our model to yield a condition that may help infer whether or not a socially triggered behavior is manipulated (see Doncaster et al. (2013) for a similar objective). We compare the conditions for the evolution of manipulated behavior to those for non-manipulated behavior; that is, behavior that is fully under control of the individuals expressing it. As stated above, we refer to non-manipulated behavior as spontaneous behavior.

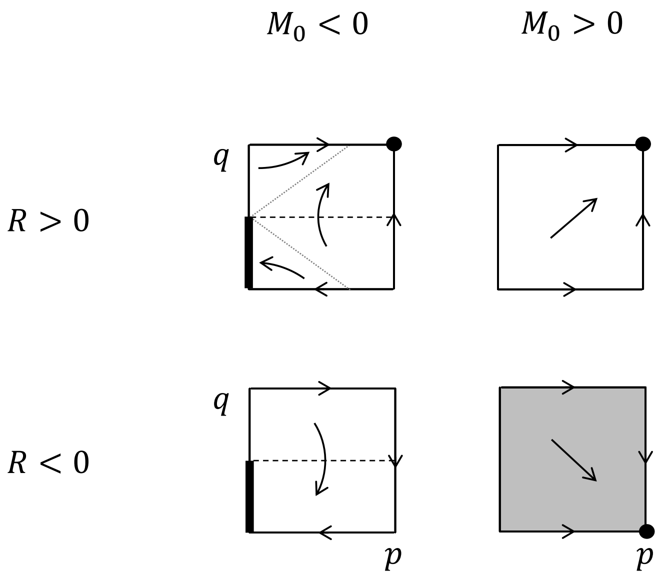

Figure 1.3: Coevolutionary dynamics of manipulation and resistance when $r_{sm} < -c_m/c_r$. See the legend in figure 1.2 for explanation.

Let the probability φ that an individual expresses the same focal social behavior as before be now under entire control of this individual. Define φ in such a way that the fitness effect b to recipients is the same as for manipulated behavior. Let c_s be the cost to actors of this spontaneous social behavior ($c_s > 0$). Spontaneous social behavior evolves when $br > c_s$ where r is the life-for-life relatedness of actor to recipient (Hamilton, 1972; Frank, 1998). We assume that the cost of spontaneous behavior (c_s) is approximately the same as the cost of acquiescence (c_a; i.e., $c_s \approx c_a$) and that relatedness for spontaneous behavior (r) is analogous to that of manipulated behavior (r_{ts}; i.e., $r \approx r_{ts}$). Manipulated behavior can be established under less stringent conditions than spontaneous behavior when inequalities (1.10) hold and $br_{ts} < c_a$. This happens when manipulation is favored in the absence of resistance (inequality (1.10b) holds) and the following condition holds:

$$0 < c_a - br_{ts} < c_r. \tag{1.13}$$

When the parameters involved in these inequalities can be measured, satisfaction of these conditions would suggest that the behavior is manipulated, provided that the assumptions of the model are approximately met. Condition (1.13) cannot be met if the cost of resistance $c_r = 0$, which makes it explicit that the advantage of manipulated behavior over spontaneous behavior in terms of its less stringent conditions to be favored is due to the cost of resistance.

This comparison also allows one to relate the notion of manipulation that we followed to another traditional notion of manipulation; that is, when the manipulated behavior goes against the fitness interests of the manipulated individual (Alexander, 1974; Hughes et al., 2012). Although it is a matter of interpretation, manipulated behavior can be said to follow this notion when it is established but spontaneous behavior is not favored.

Hypothetical example for maternal manipulation

We now illustrate our model by applying it to the evolution of eusociality via maternal manipulation. The relevant genetic variation for manipulation may be available to mothers due to the substantial maternal influence on offspring phenotype (Linksvayer and Wade, 2005; Schwander et al., 2008; Russell and Lummaa, 2009; Uller et al., 2009; Maestripieri and Mateo, 2009). The evolution of maternal (or parental) manipulation has been studied from various perspectives, sometimes with an account of offspring's resistance (Alexander, 1974; Trivers, 1974; Michener and Brothers, 1974; Charlesworth, 1978; Charnov, 1978; Parker and Macnair, 1978; Stamps et al., 1978; Craig, 1979; Emlen, 1982; Vehrencamp, 1983; Stubblefield and Charnov, 1986; Kirkpatrick and Lande, 1989; Ratnieks, 1988; Pamilo, 1991; Frank, 1995; Moore et al., 1997; Wolf et al., 1999; Johnstone, 2000; Crespi and Ragsdale, 2000; Chapman, 2003; Wenseleers et al., 2004a; Shen and Reeve, 2010; McGlothlin et al., 2010; Uller and Pen, 2011). Our model integrates, extends, and generalizes various features of these studies. Here we only illustrate when our model would predict that a maternally triggered social behavior is manipulated. This inference has been particularly challenging because high relatednesses also allow for the behavior to be spontaneous (Bourke and Franks, 1995).

Consider a sexual population in which mothers produce two broods. One or both parents provide parental care (e.g., provisioning or defense), and adult offspring disperse from the maternal site to mate and start a new site. Suppose that mothers can manipulate first-brood offspring to stay in the maternal site for a fraction of their adulthood. Acquiescing offspring stay, and may express parental care at the maternal site increasing fitness of the second-brood offspring. Resisting offspring disperse without delay. Manipulation may occur, for example, by disrupting offspring's development physiologically or psychologically; specifically, by feeding offspring poorly (Brand and Chapuisat, 2012; Tibbetts et al., 2013) or by inducing stress via aggression (Young et al., 2006). How manipulation is executed affects the nature of costs and benefits. For instance, the cost of resistance would in principle be more substantial for differential feeding than for psychological manipulation (Metcalfe and Monaghan, 2001), yet differential feeding might make poorly-fed individuals able to help only in moderate amounts.

In this setting, the manipulator is the mother, the subjects of manipulation are first-brood offspring, and the targets of manipulated behavior are second-brood offspring. Assuming outbreeding, single mating, even sex ratios and no sex discrimination, the relevant relatednesses for either diploids or haplodiploids take the following values (Bulmer, 1994): for first-brood offspring to second-brood offspring $r_{ts} = 1/2$, for mother to first-brood offspring $r_{sm} = 1/2$, and for mother to second-brood offspring $r_{tm} = 1/2$. From condition (1.10b), it follows that when the benefit b is greater than $T_p = (c_m + c_a r_{sm})/r_{tm}$, manipulation is favored in the absence of resistance. From condition (1.10a), we have that when b is greater than $T_q = (c_a - c_r)/r_{ts}$, acquiescence is favored. Similarly, when b is greater than $T_s = c_a/r_{ts}$, spontaneous behavior is favored. Finally, from condition (1.11), if resistance q is initially smaller than $T_p^* = q^* + pu$, then manipulated behavior is obtained when both manipulation in the absence of resistance and acquiescence are favored. Assume that manipulation is of little cost to the mother;

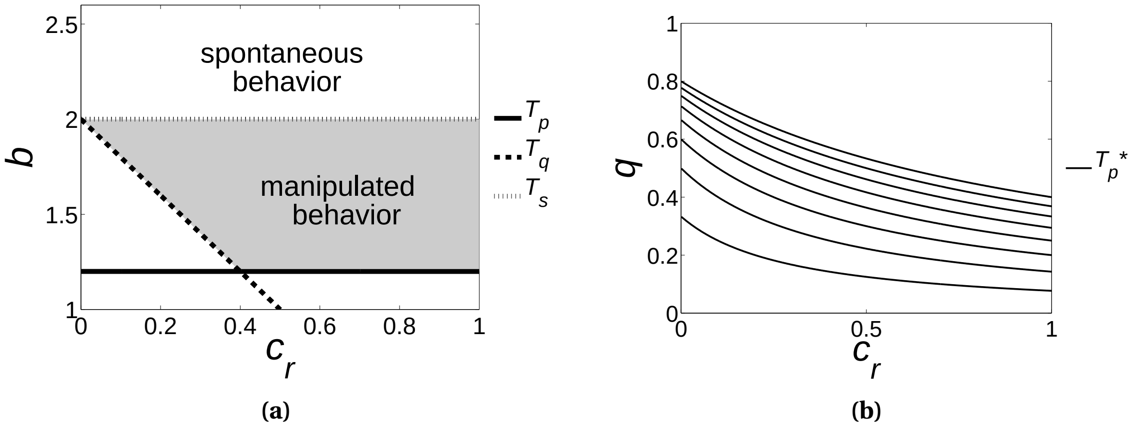

Figure 1.4: Illustration for maternally manipulated behavior. (**a**) When the benefit b is greater than T_p manipulation in the absence of resistance is favored, than T_q acquiescence is favored, and than T_s spontaneous behavior is favored. (**b**) When resistance q is initially below T_p^* manipulated behavior is obtained if both manipulation in the absence of resistance and acquiescence are favored. Parameter values are $c_a = 1$, $c_m = 0.1$, and $r_{ts} = r_{tm} = r_{sm} = \frac{1}{2}$. For T_p^*, we let $p = 0$ and lines from bottom to top are for b from 1.3 to 2.

in particular, of 10% the baseline fitness: $c_m = 0.1$. Suppose further that individuals staying in the maternal nest as adults entirely give up their reproduction (i.e., $c_a = 1$), and that manipulation is initially absent (i.e., $p = 0$). Figure 1.4(**a**) plots thresholds T_p, T_q, and T_s and shows a region in which manipulated behavior is obtained although spontaneous behavior is not favored (gray area), provided that resistance is initially below the thresholds T_p^* in figure 1.4(**b**). In the gray region, manipulated behavior requires smaller benefits than spontaneous behavior. If, for a given system, parameters could be measured that fall in the gray region, this would suggest that the behavior is manipulated to the extent that the assumptions of the model hold.

1.4 Discussion

Many social behaviors are triggered by social partners. The social trigger may sometimes be the result of manipulation, where a behavior is partly or completely under control of social partners. When this is the case, the evolution of resistance to manipulation may reduce or eliminate the manipulated behavior. Previous theoretical research has studied the evolution of manipulation and/or resistance for specific systems (Poulin, 1994; Pagel et al., 1998; Robert et al., 1999; Wenseleers et al., 2004a; Lion et al., 2006; Gandon et al., 2009; Kawatsu, 2013). Here we have studied the coevolution of manipulation and resistance in a simple but general setting. We focused on manipulated behaviors that are performed entirely by the manipulated parties, rather than on manipulated behaviors that are performed in concert between manipulated and manipulating parties. In our model, if acquiescence to manipulation is not favored (i.e., condition (1.10a) is violated), then manipulated behavior is eliminated. When acquiescence is favored, manipulated behavior can be established. It has been thought that the requirement of acquiescence, or consent, essentially makes manipulated behavior equivalent to spontaneous behavior (e.g., Hölldobler and Wilson, 1990; Bourke and Franks, 1995). We compared the conditions for the establishment of manipulated behavior with those for spontaneous behavior making use of a few assumptions. Such comparison showed that manipulated behavior can be established under less stringent conditions than spontaneous behavior. The comparison yielded an expression for the advantage of manipulated over spontaneous behavior (expression (1.13)) that may allow to infer whether an observed behavior is either manipulated or spontaneous when the assumptions of the model are approximately met. This approach can be modified to accommodate assumptions relevant to specific systems. The advantage of manipulated over spontaneous behavior is a consequence of conditional costs of resistance that do not apply to spontaneous behavior. Costs of resistance allow for manipulated behavior to evolve and be maintained with zero relatedness between actors and recipients despite positive costs (c_a, c_r) if resistance is costlier than acquiescence (inequality (1.10a)). This contrasts to spontaneous costly behavior, for which genetic or phenotypic relatedness between actor and recipient is required. Below we discuss the model and its applications.

As stated, we have considered manipulated behaviors that are expressed by the manipulated parties alone (e.g., helping rather than mating). We modeled this by taking as multiplicative the contribution of each party to trait expression (i.e., $\varphi = p(1-q)$, where φ refers to the manipulated behavior, p is the contribution of the manipulating parties and $1-q$ is the contribution of the manipulated parties). In this approach, the consent of manipulated individuals is required for the behavior to be expressed at all. This is relevant to cases in which the manipulated behavior is fully performed by an individual such as worker behaviors (Hölldobler and Wilson, 1990). In contrast, other manipulated behaviors can be performed in concert between manipulating and manipulated parties (Arnqvist and Rowe, 2005). This is typically modeled by taking as additive the contribution of each party to trait expression (i.e., $\varphi = f(x-y)$, where the manipulated behavior φ is a function of the difference between manipulation effort x and the opposition to it y; e.g., Gavrilets, 2000; Gavrilets et al., 2001; Frank and Crespi, 2011). Manipulated behaviors with additive contribution of parties can always be expressed if manipulating parties try hard enough. The relevance of one or the other modeling approaches depends on the nature of the behavior that is being manipulated.

In our model, because of multiplicative contribution to trait expression, resistance must be initially sufficiently small (condition (1.11)) if manipulators' relatedness to subjects of manipulation is large enough ($r_{sm} > -c_m/c_r$). Initially small resistance may occur when a new manipulation strategy arises since there is no previous selection pressure for resistance to it. The requirement of small resistance is not necessary when manipulators' relatedness to subjects of manipulation is small enough ($r_{sm} \leq -c_m/c_r$) because with such relatedness values, manipulators are either unaffected by or indirectly benefit from resistance. We have made the simplifying assumption that costs are independent of manipulation and resistance probabilities. This is unrealistic because costs of manipulation and resistance may often be functions of manipulation and resistance probabilities; for instance, the more subjects an individual manipulates, the larger the cost of manipulation; or the more effective resistance is, the more resources are to be invested in it. In this case, the equilibria of manipulated behavior ($p = 1, q = 0$) and neutralized manipulated behavior ($p = q = 1$) will not correspond to full manipulation and no resistance, or to full manipulation and full resistance, but to partial manipulation with no resistance, or to partial manipulation and partial resistance respectively. In addition, costs that are functions of manipulation or resistance can cause cycles of manipulation and resistance (Robert et al., 1999) because as resistance evolves high levels and eliminates manipulation, resistance becomes wasteful and diminishes, which starts a new cycle. Payoffs may also vary for other reasons. Costs and benefits vary as environmental conditions change in space and developmental or evolutionary time. Depending on how manipulation is executed, costs and benefits may be influenced by the manipulating and manipulated parties, and hence they can be subject to selection in conflicting ways. We have also made the standard assumption of constant additive genetic variances for both manipulation and resistance. In models with additive contribution to trait expression (Gavrilets, 2000; Gavrilets et al., 2001) the magnitude of the genetic variances affects the outcome of the conflict because the speed of change is important, but in our model non-zero genetic variances can only change the basin of attraction towards either outcome.

The inclusive fitness effect of manipulation (eq. (1.6a)) depends on the evolving resistance probability (q). As a result, the Hamilton's rule for manipulation ($h_p > 0$) does not determine whether manipulated behavior is obtained in the long run even if payoffs are constant. The conditions for manipulated behavior regarding manipulation are 1) that the inclusive fitness effect of manipulation in the absence of resistance is positive ($M_0 > 0$), and 2) for $r_{sm} > -c_m/c_r$, that the inclusive fitness effect of manipulation plus its relative rate of increase with acquiescence is also positive ($h_p + Mpu > 0$; eq. (A1.1)). On the other hand, the inclusive fitness effect of acquiescence (eq. (1.6b)) is different from that of spontaneous behavior ($br - c_a$). In particular, the direct fitness effect of acquiescence [i.e., $-(c_a - c_r)$] can be positive despite positive costs; that is, when resistance is costlier than acquiescence ($c_r > c_a$) (Dawkins, 1982; Pagel et al., 1998). This means that the "cost" term in the Hamilton's rule for acquiescence ($c_a - c_r$) can be negative. In such a case, acquiescence is not altruistic in Hamilton's sense (West et al., 2006) and is favored even if relatedness of acquiescing subjects toward targets is zero.

A negative "cost" is often referred to as a benefit in evolutionary parlance, but here it is only an extorted benefit that arises from acquiescence being less costly than resistance.

Although we have referred to manipulation, our model is relevant to a variety of mechanisms under other names: for example, coercion, punishment, and deception (Clutton-Brock and Parker, 1995; Holland and Rice, 1998; Cézilly and Thomas, 2012); asymmetric interactions or control of dominants over subordinates (Maynard Smith and Parker, 1976; Vehrencamp, 1983; Johnstone, 2000; Shen and Reeve, 2010); and conformity biases of individuals in groups with particular customs (Richerson and Boyd, 2005; Whiten et al., 2005). Some of these cases involve interactions among non-kin (Clutton-Brock, 2009). Although manipulated behavior can be obtained with zero relatedness between subjects of manipulation and targets of the manipulated behavior, it is useful to keep in mind that the relatednesses involved in the model stem from correlation coefficients that do not necessarily imply kinship (Queller, 1992a, 2011; Frank, 2012).

Determining whether a socially triggered behavior is spontaneous or manipulated is less difficult when there is little possibility that it confers direct or indirect benefits (Hughes et al., 2012). In other cases, determining whether a behavior is spontaneous or manipulated is particularly challenging. We used the example of workers in eusocial taxa which may be spontaneous or manipulated helpers. In such cases, the inference of ancestrally high relatedness (Hughes et al., 2008) is of little help at discerning between these two sources of behavior because high relatedness can favor both spontaneous and manipulated behavior (inequality (1.10a)). The lack of perpetual arms races and the occurrence of honest signaling are sometimes taken as evidence against manipulation (Keller and Nonacs, 1993; Keller, 2009; Heinze and d'Ettorre, 2009). However, if parties' contribution to trait expression is multiplicative, perpetual arms races need not occur as in our model above, and it is conceivable that manipulators may honestly signal components of inequality (1.10a) (e.g., b or c_r) in which case manipulated parties can be favored to attend the signal. In principle, subtle signaling such as drumming in wasps (Suryanarayanan et al., 2011) could be enough to deter individuals from developing into reproductives if it provides reliable information on the benefit to recipients or costly resistance. Deception and manipulation are not necessarily associated, and honest signaling may sometimes say little regarding whether or not a behavior is the result of manipulation.

Our analysis suggests a way in which inference regarding the above sources of behavior could be made. Although inequality (1.13) offers a condition for manipulated rather than spontaneous behavior to be expected, it is based on assumptions that are not applicable to particular systems; in particular, our assumption of constant costs. Our approach can be modified to incorporate relevant details. On the other hand, the nature of costs impose restrictions on the evolution of manipulated behavior that do not apply to spontaneous behavior thereby allowing for further distinction between the two. While the expectation of manipulated behavior would depend on how manipulation is exerted, the expectation of spontaneous behavior would not similarly vary with how it is triggered. The fact that the typical modes of helping among primitively eusocial taxa involve differential feeding or dominance interactions appears consistent with manipulated behavior in that there seems to be less reason for spontaneous behavior to be associated with these specific forms of social triggering.

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A1.1 Appendix A

Dynamic equations

In order to determine the evolutionary change of manipulation p and resistance q, consider a set of predictors (e.g., genetic loci) that specify how much of each trait is expressed by an individual. Let x_{ij} be the amount of predictor i for trait j $(= p, q)$ in a given individual. For instance, if x_{ij} is the number of alleles at locus i contributing to trait expression, then for diploids $x_{ij} = 0, 1, 2$ if the individual has non-contributing alleles, one contributing allele, or two contributing alleles respectively. Let β_{ij} be the partial regression coefficient of trait j on predictors x_{ij} across individuals. The sum $g_j = \sum_i \beta_{ij} x_{ij}$ is the additive effect of predictors, or breeding value, for trait j in a given individual. Assume that these additive effects are approximately constant in time (e.g., if there is little genetic variance and the trait changes by small amounts) and across states. Then, the evolutionary change in trait j is given by $dj/dt = v_j \partial w / \partial g_j$ evaluated at the population-average j (Frank, 1997), where v_j is the variance of breeding value g_j or additive genetic variance for trait j across individuals. For simplicity, we abuse the notation and write p and q for their population averages.

Life-for-life relatednesses are defined in terms of regression relatednesses (Hamilton, 1972; Bulmer, 1994). A regression relatedness is the regression coefficient of recipient's breeding value on actor's breeding value. For manipulation (eq. (1.5a)) the actors are manipulators (m) while for resistance (eq. (1.5b)) the actors are subjects (s). The state the focal individual is in gives the recipient state. We make the standard simplifying assumption of a 1-1 relationship of breeding value to phenotype. Thus, $dp/dg_p = \rho_{mm} = 1$ is the regression relatedness of manipulators toward themselves, $dP/dg_p = \rho_{sm}$ is that of manipulators toward reachable subjects, and $d\Pi/dg_p = \rho_{tm}$ is that of manipulators toward targets. Similarly, $dq/dg_q = \rho_{ss} = 1$ is the regression relatedness of subjects toward themselves, while $dQ/dg_q = \rho_{ts}$ is the regression relatedness of subjects toward targets. Life-for-life relatednesses are obtained when regression relatednesses are weighted by recipient-to-actor reproductive values. That is, $r_{ji} = \rho_{ji} k_j / k_i$.

A1.2 Appendix B

Analysis

Assume first that $p \neq 0$, so that some manipulation is present. Then equation (1.6b) tells us that if $R < 0$, then resistance disappears ($q \to 0$). Once $q \approx 0$, the selection gradient $h_p \approx M_0$, so that manipulation p evolves to 1 or 0 depending on whether M_0 is positive or negative. If $R > 0$, then complete resistance evolves ($q \to 1$). Once, $q \approx 1$, the selection gradient $h_p \approx M_0 - M$, so that manipulation p evolves to 1 or 0 depending on whether $M_0 - M$ is positive or negative. There are thus four cases to consider.

- If $q \to 0$, and $R < 0, M_0 > 0$, then the system evolves to $p = 1, q = 0$.
- If $q \to 0$, and $R < 0, M_0 < 0$, then the system evolves to $p = 0$.
- If $q \to 1$, and $R > 0, M_0 - M > 0$, then the system evolves to $p = 1, q = 1$.
- If $q \to 1$, and $R > 0, M_0 - M < 0$, then the system evolves to $p = 0$.

To complete the analysis we need to consider the model behavior along the line $p = 0$. If $q^* < 0$ or $q^* > 1$, then the sign of h_p does not depend on the value of q and the above analysis extends to the area of the phase-plane where $p \approx 0$. If $0 < q^* < 1$, then the sign of h_p as a function of q changes as q crosses q^*. This implies that the border $p = 0$ of the phase-plane will include a locally stable and a locally unstable segments separated by q^*. Therefore depending on initial conditions some trajectories will evolve towards the $p = 0$ line even when there are locally stable equilibria at $p = 1, q = 0$ or $p = 1, q = 1$.

The line delimiting the basin of attraction is obtained from the eigenvectors of the Jacobian of system (1.5) evaluated at the equilibrium $(p, q) = (0, q^*)$. These eigenvectors define the lines $q = q^* \pm pu$. Convergence to the equilibrium $p = 1, q = 0$ thus requires that the initial levels of resistance are $q < q^* + pu$, where $u = \sqrt{-v_q k_s R/(v_p k_m M)}$ (gray region in figure 1.2). The inequality $q < q^* + pu$ can be rearranged into

$$h_p + Mpu > 0, \tag{A1.1}$$

which states that, when $r_{sm} > -c_m/c_r$, for manipulated behavior the inclusive fitness effect for manipulation (h_p) plus its relative rate of increase with acquiescence (Mpu) must be positive.

Chapter 2

Spontaneous resolution of manipulation conflict

The following chapter is a reprint of a paper submitted for publication.

González-Forero M. Spontaneous resolution of manipulation conflict. Submitted.

Abstract

In some circumstances, individuals have the possibility to manipulate (i.e., control partially or completely) the behavior of other individuals. However, resistance to manipulation would be favored under certain conditions, which may reduce or eliminate the manipulated behavior. Such evolutionary conflicts have been studied for diverse settings including parent-offspring conflict, sexual conflict, and host-parasite coevolution. Here I show that the manipulation conflict can be resolved in a previously unidentified way that is of substantial generality. Manipulation of a social behavior creates selection pressure for increasing efficiency of the behavior before resistance is complete. The efficiency of the social behavior can become high enough so that selection for resistance disappears. The outcome is a social behavior triggered by social partners, yet the triggering and triggered parties are not in conflict anymore. Due to the final absence of conflict, I refer to this outcome as induced behavior. Induced behavior can be obtained under less stringent conditions than spontaneous (i.e., non-manipulated) social behavior. I suggest grounds for thinking that the induction of behavior is not lost after the conflict is removed. The induction may then appear as communication. Applications of these results span biology and the social sciences.

2.1 Introduction

Individuals, vaguely defined, may have the opportunity to influence the traits of other individuals (Dawkins, 1982). Influencing another individual's traits is sometimes referred to as partner control (West Eberhard, 1975; Taylor, 1988), manipulation (Alexander, 1974; Dawkins and Krebs, 1978), indirect genetic effects (Kirkpatrick and Lande, 1989; Wolf et al., 1998) or part of an individual's extended phenotype (Dawkins, 1982). I will use the term manipulation because it implies that the control of another individual's trait is not necessarily complete, and because of its implicit reference to resistance.

The ability to manipulate the traits of other individuals may be gained by direct access to such individuals' physiology, as internal parasites, parents, offspring or sexual partners with internal fertilization may have (Arnqvist and Rowe, 2005; Maestripieri and Mateo, 2009; Uller et al., 2009; Hughes et al., 2012). Manipulation can also be accomplished remotely, for example via sensory exploitation, communication or deception (Holland and Rice, 1998; Bradbury and Vehrencamp, 2011; Trivers, 2011). In addition, manipulation can be done by altering the payoffs to other individuals. This can be effected with power asymmetries, coalitions and alliances, punishment, and dominance hierarchies (Maynard Smith and Parker, 1976; Byrne and Whitten, 1988; Clutton-Brock and Parker, 1995; de Waal, 1998; Richerson and Boyd, 2005; Mesterton-Gibbons et al., 2011).

However, manipulation may or may not match the fitness interests of the manipulated individuals. If so, manipulating and manipulated parties conflict, and the manipulated individuals may be favored to resist manipulation. Resistance can then reduce or eliminate the manipulated behavior (Parker and Macnair, 1978; Robert et al., 1999; Gandon et al., 2009). Alternatively, the manipulated behavior can be maintained if resistance is costly enough (Pagel et al., 1998; González-Forero and Gavrilets, 2012) or if there is little genetic variance for resistance (Gavrilets, 2000; Gavrilets et al., 2001).

It has been pointed out that competing interactions may evolve into cooperative interactions when the evolution of payoffs is allowed (Worden and Levin, 2007; Akçay and Roughgarden, 2011). In principle, the evolution of payoffs may similarly modify the outcome of a manipulation conflict. I analyze here the effect of the evolution of payoffs on the evolution of manipulated behavior. I identify one way in which the evolution of payoffs can cause resistance to manipulation to become disfavored. This produces an agreement in the interests of manipulating and manipulated parties as a result of the selection pressures created by manipulation. Because of the absence of conflict, I do not refer to the final behavior as manipulated but as induced behavior. The conditions for induced behavior can be less stringent than those for spontaneous (i.e., non-manipulated) behavior without the need of costly resistance or diminished genetic variance for resistance. The outcome is a highly efficient socially induced behavior over which there is no actual or potential conflict between inducing and induced parties. This outcome matches some of the key features of advanced eusociality, which is one the most extreme forms of sociality (Hölldobler and Wilson, 2009). I briefly discuss further applications of these results.

2.2 Model for manipulated behavior with social efficiency

I extend the model in González-Forero and Gavrilets (2012) that studies manipulated behavior by including the evolution of social efficiency.

Consider a population where individuals can be in one of three states at a given time: "manipulator" state (m), "subject of manipulation" state (s), or "target of manipulated behavior" state (t). A single individual can be at one time a manipulator and at another time a target of manipulated behavior. A manipulator m manipulates with probability p subjects of manipulation s that are within its reach. I let p be under control of the manipulator. A manipulated subject s resists manipulation with probability q, which I let be under control of the subject. Alternatively, a manipulated subject s that acquiesces (i.e., that does not resist) expresses a focal social behavior with probability φ. Specifically, $\varphi = P(1-q)$, where P is the average manipulation probability among the manipulators that can reach the focal subject. Targets of manipulated behavior t receive the fitness effects of the social behavior φ expressed by neighboring subjects.

An acquiescing subject pays the cost c of acquiescence and causes a fitness effect b to targets. I let c be positive, but b may be positive or negative reflecting helping or harming. A highly efficient acquiescing individual causes greater fitness effects $|b|$ than a lowly efficient individual. For example, if the social trait φ refers to the probability that an individual stays in the maternal nest as an adult, social efficiency y may refer to the helping efficiency expressed by the individual in the maternal nest: φ and y can be different in this example since an individual can stay ($\varphi > 0$) and express no help (i.e., be totally inefficient $y = 0$), or any other combination of the two. To define social efficiency y, I proceed as follows.

Let $b_{\max}$ be the fitness effect that an actor provides to recipients when expressing the social behavior φ at maximum efficiency. $b_{\max}$ can be positive or negative depending on whether the social behavior is a helping or a harming one. Let y be the normalized efficiency at expressing the social behavior φ; that is, y is the fraction of $b_{\max}$ that an actor expresses. I assume social efficiency y to be controlled by the actors expressing φ. The fitness effect b to a recipient of the social behavior φ is

$$b = b_{\max} Y, \tag{2.1}$$

where Y is the average social efficiency among the actors that reach the recipient of φ.

Social efficiency y can also affect the cost c of the social behavior φ. I partition the cost c into a part c_b due to social efficiency y and a part $c_{\neg b}$ due to social inefficiency $1 - y$ ("$\neg$" means "not"; I let $c_b, c_{\neg b} \geq 0$). In the above example, the cost of social efficiency c_b may occur if effort spent helping is not spent reproducing, while the cost of social inefficiency $c_{\neg b}$ may happen if lack of helping translates into ineffective reproduction, for example due to overcrowding of the maternal nest with siblings and own offspring or to poor parenting skills from lack of alloparenting practice (Emlen, 1982). Hence, the cost of the social trait φ is

$$c = yc_b + (1 - y)c_{\neg b}. \tag{2.2}$$

This yields dynamic equations for the coevolution of manipulated behavior φ and social efficiency y (Appendix).

2.3 Results

Equations (2.9) in the Appendix specify the Hamilton's rule for increase in each trait (i.e., $h_i > 0$). They involve the life-for-life relatedness r_{ji} of actor i toward recipient i, as illustrated in Fig. 2.1. Life-for-life relatedness measures the correlation of the heritable component of the trait values between the social partners (Hamilton, 1972). Because the model uses techniques that allow for non-genetic inheritance (e.g., via learning), relatedness here need not refer to genetic relatedness (Frank, 1998). Manipulation increases when $br_{tm} > cr_{sm}$ as long as resistance is not complete (eq. (2.9a)). Acquiescence to manipulation increases when $br_{ts} > c$ provided there is some manipulation (eq. (2.9b)). Social efficiency increases when $br_{ts} > c - c_{\neg b}$ if there is some manipulated behavior (eq. (2.9c)). The different condition for social efficiency when compared to that for acquiescence allows for social efficiency to increase when acquiescence is not favored. As a result, Hamilton's rule for acquiescence can become satisfied in the long run.

Fig. 2.2 shows that the evolution of social efficiency can eliminate resistance. The process is the following. Under conditions of conflict, as soon as there exists manipulation, resistance becomes favored and if there is no genetic variation for social efficiency, then resistance eliminates the manipulated behavior (Fig. 2.2A). With some genetic variation, social efficiency is favored to increase even though resistance is also favored (Fig. 2.2B). For example, before resistance is complete, an offspring manipulated by its mother to help stays in the maternal nest with some probability; in

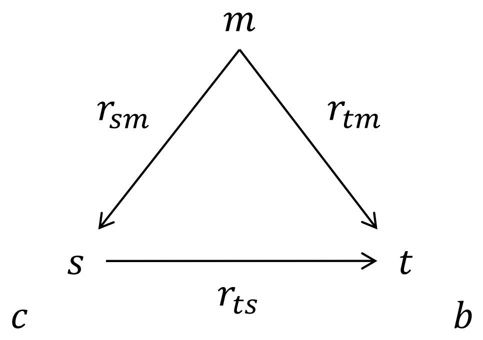
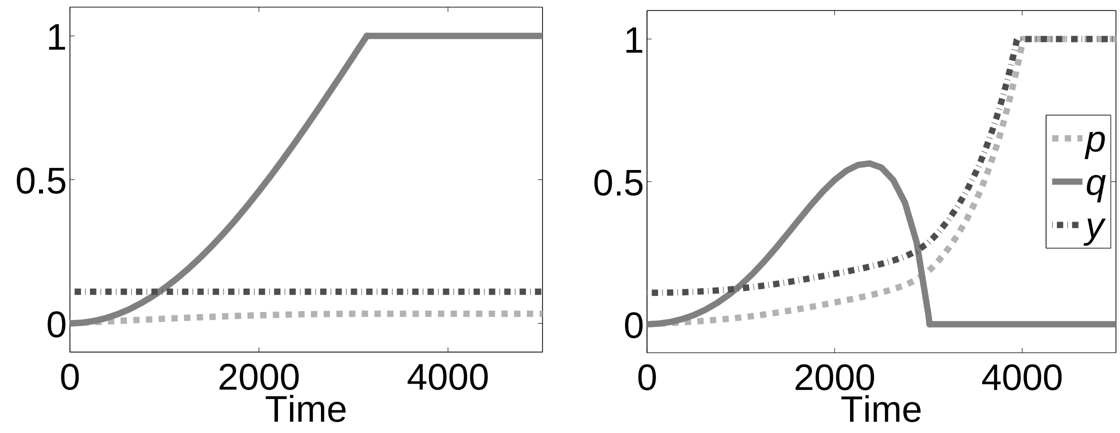


Figure 2.1: Relatednesses among social partners and their corresponding payoffs. Individuals at a given time are either manipulators (m), subjects of manipulation (s), or targets of manipulated behavior (t). Arrows correspond to the life-for-life relatedness r_{ji} of actor i to recipient j. A manipulator m can be a target of manipulation t at another time, in which case $r_{tm} = 1$. Also indicated are the payoffs to each state: subjects of manipulation s can pay the cost of acquiescence c, and targets of manipulated behavior t receive a fitness effect b from acquiescing subjects.

such a case, the manipulated offspring can be favored to be an efficient helper if there is a cost for inefficiency (see above). Social efficiency can then increase up to a point where resistance becomes selected against (Fig. 2.2B). At the end of the process, there is no conflict between manipulator and subject, as both agree on the expression of the social behavior by the latter. I characterize the conditions for this to happen.

The coevolutionary dynamics between resistance and social efficiency are in Fig. 2.3. If Hamilton's rule for acquiescence cannot be satisfied for any social efficiency (Fig. 2.3**a**), resistance eliminates the manipulated behavior. In contrast, if Hamilton's rule can be satisfied for some social efficiency (i.e., above the dashed line in Fig. 2.3**b**), the system can converge to a point of full manipulation, no resistance, and maximum social efficiency (dot in Fig. 2.3**b**). In this point, there is no (actual or potential) conflict between manipulator and subject and I refer to it as induced behavior. The system converges to induced behavior if it starts in the gray area of Fig. 2.3**b**. This shows that Hamilton's rule for acquiescence need not be initially satisfied for induced behavior, provided that resistance probability is initially sufficiently small. Instead, the condition for induced behavior is that the system starts above the oblique line delimiting the gray



(a) **(b)**

Figure 2.2: Coevolution of manipulation p, resistance q, and social efficiency y. Numerical solutions to the differential equations defined by (2.9) are plotted. (**a**) Genetic variation for social efficiency is zero ($v_y = 0$) and resistance evolves and eliminates any manipulated behavior [i.e., the manipulated behavior $\varphi = p(1-q) = 0$ in the end]. (**b**) Genetic variation for social efficiency is non-zero ($v_y = 0.001$) and social efficiency increases causing resistance to eventually decrease and be eliminated. The remaining parameter values for A and B are $p(0) = q(0) = 0$, $y(0) = 0.11$, $r_{ts} = r_{sm} = r_{tm} = 1/2$, $c_b = c_{\neg b} = 1$, $b_{\max} = 10$, $v_p = 0.001$, $v_q = 0.1$, $k_m = k_s = k_t = 1/3$, and hence $S = S_m = 5$.

area in Fig. 2.3**b**. This line is determined in the SI, and hence the condition that must be met at the start of the evolutionary process is

$$br_{ts} + (1-q)S\sqrt{v_y/v_q} > c, \tag{2.3a}$$

where

$$S = b_{\max}r - (c_b - c_{\neg b}). \tag{2.3b}$$

The quantity S measures individuals' evolutionary interest in their own social efficiency, as shown by the right-most expression in eq. (2.9c). v_y and v_q are the additive genetic variances of social efficiency and resistance respectively. Condition (2.3a) is a relaxed Hamilton's rule, and its relaxing term $[(1-q)S\sqrt{v_y/v_q}]$ measures the speed of increase in social efficiency relative to resistance.

In the online Supporting Information, I build an analogous model in which the probability of expressing the focal trait φ is completely under control of the individuals

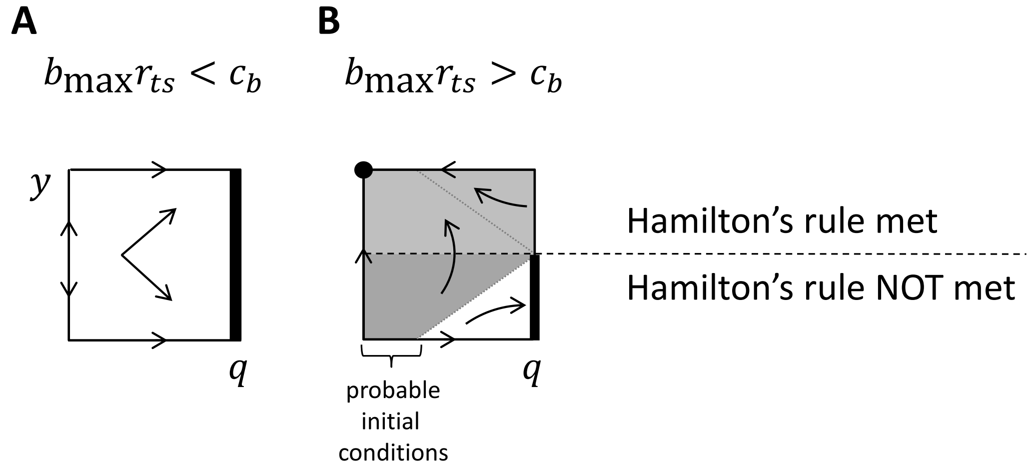


Figure 2.3: Coevolutionary dynamics of resistance q and social efficiency y. The arrows indicate the direction of change. The dashed line is the level $y^* = c_{\neg b}/S$ of social efficiency at which Hamilton's rule for spontaneous behavior φ becomes satisfied ($br = c$). Thick strokes indicate stable equilibria. In the gray area, the system converges to acquiescence and maximum social efficiency. For initially small probability of resistance, Hamilton's rule for the focal behavior need not be satisfied initially.

expressing it. I refer to this case as spontaneous behavior. The coevolution of spontaneous behavior φ and social efficiency y also allows for the spontaneous behavior to be obtained when a relaxed Hamilton's rule is satisfied (condition (S7a) in SI). The relaxed Hamilton's rule for spontaneous behavior is entirely analogous to that for manipulated behavior (2.3a), except that the factor $1 - q$ is replaced by the probability φ of expressing the spontaneous behavior. As a result, if the probability φ of spontaneous behavior is initially small, the relaxed Hamilton's rule for spontaneous behavior reduces to Hamilton's rule ($br > c$). In contrast, if the probability q of resistance is initially small, the relaxed Hamilton's rule for manipulated behavior is maintained. In principle, initially small probability of resistance may be expected when a novel manipulation strategy arises. The reason is that before the new manipulation strategy arises, there is no selection pressure for resistance. This, however, is an empirical question that must be addressed on a case by case basis and whose answer may be affected by selection for homeostasis in particular systems.

A numerical illustration of the coevolution of manipulation, resistance, and social efficiency is given in Fig. 2.4. The gray plane, defined by condition (2.3a), specifies the region for convergence to induced behavior. The full set of conditions for induced behavior are the following (see SI). When manipulation and resistance are initially small, fully efficient socially induced behavior $[(p,q,y)=(1,0,1)]$ is obtained when the following conditions hold:

$$br_{ts}+S\sqrt{v_y/v_q}>c \tag{2.4a}$$

$$b_{\max}r_{ts}>c_b \tag{2.4b}$$

$$br_{tm}>cr_{sm} \qquad \text{if } r_{sm}>0 \tag{2.4c}$$

$$b_{\max}r_{tm}>c_b r_{sm} \qquad \text{if } r_{sm}\leq 0. \tag{2.4d}$$

Condition (2.4a) states that acquiescence must become favored for some social efficiency; condition (2.4b) that acquiescence can be favored for some social efficiency; condition (2.4c) that manipulation is favored; and condition (2.4d) that manipulation does not become disfavored at high social efficiency. The latter condition stems from the fact that manipulation is favored when it harms sufficiently unrelated subjects (González-Forero and Gavrilets, 2012).

Comparison between spontaneous and induced behavior.

Comparing the models for manipulated and spontaneous behavior yields a condition that specifies when induced behavior can require less stringent conditions than spontaneous behavior. This occurs when induced behavior is obtained even though spontaneous behavior is not. This is the case when initially the relaxed Hamilton's rule for acquiescence is satisfied (ineq. (2.3a)), but the relaxed Hamilton's rule for spontaneous behavior is not (ineq. (S7a) in SI does not hold). Assume that spontaneous behavior, manipulation, and resistance are all initially small (i.e., $\varphi,p,q\approx 0$ initially). Also assume that the relatedness of actors to recipients for the spontaneous behavior is

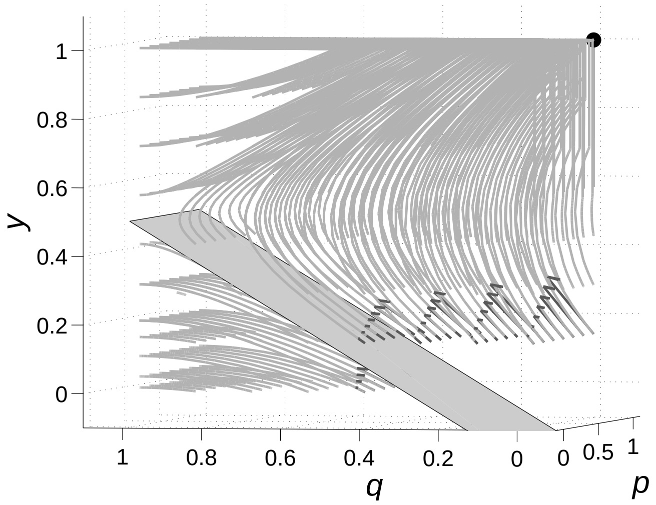


Figure 2.4: Example of numerical solutions for the three dimensional system of manipulation, resistance and social efficiency (p,q,y). Numerical solutions for different initial conditions are in gray, and arrows indicate the direction and speed (length of the arrow) of change. The outcome of induced behavior is indicated by the dot, where $(p,q,y) = (1,0,1)$. The plane is $y = y^* - (1-q)\sqrt{v_y/v_q}$ (or equivalently, $br_{ts} + (1-q)S\sqrt{v_y/v_q} = c$) which is constant with respect to manipulation p. No solution crosses the plane, which divides the basin of attraction for any manipulation p. The parameter values are $v_p = 0.001$, $v_q = 0.1$, $v_y = 0.05$, $k_m = k_s = 1/3$, $r_{ts} = r_{sm} = r_{tm} = 1/2$, $c_b = c_{\neg b} = 1$, and $b_{\max} = 4$.

analogous to the relatedness of subjects to targets for the manipulated behavior (i.e., $r \approx r_{st}$). Therefore, induced behavior requires less stringent conditions than spontaneous behavior if at the start of the process

$$0 < c - br_{ts} < S\sqrt{v_y/v_q}, \tag{2.5}$$

provided that the remaining conditions (2.4) hold. Expression (2.5) makes it transparent that it is the evolution of social efficiency (measured by S and v_y) that allows for the advantage of induced behavior to occur, since expression (2.5) cannot be satisfied if $Sv_y = 0$.

2.4 Discussion

The expression of social behaviors often requires the proper triggering by social partners. Signals are a pervasive feature in nature. The seemingly high incidence of social triggering of behavior relative to other means (e.g., abiotic cues or information intrinsic to the individual expressing the behavior, such as age) may be the result of the benefits of information or of the relatively lax conditions for manipulation to evolve. A difficulty with the latter case is that manipulation may favor the evolution of resistance which can reduce or eliminate the expression of manipulated behavior (Trivers, 1974; Dawkins and Krebs, 1979; Keller and Nonacs, 1993; Bourke and Franks, 1995; Ratnieks and Wenseleers, 2008). I have shown that manipulated behavior could persist despite the evolution of resistance because of the evolution of payoffs. The outcome is socially induced behavior over which there is no (actual or potential) conflict between manipulating and manipulated parties. Due to the lack of conflict, I have referred to this outcome as induced behavior. The conditions for induced behavior to evolve can be less stringent than the conditions for spontaneous behavior (i.e., behavior fully under control of the individuals expressing it). Below I discuss the model, reinterpretations of data as suggested by the model, and possible applications.

The model presented above is deliberately simple so that complete analytic treatment is possible. I obtained analytical conditions for induced behavior and compared them to those for spontaneous behavior. Induced behavior can require less stringent conditions than spontaneous behavior because of the evolution of the fitness effect b to recipients of the manipulated behavior. This advantage of induced behavior is possible for two reasons. First, the conditions for selection of a social trait (h_φ) may be different from the conditions for selection of the social trait's efficiency (h_y). This difference arises because of costs of social inefficiency $c_{\neg b}$. The selective difference between the social trait and its efficiency allows for social efficiency to evolve when the social trait is not favored. The evolution of social efficiency can make the Hamilton's rule for the social trait to become eventually satisfied even though it initially is not. In a sense, the evolution of social efficiency rescues the social trait. Second, the initial conditions that allow for rescue of the social trait might more easily hold when the social trait is manipulated rather than spontaneous. In particular, when the social behavior is manipulated, the resistance probability to manipulation may be initially small, which translates into initially large probability of acquiescence. This allows for social efficiency to evolve when the social behavior is not favored. While the first reason above applies to both spontaneous and induced behavior, the second reason preferentially holds for induced behavior to the extent that the probability of expressing spontaneous social behavior is initially small. Therefore, it is the second reason that can ultimately cause induced behavior to require less stringent conditions than spontaneous behavior, which is made explicit by expression (2.5).

As a result of these two reasons, induced behavior can be obtained when a relaxed Hamilton's rule for acquiescence holds (ineq. (2.3a)). The relaxing term is a function of how much social efficiency is favored from the point of view of the subjects of manipulation (measured by S). In addition, the relaxing term is also a function of the genetic variances of social efficiency v_y and resistance v_q. Depending on the value of these quantities, the magnitude of the relaxing term can be substantial. It is a noticeable fact that the relaxing term is not eliminated with initially small manipulation probability p as illustrated by Fig. 2.4. This is because p multiplies the entire inequality (2.3a), as it equally affects the rate of change of resistance and social efficiency.

The simplicity of the model, however, gives room for an objection, that in turn suggests a hypothesis that links manipulation to communication. When social efficiency crosses the point at which acquiescence becomes favored (y^* in Fig. 2.3), the social behavior is favored regardless of whether or not there is manipulation. This raises the question of what would maintain the social triggering of behavior after this threshold is crossed. In particular, manipulation would be wasteful if the social behavior is expressed even without it, and the social behavior does not need manipulation anymore for it to be expressed. These were not issues in the model above because manipulation was assumed to be costless, and the social behavior could only be expressed if there was manipulation. Even if these two aspects were modified in the model, an interesting possibility is that the reduction of social triggering causes dissipation of the high fitness effect b that made the spontaneous behavior favored in the first place. For example, if manipulators are mothers of two subsequent broods where first-brood offspring are subjects of manipulation and second-brood offspring are targets of manipulated behavior, reduction of social triggering may cause some second-brood offspring to develop as helpers. The helping offered to second-brood helpers would be a waste if second-brood helpers are unable to help further broods or reproduce themselves. The fitness effect b averaged across recipients would then be smaller if offspring developed as helpers without information about the brood they belong to. As a result, spontaneous behavior that ignores manipulation can be disfavored because it dissipates the fitness effect b. If so, the spontaneous behavior would be expressed only when manipulated, and hence reduced manipulation would be disfavored because the focal social behavior would also be reduced. To the extent that this holds, the social triggering may be interpreted as being coopted to serve communication purposes. Manipulation would thus produce induced behavior that is maintained by the cooption of manipulation as communication. However, a formal exploration of this possibility is beyond the scope of the present paper.

The results reported here are immediately relevant to discussions of the evolution of eusociality. Parental manipulation, where eusocial workers are manipulated by their parents to help, is a classic hypothesis for the evolution of eusociality (Alexander, 1974; Michener and Brothers, 1974; Bourke and Franks, 1995). However, offspring consent to manipulation is considered to be necessary for offspring to express helping, specially in the large colonies of advanced eusocial taxa where mothers would not be able to coerce offspring into helping (Hölldobler and Wilson, 1990; Bourke and Franks, 1995; Keller and Nonacs, 1993; Ratnieks and Wenseleers, 2008). Evidence supporting offspring-favored outcomes in parent-offspring conflicts has served to support this view (Trivers and Hare, 1976; Keller and Nonacs, 1993; Heinze and d'Ettorre, 2009; West, 2009). The results reported here show that manipulation can create consent in the manipulated parties. The outcome of a parent-offspring conflict may thus appear as if offspring have won, given that in the end helping occurs and its Hamilton's rule is satisfied. However, in a sense, both parties win. For example, queen pheromones, which are subtle mechanism for social triggering of behavior in advanced eusocial taxa, often honestly signal queen fertility (Keller and Nonacs, 1993; Heinze and d'Ettorre, 2009). Such honesty has suggested that queen pheromones are not manipulative (Keller and Nonacs, 1993; Heinze and d'Ettorre, 2009). A different interpretation suggested by the results reported here is that queen pheromones might be the result of ancestral manipulation. The results above show how Hamilton's rule could mark the end point at which the social trait becomes favored, while the initial points that bring the system toward satisfaction of the rule may be decisive in the final form of the social behavior observed.

The evolution of social efficiency y can in the case of eusociality represent worker specialization. Worker specialization is one of the key components of advanced eusociality (where another component is queen specialization which is not captured by the model above) (Hölldobler and Wilson, 2009). The results above show that manipulation could produce socially induced behavior, worker specialization, and low level of conflict between inducing and induced parties, all of which match defining features of advanced eusociality (Hölldobler and Wilson, 2009). More broadly, these results offer a distinct mechanism for the evolution of division of labor applicable to a variety of contexts. In particular, manipulation of social behavior can bring specialization that only later in the process becomes in the interests of the highly specialized laborers. This contrasts with previous theories that regard specialization as bringing direct or indirect benefits from the start of the process (Smith, 1776; Oster and Wilson, 1978; Beshers and Fewell, 2001; Wahl, 2002).

The model is general in that it does not imply particular kinds of interactions such as parent-offspring, male-female, or unrelated host and parasite. Interactions can be between rather arbitrary social partners. The type of interaction can be specified by the relatednesses involved. Relatednesses are here defined in their general form

(Frank, 1998, 2013): they measure the correlation in the heritable components of the traits between actors and recipients of the traits. These correlations need not arise from kinship (kin selection) (Hamilton, 1964a, 1970), but may arise through conditional response to partner's behavior (which allows for reciprocity to evolve) (Queller, 1985; Frank, 1994; Fletcher and Zwick, 2006), biased assortment among groups (which allows for group selection) (Queller, 1985; Fletcher and Doebeli, 2009), manipulation, punishment, partner choice (Queller, 2011), or any other mechanism that creates such correlations. In addition, the traits need not have a genetic basis. Heritability can be cultural (e.g., through learning) or in any other way that correlates the phenotype of "parents" and "offspring" (Frank, 1998; Richerson and Boyd, 2005). Therefore, these results are also relevant to cultural manipulation.

As an example, central governments are regarded as particularly powerful drivers of social change (Hobbes, 1651; Rousseau, 1762; Pettit, 1997). For instance, they have been suggested to be key promoters of a large-scale tendency of violence decline across human history (Pinker, 2011). The results presented here illustrate one way in which government effectiveness can be achieved. In particular, the introduction of a new policy by a ruling government can cause citizens to revolt. As affected citizens pursue attempts to revert the policy, such citizens may be simultaneously favored to find ways of thriving in the recently established system (e.g., in terms of the model, if there is a cost of social inefficiency). Citizens may then eventually become sufficiently proficient in the new system so that reasons to attempt policy reversal dissolve. If one had not seen that the initial process started from governmental influence (as would be the case for ancestral biological manipulation), the outcome of the manipulation conflict would in the end appear as if the subjects of manipulation had won since Hamilton's rule for acquiescence is satisfied. However, in a certain sense, both parties win given that the conflict disappears.

The models presented here are deliberately simple so that complete analytical treatment is possible. Enhancing their realism will necessarily affect many of their specifications. Stochastic effects can take the evolutionary trajectories out of the basin of attraction toward induced behavior. Variable costs of manipulation and resistance, and time-dependence of quantities that were here assumed to be constant will change the dynamics. However, the qualitative understanding provided by the models may prove more robust.

Appendix

For simplicity, I assume that there are no costs of manipulation and resistance. Because manipulators pay no cost of manipulation and the fitness effects of the social behavior φ are received by targets, the fitness payoff to a manipulator m is the baseline fitness which I let be $w_m = 1$. On the other hand, an acquiescing subject of manipulation s pays the cost of acquiescence c. Then, the payoff to a subject of manipulation is

$$\begin{aligned} w_s &= P(1-q)(1-c) + Pq + (1-P) \\ &= 1 - cP(1-q). \end{aligned} \tag{2.6}$$

A target of manipulated behavior t receives a fitness effect b from its acquiescing neighbors. The fitness effect b can be positive or negative. The average resistance probability among subjects of manipulation in the focal patch is Q. Thus, the payoff to a target of manipulated behavior is

$$\begin{aligned} w_t &= P(1-Q)\,(1+b) + PQ + (1-P) \\ &= 1 + bP(1-Q). \end{aligned} \tag{2.7}$$

As before, let k_j be the reproductive value of state j $(= m, s, t)$. Therefore, the fitness of a random individual is $w = \sum k_j w_j$ which becomes

$$w = 1 - k_s cP(1-q) + k_t bP(1-Q). \tag{2.8}$$

The payoffs b and c are defined as in equations (2.1) and (2.2), where the social efficiency y of an acquiescing subject is under the acquiescing subject's control and Y is the average social efficiency among acquiescing subjects in the patch.

Resulting dynamic equations.

Assuming negligible association between the traits, the resulting dynamic equations are $di/dt = v_i k_{\text{act}} h_i$, where di/dt is derivative of i with respect to time ($i = p, q, y$, which denote population averages) (Frank, 1998). v_i is the additive genetic variance of i ("genetic" is the customary name, but it also refers to non-genetic inheritance–e.g., via learning). k_{act} is the class reproductive value of the actors of trait i. The actors for the equation of manipulation p are manipulators m while the actors for the equations of resistance q and social efficiency y are subjects of manipulation s. h_i is the inclusive fitness effect of trait i. They are

$$h_p = (1-q)(br_{tm} - cr_{sm}) \qquad = (1-q)(yS_m - c_{\neg b} r_{sm}) \tag{2.9a}$$

$$h_q = -p(br_{ts} - c) \qquad = -p(yS - c_{\neg b}) \tag{2.9b}$$

$$h_y = \frac{p(1-q)}{y}[br_{ts} - (c - c_{\neg b})] \qquad = p(1-q)S. \tag{2.9c}$$

Here $r_{ji} = k_j/k_i \rho_{ji}$ is the life-for-life relatedness of actor i to recipient j (where $i = m, s$, and $j = s, t$). The regression relatednesses ρ_{ji} are: for manipulators to subjects $\rho_{sm} = dP/dg_p$, for manipulators to targets $\rho_{tm} = dP/dg_p$, for subjects to themselves $\rho_{ss} = dq/dg_q = dy/dg_y = 1$, and for subjects to targets $\rho_{ts} = dQ/dg_q = dY/dg_y$. The quantity $S_m = b_{\max} r_{tm} - r_{sm}(c_b - c_{\neg b})$ measures manipulators' interest in subjects' social efficiency.

The inclusive fitness effects of resistance and social efficiency (eqs. (2.9b) and (2.9c)) are analogous to those of spontaneous behavior and social efficiency in the spontaneous behavior model (eqs. (S5) in SI), except that the one for resistance (eq. (2.9b)) has the opposite sign to that of spontaneous behavior (eq. (S5a) in SI). This only means that when the Hamilton's rule for acquiescence (i.e., $br_{ts} > c$) is satisfied, resistance decreases. The inclusive fitness effect of manipulation (eq. (2.9a)) shows that manipulation is favored under different conditions than acquiescence (eq. (2.9b)), which allows for conflict over the social trait φ between the controlling parties. A more subtle difference with the system of the spontaneous behavior model which is key for the results reported here is that the inclusive fitness effect of social efficiency in the manipulated behavior model (eq. (2.9c)) depends on $p(1-q)$, rather than on the spontaneously controlled φ in eq. (S5b) in SI. In consequence, $p(1-q)$ can become non-zero when manipulation is favored ($br_{tm} > cr_{sm}$) even if acquiescence is not ($br_{rs} < c$) as long as resistance is small. This contrasts with the model for spontaneous behavior for which φ becomes non-zero only if the spontaneous behavior is favored ($br > c$). That is, social efficiency can here start evolving when manipulation arises rather than when the spontaneous behavior arises.

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A2.1 Supporting Information

The models use techniques (Frank, 1998) derived from the Price (1970) equation and hence relatively few assumptions are necessary.

A2.2 Spontaneous behavior

In this section, I develop a simple model for the evolution of payoffs in a common evolutionary model of social behavior (Hamilton, 1970; Taylor and Frank, 1996; Frank, 1998). This illustrates the basic effect of the evolution of payoffs that will be of interest in the manipulated behavior section. Here I assume that the social trait is fully under control of the individual expressing it and I refer to such a trait as spontaneous.

A2.2.1 Model for spontaneous behavior

Fitness

Consider a population of individuals so that at a given time, each individual is in one of two states: actor or recipient. An individual in the actor state expresses some focal social trait (e.g., helping or harming) with probability φ, which is under control of the actor. A reachable individual in the recipient state receives a fitness effect b from the actor. The fitness effect b can either be positive or negative, reflecting the helping or harming of recipients respectively.

Actors that express the social trait pay a cost c (I let all direct fitness effects of the social trait be non-negative, reflecting costs). Letting the baseline fitness be 1, the fitness payoff for an actor is

$$\begin{aligned} w_{\text{act}} &= \varphi(1-c) + (1-\varphi) \\ &= 1 - \varphi c. \end{aligned} \tag{A2.1}$$

The average probability of expressing the social trait over actors that can reach a focal recipient is Φ. Then, the payoff to a recipient is

$$\begin{aligned} w_{\mathrm{rec}} &= \Phi(1+b) + (1-\Phi) \\ &= 1 + \Phi b. \end{aligned} \tag{A2.2}$$

Actors and recipients may have intrinsically different possibilities of leaving descendants (e.g., if actors are typically older than recipients (Charlesworth, 1994), or if the genetic system is haplodiploid so that males are haploid and always contribute the same genes to their female offspring but no genes to next generation's males (Bulmer, 1994)). For the sake of generality, I do not specify how the intrinsic differences in leaving descendants arise. As a result, the calculation of fitness of a random individual in the population requires that the fitness of an individual in a given state (or class) is weighted by the state's reproductive value (Taylor, 1990; Taylor and Frank, 1996). The reproductive value of state j, which I will denote by k_j, is the probability that an individual in the long-term future of the population descends from a state j individual in the current population ($\sum k_j = 1$). Therefore, the fitness of a random individual in the population is $w = \sum k_j w_j$ (Taylor, 1990; Taylor and Frank, 1996) which in the present model becomes

$$w = 1 - k_{\mathrm{act}} \varphi c + k_{\mathrm{rec}} \Phi b. \tag{A2.3}$$

This is a standard expression for the fitness of socially behaving individuals that applies to arbitrary genetic (and non-genetic) systems (Hamilton, 1970; Frank, 1998).

I use this model to illustrate the effect of the evolution of payoffs b and c on the evolution of the social behavior φ. Payoffs b and c are defined by eqs. (2.1) and (2.2) in the main text. I study the coevolution of the spontaneous behavior φ and social efficiency y.

Resulting dynamic equations

I use the techniques of (Taylor and Frank, 1996) and (Frank, 1997) to obtain dynamic equations for the approximate evolutionary change in trait i ($= \varphi, y$) due to selection. The equation for trait i is given by $v_i \partial w / \partial g_i$ evaluated at the population average values, where v_i is the additive genetic variance of trait i and g_i is the trait's breeding value (or heritable component) in the actor (Taylor and Frank, 1996; Frank, 1997). The additive genetic variance v_i is the variance in the breeding value g_i which need not refer to genes if the trait can be inherited by other means (e.g., via learning). Thus, neither the additive genetic variance v_i nor the breeding value g_i assume that the trait is necessarily under genetic control. This is important for cultural evolution and other applications.

Therefore, assuming that the traits are uncorrelated, the dynamic equation for trait i is

$$\frac{di}{dt} = v_i k_{\text{act}} h_i, \tag{A2.4}$$

where h_i is the inclusive fitness effect of trait i on actors. The inclusive fitness effects of spontaneous behavior φ and social efficiency y are

$$\begin{aligned} h_\varphi &= br - c & &= yS - c_{\neg b} & \text{(A2.5a)} \\ h_y &= \frac{\varphi}{y}\left[br - (c - c_{\neg b})\right] & &= \varphi S. & \text{(A2.5b)} \end{aligned}$$

Here $r = k_{\text{rec}}/k_{\text{act}}\rho_{\text{rec,act}}$ is the life-for-life relatedness of actors to recipients (Hamilton, 1972; Bulmer, 1994), which is defined in terms of the regression coefficient of relatedness of actors to recipients $\rho_{\text{rec,act}} = d\Phi/dg_\varphi = dY/dg_y$ (Hamilton, 1970; Queller, 1992a; Taylor and Frank, 1996). The regression relatedness $\rho_{\text{rec,act}}$ is the regression coefficient of recipients' breeding value on actors' breeding value, and therefore relatedness here can be caused by but does not necessarily refer to genetic association.

The dynamic analysis of system (A2.4) is facilitated by rearranging inclusive fitness effects h_i in terms of the quantity S as defined by eq. (2.3b) in the main text. S measures actors' evolutionary interest in their own social efficiency, as shown by eq. (A2.5b).

When social efficiency is minimal ($y = 0$), the inclusive fitness effect of spontaneous behavior becomes $h_{\varphi} = -c_{\neg b}$ in which case the spontaneous behavior decreases. When social efficiency is maximal ($y = 1$), the inclusive fitness effect of the spontaneous behavior reduces to $h_{\varphi} = b_{\max} r - c_b$. Hence, if $b_{\max} r < c_b$, the spontaneous behavior decreases for any social efficiency y. The dynamics in this case are illustrated in Fig. A2.1A. Whether or not social efficiency y increases depends on the sign of S. In any case, the outcome is the loss of the spontaneous social behavior $[(\varphi, y) = (0, y)]$.

If $b_{\max} r > c_b$, Hamilton's rule for the spontaneous behavior becomes satisfied when $y > y^*$, where $y^* = c_{\neg b}/S$ is the critical social efficiency at which the Hamilton's rule for the spontaneous behavior becomes satisfied. The point $(\varphi, y) = (0, y^*)$ is an equilibrium and defines the global dynamics because of the linearity of system (A2.4). It is easily checked that this equilibrium is a saddle and, therefore, that the dynamics of the system are as illustrated in Fig. A2.1B.

The line delimiting the gray region in Fig. A2.1 can be obtained from the eigenvectors of the Jacobian of system (A2.4) that define lines with negative slope with respect to φ. Such eigenvectors are proportional to $(-\sqrt{v_{\varphi}/v_y}, 1)$. Because the intercept with the y axis is at y^*, these eigenvectors occur in the line $y = y^* - \varphi\sqrt{v_y/v_{\varphi}}$. This shows that the condition for the system to be in the gray region is

$$y > y^* - \varphi\sqrt{v_y/v_{\varphi}}. \tag{A2.6}$$

A2.2.2 Results for the spontaneous behavior model

Eqs. (A2.5) show that the Hamilton's rules (i.e., $h_i > 0$) for spontaneous behavior and its efficiency are different. That is, the spontaneous behavior φ and its efficiency y can increase under different conditions. The former increases when $br > c$, while the latter increases when $br > c - c_{\neg b}$ provided that the probability of expressing the spontaneous behavior is non-zero ($\varphi > 0$). This difference in selection, caused by the cost of social inefficiency $c_{\neg b}$, allows for social efficiency to increase even though spontaneous behavior is not favored.

In this model, there are two possible outcomes: either the spontaneous behavior disappears $[(\varphi, y) = (0, y)]$ or it evolves to maximum efficiency $[(\varphi, y) = (1, 1)]$. Spontaneous behavior with maximum social efficiency $(\varphi, y) = (1, 1)$ is obtained when

$$br + \varphi S\sqrt{v_y / v_\varphi} > c \tag{A2.7a}$$

$$b_{\max} r > c_b. \tag{A2.7b}$$

Inequality (A2.7a) is a rearrangement of inequality (A2.6). Inequality (A2.7b) guarantees both that Hamilton's rule for spontaneous behavior can be satisfied for some social efficiency y and that social efficiency is favored (i.e., that $S > 0$). Inequality (A2.7a) is a relaxed Hamilton's rule for spontaneous behavior since it requires a smaller br/c ratio to be satisfied than the Hamilton's rule for spontaneous behavior. This is because the term $\varphi S\sqrt{v_y / v_\varphi}$ is non-negative if condition (A2.7b) holds. This term measures selection for social efficiency (φS) and the genetic variation of social efficiency relative that for the social behavior ($\sqrt{v_y / v_\varphi}$). Hence, the Hamilton's rule for spontaneous behavior need not be satisfied initially for fully efficient social behavior to be obtained if the term $\varphi S\sqrt{v_y / v_\varphi}$ is large enough. For Fig. A2.1A, the Hamilton's rule for the spontaneous behavior cannot be satisfied and the spontaneous behavior always disappears. For Fig. A2.1B, the Hamilton's rule for the spontaneous behavior is not satisfied in the region below the dashed line ($br < c$), but it becomes satisfied in the region above it ($br > c$). When the system starts in the gray region, it converges to spontaneous behavior and maximum social efficiency $[(\varphi, y) = (1, 1)]$. Hence, to obtain fully efficient spontaneous behavior it is not required that the Hamilton's rule for the spontaneous behavior ($br > c$) is satisfied initially (Fig. A2.1). That is, if the spontaneous behavior φ is not favored but it is initially high enough so that the system falls in the gray area, the evolution of social efficiency y causes the spontaneous social behavior to eventually become favored as its

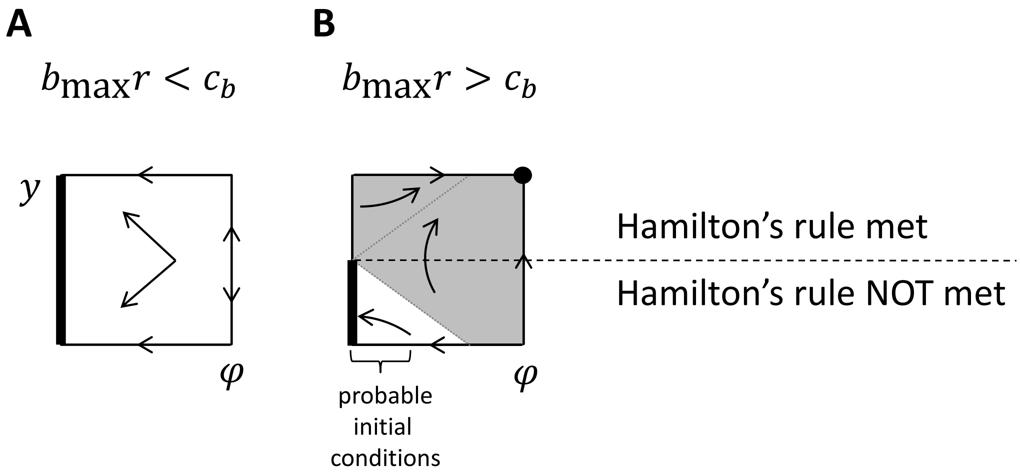


Figure A2.1: Coevolutionary dynamics of spontaneous behavior φ and social efficiency y. The arrows indicate the direction of change. The dashed line is the level $y^* = c_{\neg b}/S$ of social efficiency at which Hamilton's rule for spontaneous behavior φ becomes satisfied ($br = c$). Thick strokes indicate stable equilibria. In the gray region the system converges to spontaneous behavior. For initially small probability of spontaneous behavior, Hamilton's rule for the focal behavior must be satisfied initially.

Hamilton's rule becomes satisfied. The exact condition for the system to be in the gray area is given by inequality (A2.7a).

However, the term $\varphi S\sqrt{v_y/v_\varphi}$ in inequality (A2.7a) is proportional to φ. At the start of the coevolutionary process, the spontaneous behavior φ may often be generally close to zero in which case the relaxing term disappears. In this case, spontaneous behavior still requires its Hamilton's rule to be satisfied. This feature is reverted for manipulated behavior.

A2.3 Results for the manipulated behavior model

Dividing by p the system specified by eqs. (2.9) in the main text produces equations on q and y that are independent of p and hence can be studied independently. The analysis of the dynamics of the resulting system (q, y) is analogous to that for the system of spontaneous behavior (φ, y) (eqs. (A2.5)). This analysis shows that the system of resistance and social efficiency (q, y) is a mirror image of the system for spontaneous behavior (Fig. 2.3 in the main text). This system has two outcomes: either resistance becomes complete $[(q, y) = (1, y)]$, or fully efficient acquiescence is established $[(q, y) = (0, 1)]$. In particular, for Fig. 3A resistance is established, while for Fig. 3B fully efficient acquiescence is obtained in the gray region. As before, Hamilton's rule for acquiescence becomes satisfied above the dashed line ($br_{ts} > c$), but the evolution of social efficiency allows for convergence to acquiescence even if its Hamilton's rule is not satisfied (dark gray region). This requires that resistance is initially small so that the system falls within the dark gray region.

Proceeding as before, the reduced system (q, y) converges to acquiescence and maximum social efficiency $(q, y) = (0, 1)$ when

$$br_{ts} + (1-q)S\sqrt{v_y/v_q} > c \tag{A2.8a}$$

$$b_{\max} r_{ts} > c_b. \tag{A2.8b}$$

Inequalities (A2.8) have analogous interpretations to those of inequalities (A2.7). Thus, condition (A2.8b) allows the Hamilton's rule for acquiescence to be satisfied for some social efficiency, and condition (A2.8a) is a relaxed Hamilton's rule for acquiescence. However, the relaxing term $(1-q)S\sqrt{v_y/v_q}$ is now proportional to $1-q$ instead of φ, and hence such a term is not necessarily negligible if resistance is small. Initially small resistance may occur if the initial absence of manipulation causes an initial absence of selection pressure for resistance. When this is so, the Hamilton's rule for acquiescence does not need to be satisfied initially for highly efficient acquiescence to be obtained.

An important feature of the relaxed Hamilton's rule (A2.8a) is that it holds for any manipulation p, and hence its relaxing term is not the only one multiplied by p in the full system (p, q, y). Therefore, the relaxing term in (A2.8a) does not disappear for initially small p in the full system (p, q, y). This is illustrated in Fig. (2.4) in the main text. In the figure, solutions for the full system (p, q, y) are plotted. Condition (A2.8a) holds above the gray plane. No evolutionary path crosses the plane, which delimits the basin of attraction for any p. That is, the relaxing term $(1-q)S\sqrt{v_y/v_q}$ applies to the full system (p,q,y) and does not disappear for small p.

System (2.9) in the main text can also be divided by $1-q$ and the resulting system produces equations for p and y that are independent of q and can then be studied independently. The dynamics are as follows. When social efficiency is minimal $(y=0)$, the inclusive fitness effect for manipulation becomes $h_p = -c_{\neg b}r_{sm}$, the sign of which depends on the sign of the relatedness of manipulators toward subjects r_{sm}. When social efficiency is maximal $(y=1)$, the inclusive fitness effect for manipulation becomes $h_p = b_{\max}r_{tm} - c_b r_{sm}$. Therefore, when $r_{sm} > 0$ and $b_{\max}r_{tm} < c_b r_{sm}$, manipulation decreases for any social efficiency y, as illustrated in Fig. A2.2A,C. In contrast, when $r_{sm} > 0$ and $b_{\max}r_{tm} > c_b r_{sm}$, manipulation becomes favored at some social efficiency. Specifically, manipulation increases if $y > y_p^*$, where $y_p^* = c_{\neg b}/S_m$ is the social efficiency at which Hamilton's rule for manipulation becomes favored (i.e., $br_{tm} > cr_{sm}$). This defines an equilibrium at $(p,y) = (0,y_p^*)$ which, because of the linearity of the reduced system, defines the global dynamics. It is easy to verify that the equilibrium is a center if $S<0$ and a saddle if $S>0$. Hence, the dynamics are those in Fig. A2.2B,D. The basin of attraction towards the equilibrium $(p,y)=(1,1)$, calculated as before, is given by

$$y > y_p^* - p\sqrt{v_y k_s S/(v_p k_m S_m)}. \tag{A2.9}$$

For $r_{sm} < 0$, when social efficiency is minimal $(y=0)$, the inclusive fitness effect for manipulation is positive $(h_p = -c_{\neg b}r_{sm} > 0)$. Manipulation is thus favored even though subjects are entirely socially inefficient $(y=0)$. If the inclusive fitness effect of manipulation at maximal social efficiency is negative $(h_p = b_{\max}r_{tm} - c_b r_{sm} < 0)$, manipulation becomes disfavored at the social efficiency $y = y_p^*$. In this case, the equilibrium $(p,y) = (0,y_p^*)$ is a saddle if $S<0$ and a center if $S>0$, producing the dynamics in Fig. A2.3A,C. If the inclusive fitness effect of manipulation at maximal social efficiency is positive $(h_p = b_{\max}r_{tm} - c_b r_{sm} > 0)$. The resulting dynamics are those in Fig. A2.3B,D. These dynamics arise because the negative relatedness of manipulators toward

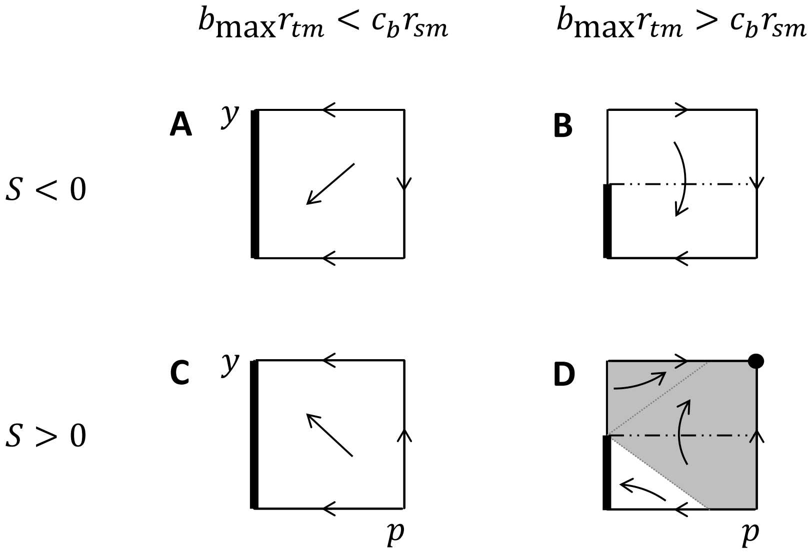


Figure A2.2: Coevolutionary dynamics of manipulation p and social efficiency y with positive relatedness of manipulators toward subjects of manipulation ($r_{sm} > 0$). See the legend of Fig. A2.1 for explanation. Here the dashed-and-dotted line corresponds to the critical social efficiency for manipulation $y_p^* = c_{\neg b}/S_m$ above which the Hamilton's rule for manipulation becomes satisfied (i.e., above which manipulation becomes favored). In the gray area the system converges to manipulation and full social efficiency.

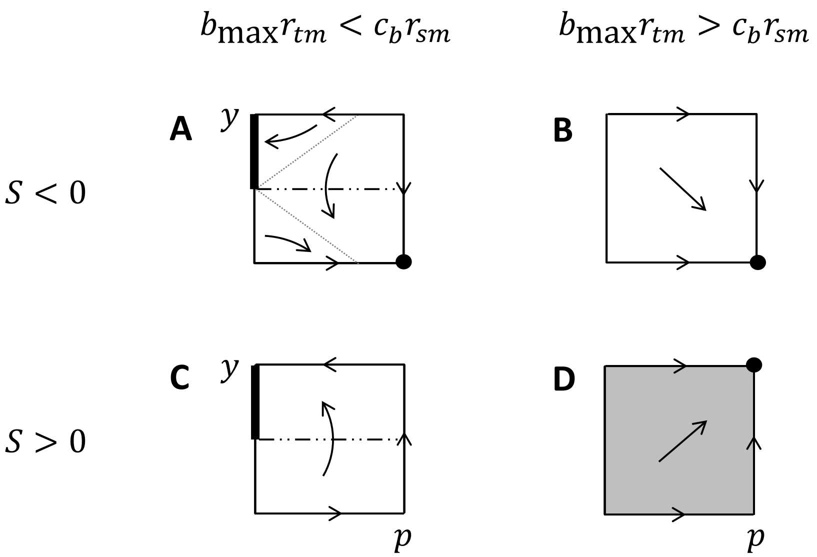


Figure A2.3: Coevolutionary dynamics of manipulation p and social efficiency y with negative relatedness of manipulators toward subjects of manipulation ($r_{sm} < 0$). See the legend of Fig. A2.2 for explanation. In the gray area, full manipulation and social efficiency is obtained.

subjects causes manipulation to be favored even if subjects are completely inefficient since manipulation harms the subjects (provided that $c_{\neg b} > 0$) (as in (González-Forero and Gavrilets, 2012)).

Hence, in the reduced system of manipulation and social efficiency (p, y), there are three possible outcomes: 1) no manipulation $[(p, y) = (0, y)]$, 2) full manipulation of inefficient behavior $[(p, y) = (1, 0)]$, or 3) full manipulation of fully efficient behavior $[(p, y) = (1, 1)]$. If relatedness of manipulators to subjects of manipulation is positive ($r_{sm} > 0$), the reduced system (p, y) converges to manipulation of efficient behavior $[(p, y) = (1, 1)]$ when

$$b_{\max} r_{tm} > c_b r_{sm} \tag{A2.10a}$$

$$b_{\max} r_{ts} > c_b - c_{\neg b} \tag{A2.10b}$$

$$b r_{tm} + p S_m \sqrt{v_y k_s S / (v_p k_m S_m)} > c r_{sm}. \tag{A2.10c}$$

Condition (A2.10a) guarantees that the Hamilton's rule for manipulation is satisfied for sufficiently high social efficiency (i.e., that $br_{tm} > cr_{sm}$ for some high y). Inequality (A2.10b) is the condition for social efficiency to be favored (i.e., $S > 0$). Condition (A2.10c) is a relaxed Hamilton's rule for manipulation. The evolutionary dynamics for the reduced system (p, y) when $r_{sm} > 0$ are illustrated in Fig. A2.2. Similarly to the results above, in Fig. A2.2A,C, manipulation cannot be favored. In Fig. A2.2B,D, the Hamilton's rule for manipulation is not satisfied below the dashed-and-dotted line (i.e., $br_{tm} < cr_{sm}$) but it is satisfied above the line ($br_{tm} > cr_{sm}$). The gray area gives the region for which manipulation of efficient behavior is obtained. As seen from both Fig. A2.2D and from the relaxing term of condition (A2.10c), if p is small initially, the relaxing term in the Hamilton's rule for manipulation is negligible.

The evolutionary dynamics of the system of manipulation and social efficiency (p, y) are different when manipulators' relatedness to subjects is negative ($r_{sm} < 0$). In this case, the reduced system (p, y) converges to manipulation of efficient behavior $(p, y) = (1, 1)$ in the same conditions (A2.10) except that condition (A2.10c) is not necessary. The dynamics when relatedness of manipulators toward subjects is negative are described in Fig. A2.3. Because of the negative relatedness of manipulators toward subjects, for Fig. A2.3B,D the Hamilton's rule for manipulation holds for any social efficiency y. However, for Fig. A2.3A,C, manipulation becomes disfavored above the dashed-and-dotted line. The reason is that sufficiently high social efficiency can cause the Hamilton's rule for manipulation to be unsatisfied due to either high harming of targets that are related to manipulators or high benefits to targets that are negatively related to manipulators. The outcome of full manipulation of inefficient behavior [$(p, y) = (1, 0)$; outcome 2 above] is thus made possible by $r_{sm} < 0$. The case in which $r_{sm} = 0$ is captured by Fig. A2.3 by setting $y_p^* = 0$ in all panels. In such a case, the outcomes for Fig. A2.3A-B are 1) no manipulation [$(p, y) = (0, y)$] or 2') no social efficiency [$(p, y) = (p, 0)$], while the outcomes for Fig. A2.3C-D remain the same. Hence, the conditions for the outcome of manipulation of efficient behavior given above still apply.

Chapter 3

Queen specialization eliminates manipulation conflict

The following chapter is a reprint of a paper to be submitted for publication.

González-Forero M. Queen specialization eliminates manipulation conflict. To be submitted.

Abstract

Advanced eusociality is a quintessential form of sociality (Wheeler, 1911; Hölldobler and Wilson, 2009). Advanced eusocial colonies are composed of up to millions of members produced by a single or relatively few individuals (Wilson, 1971; Seeley, 1995). Colony members divide labor sometimes through extreme morphological specialization while displaying negligible conflict (Seeley, 2010; Bignell et al., 2011). The evolution of advanced eusociality is currently explained by kin-selected altruism (Hamilton, 1964b; Boomsma, 2009) compounded with policing (Ratnieks, 1988; Frank, 1995) and colony efficiency (Oster and Wilson, 1978; Ratnieks and Helanterä, 2009). A classic alternative for the evolution of eusociality is parental manipulation (Alexander, 1974; Michener and Brothers, 1974), but it is thought to be of little relevance to advanced eusociality (Keller and Nonacs, 1993; Bourke and Franks, 1995). Here I show that a key factor of advanced eusociality, namely queen specialization, can be more likely to stem from maternal manipulation than from altruism. In particular, maternal manipulation of offspring social behavior causes the evolution of queen specialization (decreased maternal care and increased maternal fertility) which eliminates offspring resistance to manipulation. That is, queen specialization eliminates the mother-offspring conflict created by manipulation, which in principle may allow the mother to induce helping by non-coercive means such as pheromones. I also show that queen specialization can evolve under less stringent conditions with manipulation than purely as a result of altruism. Recent work (González-Forero, 2013) has found that worker specialization can also evolve under less stringent conditions via manipulation than via altruism. Together, these results indicate that defining aspects of advanced eusociality (queen and worker specialization, queen pheromones, large colony sizes, and negligible conflict) may simultaneously be better explained by maternal manipulation than by altruism. Thus, some of the quintessential examples of sociality may be particularly likely to occur via the long-neglected alternative of manipulation.

3.1 Introduction

Eusociality involves groups of individuals where some group members do not reproduce and instead help group mates do so (Michener, 1969; Wilson, 1971). Eusociality can be subdivided into so-called primitive and advanced (Michener, 1969; Wilson, 1971). Primitive eusociality involves relatively small colonies (up to hundreds of members) in which the division of reproductive labor is primarily behavioral rather than morphological, and conflict among members is substantial. In contrast, advanced eusociality comprises relatively large colonies (up to millions of members) in which the division of reproductive labor can be morphological and permanent, and in which conflict among members is remarkably small. A currently prominent explanation for the evolution of advanced eusociality can be summarized as follows: 1) Selection initially favors altruism towards sufficiently close kin under certain ecological conditions (Hamilton, 1964b; Boomsma, 2009). 2) Altruists become highly specialized due to kin or group selection for colony-level efficiency (Oster and Wilson, 1978). Specialization causes altruists to become unable to mate (Oster and Wilson, 1978). 3) Despite their inability to mate, conflict remains favoring hymenopteran (e.g., wasps, bees, and ants) workers to produce male offspring asexually (Trivers and Hare, 1976). 4) Queens are then favored to mate multiply (polyandry) as this increases colony productivity (Mattila and Seeley, 2007), partly because workers become favored to police conflicting mates (Ratnieks, 1988). That is, with polyandry, workers become favored to destroy other workers' offspring rather than attempt to become reproductively independent given that they are already unable to mate (Ratnieks and Helanterä, 2009). As a result, policing diminishes conflict and enhances the levels of cooperation within the colony (Frank, 1995), thereby yielding advanced eusociality.

Two key difficulties can be identified with this explanation. First, objections can be raised regarding the purported inability of workers to regain their ability to mate. Second, this explanation applies only to hymenopteran advanced eusociality, which involves haplodiploid genetics where males are produced asexually. However, advanced eusociality also occurs in termites (Bignell et al., 2011) and to some extent in naked mole rats (Sherman et al., 1991), which have diploid genetics. In principle, the selection pressures that produced advanced eusociality in diploids might also have been relevant for haplodiploids. This point raises the question of whether advanced eusociality actually needed policing even for hymenoptera.

Here I develop a different pathway to advanced eusociality, in particular via maternal manipulation. Maternal manipulation is a classic alternative to altruism for the evolution of eusociality (Alexander, 1974; Michener and Brothers, 1974). The hypothesis states that, instead of helpers being favored to help spontaneously (hereafter, "altruism"), mothers manipulate some of their offspring to help raise their siblings (Alexander, 1974; Michener and Brothers, 1974). However, this hypothesis has remained neglected, partly because manipulation can promote the evolution of resistance to manipulation (Trivers, 1974; Trivers and Hare, 1976; Keller and Nonacs, 1993). Acquiescence (i.e., no resistance) to manipulation has recently been found to evolve under less stringent conditions than those required for altruism (González-Forero and Gavrilets, 2012; González-Forero, 2013). The social behaviors obtained via manipulation appear consistent with both primitive eusociality (González-Forero and Gavrilets, 2012) and worker specialization in advanced eusociality (González-Forero, 2013). In both cases, the initial point is a population where the only social behavior present is parental care. Here I show how maternal manipulation can produce specialized queens as in advanced eusociality, also from an initial population with only parental care. Despite the possible evolution of resistance to manipulation, acquiescence to manipulation is obtained because of the evolution of maternal exploitation. That is, once the mother has help available due to manipulation, she becomes a better exploiter of this help by increasing her fertility and decreasing her maternal care. The latter two are defining features of the highly specialized queens in advanced eusociality. This process causes selection for resistance to manipulation to disappear. In addition, queen specialization can evolve and be stable via manipulation under less stringent conditions than those required via altruism.

The key factors yielding these results are that the benefit to the recipients of help depends on the recipient's condition, and that an individual's condition is under maternal influence. I assume that poor-condition individuals get larger benefits from receiving the same amount of help than good-condition individuals (West Eberhard, 1975). Hence, when a manipulating mother has help from manipulated offspring, she can become favored to decrease the maternal care to the offspring who will instead be cared for by helpers. The decrease in maternal care makes the to-be-helped offspring be in poor-condition at the time of receiving help. This can yield sufficiently large average benefits to the recipients of help, so that helpers stop being selected to resist manipulation. That is, Hamilton's rule for acquiescence becomes satisfied when the mother becomes a sufficiently good exploiter despite Hamilton's rule not being satisfied at the start of the process. I obtain these results using a set of simple mathematical models.

3.2 Model

Consider a population where mothers produce two subsequent broods (Fig. 3.1). One or both parents provide parental care to offspring. Adult offspring disperse from the maternal site, mate, and start a new site. With probability p, mothers manipulate first-brood offspring to stay in the maternal site as adults. Manipulation may occur, for example, by disrupting offspring's development by feeding them poorly (Brand and Chapuisat, 2012; Tibbetts et al., 2013). Manipulated offspring resist manipulation with probability q in which case they disperse without delay. Alternatively, manipulated offspring acquiesce to manipulation with probability $1 - q$ in which case they stay as adults in the maternal site. Acquiescing offspring pay the cost of acquiescence c. In addition, acquiescing offspring express parental care in the maternal site, giving a fitness benefit b to second-brood offspring (see ref. (González-Forero, 2013) for the conditions for which such helping is selected).

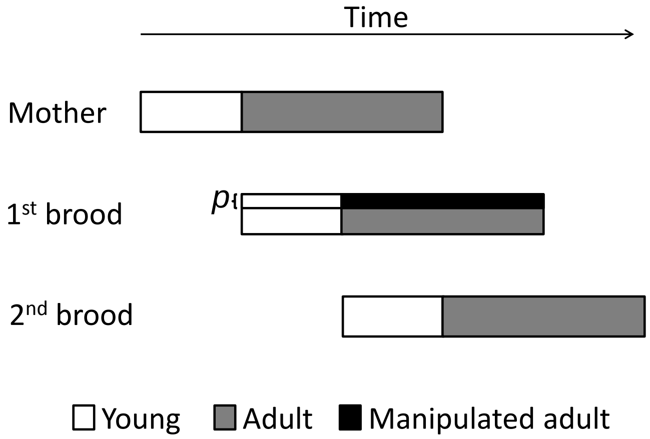


Figure 3.1: Life cycle. The mother produces two subsequent broods. When individuals are young (white) they stay in the maternal site, but disperse as adults (gray). The mother manipulates a fraction p of the first brood to stay as adults.

Mothers provide maternal care to a fraction z of their second-brood offspring, hence paying the cost c_c of providing maternal care. A second-brood individual receiving maternal care is in good condition at the time in which it receives help from first-brood offspring. Alternatively, a second-brood individual not receiving maternal care is in poor condition when it receives help. Poor-condition individuals pay the cost of not receiving maternal care $c_{\neg c}$. A second-brood individual in good (poor) condition receives a benefit b_g (b_p) when helped by a random first-brood individual. I assume $b_p > b_g$. Thus, an acquiescing individual provides a benefit to a random second-brood offspring of

$$b = zb_g + (1-z)b_p. \tag{3.1}$$

Although poor-condition individuals benefit more from receiving the same amount of help than good-condition individuals, it is possible that poor-condition individuals are costlier to raise if they demand more care. The cost of acquiescence then depends on whether recipients are in good or poor condition. Hence, the cost of acquiescence is

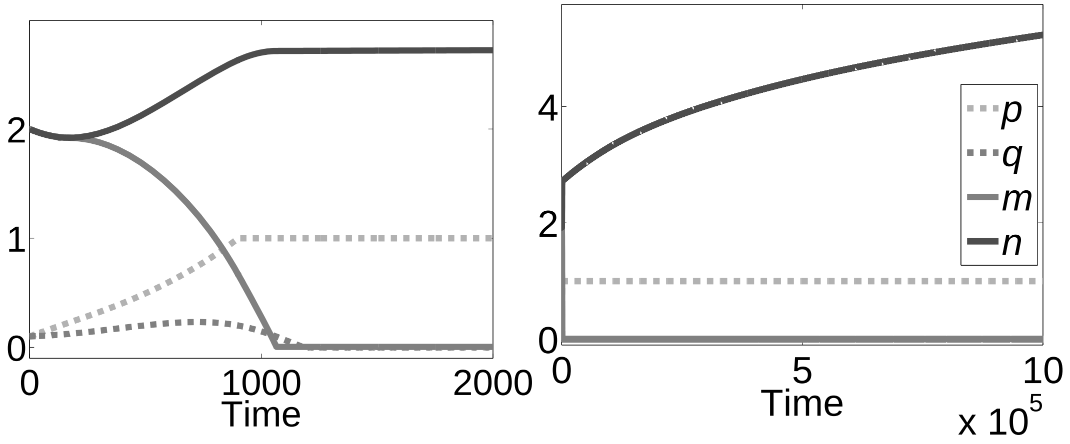
$$c = zc_g + (1-z)c_p, \tag{3.2}$$

where c_g (c_p) is the cost of acquiescence due to helping recipients in good (poor) condition. I study the coevolution of maternal manipulation p, offspring resistance q, and the probability z that second-brood offspring receive maternal care. The probability z is the ratio of the number m of second-brood offspring the mother provides care to (hereafter, "maternal care") and the number n of second-brood offspring (hereafter, "maternal fertility"). I assume offspring resistance q to be under offspring control, and the remaining variables (maternal manipulation p, care m, and fertility n) to be under maternal control. These considerations yield an expression for the fitness of a random individual in the population, which specifies the coevolutionary dynamics (see Methods Summary).

3.3 Results

An illustration of the resulting coevolutionary dynamics is given in Fig. 3.2. The process shown in the figure is the following. Once there exists manipulation and before resistance to manipulation is complete, the mother has help available. She is then selected to reduce her maternal care and increase her fertility. This yields an increasing proportion of poor-condition recipients of help, which causes the benefit b to increase up to a point where Hamilton's rule for acquiescence becomes satisfied. As a result, resistance becomes selected against and in the end, the mother manipulates her entire first brood, all showing no resistance. The second brood is at this point raised only by the first brood. In addition, at the end of the process, the mother is maximally fertile in terms of the number of second-brood offspring. Notice that the evolution of maternal fertility in terms of her first-brood offspring is not modeled here explicitly. For simplicity, I refer to the outcome of manipulation, acquiescence, no maternal care and maximum fertility in terms of second-brood offspring $(p,q,m,n) = (1,0,0,n_{\max})$ as queen specialization via maternal manipulation.

Simple conditions for this outcome can be obtained (see Supplementary Information). To simplify the analysis, I assume the cost to the mother for providing maternal



(a) **(b)**

Figure 3.2: Conflict resolution with the evolution of maternal exploitation. Numerical solutions for a given set of initial conditions. **a**, Resistance q initially increases but is later eliminated by the evolution of reduced maternal care m and increased maternal fertility n. In the end, there is no mother-offspring conflict. The time span is 2000 generations. **b**, The same scenario is shown but the time span is 10^6 generations. Maternal fertility increases up to its maximum $n_{\max}$ at the decreasing rate of m/n^2. For both panels the parameter values are: $v_p = v_q = 0.01$, $v_m = v_n = 0.1$ (v_i: additive genetic variance of trait i), $k_m = k_1 = 1/3$, $r_m = r = 1/2$ (r_m, r: life-for-life relatedness (Hamilton, 1972; Bulmer, 1994) of mother to offspring and of first-brood offspring to second-brood offspring respectively), $b_p = 2.5$, $b_g = 1.5$, $n_{\max} = 10$, $c_p = c_g = 1$, $c_c = 0.4$, and $c_{\neg c} = 1$.

care is approximately the same as the cost to offspring for not receiving maternal care weighted by the life-for-life relatedness (Hamilton, 1972; Bulmer, 1994) of mother to offspring (i.e., $c_c \approx r_m c_{\neg c}$). In such a case, when manipulation and resistance are initially small, queen specialization via maternal manipulation is obtained if at the start of the evolutionary process the following four conditions hold:

$$b_p r > c_p \tag{3.3a}$$

$$b_p - b_g > c_p - c_g \tag{3.3b}$$

$$b > c \tag{3.3c}$$

$$br + \frac{A}{n} > c, \tag{3.3d}$$

where A measures the increase in selection for acquiescence as maternal care decreases (defined in the Methods Summary). Condition (3.3a) states that acquiescence must be favored for poor-condition recipients of help; condition (3.3b) that the probability z of giving maternal care must be favored to decrease if the mother has some help; condition (3.3c) that maternal manipulation must be favored; and condition (3.3d) that acquiescence can become favored as a result of the evolution of maternal exploitation. That is, Hamilton's rule for acquiescence (i.e., $br > c$) need not be initially satisfied.

Analogous conditions can be obtained for queen specialization via altruism (i.e., when first-brood offspring stay in the maternal nest without being manipulated by the mother; the conditions for queen specialization via altruism are inequalities (S8) in SI). If the probability of expressing altruism is initially small, then queen specialization via manipulation can be obtained under less stringent conditions than via altruism if at the start of the process

$$0 < c - br < \frac{A}{n}. \tag{3.4}$$

This advantage of queen specialization via manipulation is illustrated in Fig. 3.3. Fig. 3.3 shows that in the outcome of queen specialization via maternal manipulation, Hamilton's rule for acquiescence is satisfied. That is, there is not mother-offspring conflict in the end. However, as shown in Fig. 3.3, Hamilton's rule need not be satisfied at the start of the process. The rule can become satisfied as maternal care decreases and maternal fertility increases, which eliminates the mother-offspring conflict. Instead of Hamilton's rule, the necessary condition for queen specialization via maternal manipulation is a relaxed Hamilton's rule (inequality (S50e) in SI) that, when resistance probability is initially small, reduces to condition (3.3d).

3.4 Discussion

These results show how queen specialization can be obtained under less stringent conditions (smaller b/c ratios) via maternal manipulation than via offspring altruism. This occurs because of the evolution of maternal exploitation (measured by A/n; see condition (3.3d)). Offspring can eventually become favored to acquiesce to manipulation without the need of resistance costs (González-Forero and Gavrilets, 2012) or the evolution of helping efficiency (González-Forero, 2013). Because resistance costs are not necessary, manipulation may occur via non-coercive means, for instance, via pheromones. Queen specialization via maternal manipulation yields maternally-induced workers with no conflict with the mother: both mother and helping offspring agree on the latter helping status despite the latter not being initially selected to help. As with the evolution of helping efficiency (González-Forero, 2013), the evolution of maternal exploitation can cause the evolution of offspring consent to maternal manipulation. Queen specialization and socially induced, yet non-conflicting, workers are consistent with key features of advanced eusociality (Hölldobler and Wilson, 2009). A remaining defining feature of advanced eusociality, namely worker specialization, can also be obtained under less stringent conditions via manipulation than via altruism (González-Forero, 2013).

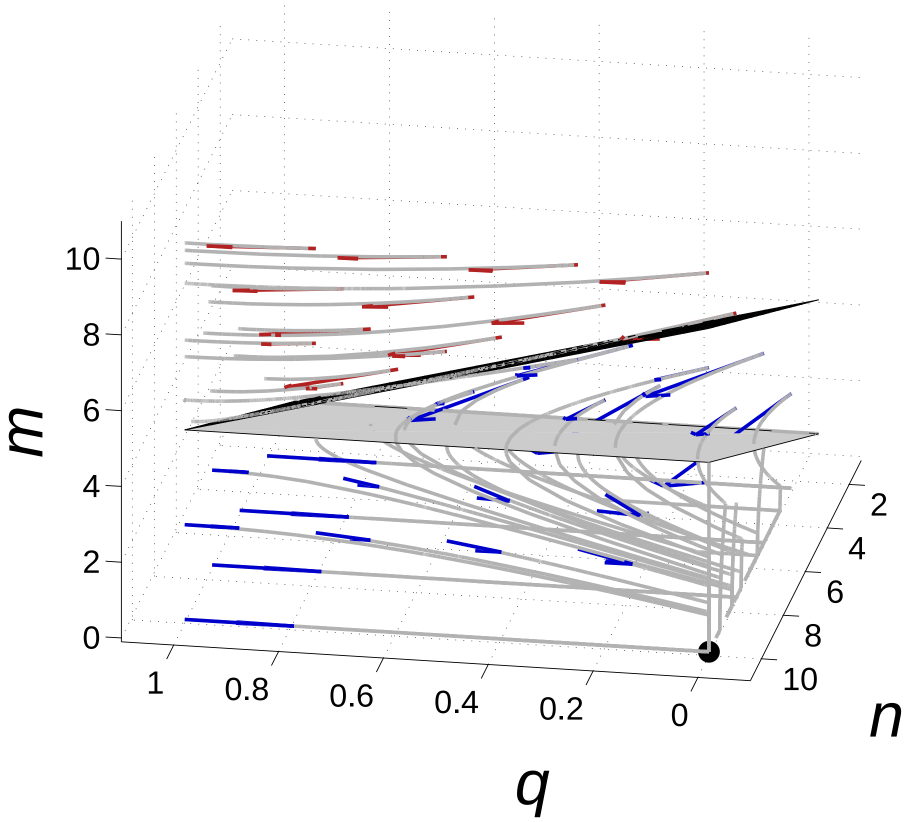


Figure 3.3: Relaxed Hamilton's rule due to the evolution of maternal exploitation. Evolutionary trajectories (gray lines; numerical solutions for system (A3.28)) are shown for different initial conditions for the complete system (p, q, m, n). Only three dimensions are plotted (q, m, n). Arrows indicate the direction of change. Hamilton's rule for acquiescence is satisfied (unsatisfied) in the region below (above) the gray plane. A relaxed Hamilton's rule for acquiescence (inequality (S50e) in SI) is satisfied (unsatisfied) below (above) the black plane. Trajectories starting below the black plane (blue arrows) converge to queen specialization $(p, q, m, n) = (1, 0, 0, n_{\max})$ (black dot), otherwise (red arrows) they converge to full resistance $(p, q, m, n) = (p, 1, m, n)$. Hence, Hamilton's rule is not necessary for convergence to queen specialization via manipulation if resistance is initially incomplete. Parameter values are: $v_p = v_q = 0.01$, $v_m = v_n = 0.1$, $k_m = k_1 = 1/3$, $r_m = r = 1/2$, $b_p = 2.5$, $b_g = 1.5$, $c_p = c_g = 1$, $c_c = 0.5$, $c_{\neg c} = 1$, $n_{\max} = 10$ and the time span is 10^6. The initial manipulation probability is $p(0) = 0.1$.

Maternal manipulation may thus account for advanced eusociality in both diploids (e.g., termites) and haplodiploids (e.g., wasps, bees, and ants). In the mechanism developed here, polyandry is not a cause of advanced eusociality, but may instead be a consequence. For instance, as high benefits to recipients evolve as a result of maternal exploitation or helping efficiency (González-Forero, 2013), the lower relatedness caused by polyandry still allows for acquiescence to be favored. The evolution of polyandry, for example favored because of benefits to the mother (Mattila and Seeley, 2007), need not then disrupt sufficiently advanced eusociality. The results presented here offer a novel mechanism for the origin of advanced eusociality which, as shown here, may be comparatively particularly powerful.

Methods Summary

For simplicity, I assume no costs of manipulation or of resistance to manipulation. The baseline fitness is 1. The cost to a mother for providing maternal care is c_c. The fitness payoff to a mother is

$$\begin{aligned} w_m &= z(1-c_c)+(1-z) \\ &= 1-c_c z. \end{aligned} \tag{3.5a}$$

The fitness payoff to first-brood offspring is

$$\begin{aligned} w_1 &= p(1-q)(1-c)+pq+(1-p) \\ &= 1-cp(1-q). \end{aligned} \tag{3.5b}$$

The average resistance probability among the first-brood offspring of a mother is Q. The cost to second-brood offspring for not receiving maternal care is $c_{\neg c}$. The fitness payoff to second-brood offspring is

$$\begin{aligned} w_2 &= z[p(1-Q)(1+b_g) + pQ + (1-p)] \\ &\quad + (1-z)[p(1-Q)(1-c_{\neg c} + b_p) + pQ(1-c_{\neg c}) + (1-p)(1-c_{\neg c})] \\ &= 1 + bp(1-Q) - (1-z)c_{\neg c}. \end{aligned} \tag{3.5c}$$

The fitness of a random individual is $w = \sum k_j w_j$ where k_j is the reproductive value of state j $(= m, 1, 2$ for mother, first-brood offspring, and second-brood offspring respectively) (Taylor, 1990; Frank, 1998). That is,

$$w = 1 - k_m c_c z - k_1 cp(1-q) + k_2[bp(1-Q) - c_{\neg c}(1-z)]. \tag{3.6}$$

This expression yields the dynamic equations derived in §2 of the Supplementary Information.

The quantity A involved in condition (3.3d) is

$$A = \sqrt{\frac{k_m r_m H_m}{k_1 H} \frac{v_m H^2 + v_n H_0^2}{v_q}}, \tag{3.7a}$$

where H_0 measures selection for acquiescence in the absence of maternal care, H is the reduction in H_0 when there is full maternal care, and H_m measures the increase in selection for manipulation as maternal care decreases. The latter three terms are given by:

$$H_0 = b_p r - c_p \tag{3.7b}$$

$$H = (b_p - b_g)r - (c_p - c_g) \tag{3.7c}$$

$$H_m = b_p - b_g - (c_p - c_g). \tag{3.7d}$$

If $H < 0$, then condition (3.3d) implies $br > c$ and in such case condition (3.3d) is unnecessary.

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A3.1 Supplementary Methods

A3.2 Spontaneous helping (altruism)

In this section I analyze a model where helping is only under control of the helper. I refer to this case as spontaneous helping. Let x be the probability that a first-brood individual stays as an adult in the maternal site (i.e., the individual's probability of spontaneous helping or altruism). Assume x to be under the control of the first-brood individual. Hence, the fitnesses of mother (w_m), first-brood offspring (w_1) and second-brood offspring (w_2) take analogous forms to eqs. (5) in the main text. They are

$$\begin{aligned} w_m &= z(1-c_c)+(1-z) \\ &= 1-c_c z, \qquad \text{(A3.1a)} \\ w_1 &= x(1-c)+(1-x) \\ &= 1-cx, \qquad \text{(A3.1b)} \\ w_2 &= z[X(1+b_g)+(1-X)] \\ &\quad +(1-z)[X(1-c_{\neg c}+b_p)+(1-X)(1-c_{\neg c})] \\ &= 1+bX-(1-z)c_{\neg c}, \qquad \text{(A3.1c)} \end{aligned}$$

where X is the average probability of spontaneous helping among first-brood offspring. The fitness of a random individual ($w=\sum k_j w_j$) is thus

$$w = 1-k_m c_c z - k_1 c x + k_2[bX - c_{\neg c}(1-z)]. \qquad \text{(A3.2)}$$

Let v_i be the additive genetic variance of trait i $(= x, z)$, and g_i the breeding value for trait i in the actor (i.e., the individual controlling trait i). Hence, assuming that association between the traits is negligible, the evolutionary change in trait i can be approximated by $di/dt = v_i \partial w/\partial g_i$ (Frank, 1998).

A3.2.1 Maternal care probability

In this subsection I do not specify the components of the maternal care probability z, which allows for a simpler analysis. This yields that the evolutionary change in trait i is $di/dt = v_i k_{\text{act}} h_i$ where k_{act} is the class reproductive value of actors (i.e., first-brood offspring for spontaneous helping x and mothers for the maternal probability z) and h_i is the inclusive fitness effect of trait i on actors. Specifically,

$$\begin{aligned} h_x &= \quad br - c \quad &&= H_0 - zH && \text{(A3.3a)} \\ h_z &= \quad -\{r_m x[b_p - b_g - (c_p - c_g)] + c_c - r_m c_{\neg c}\} \quad &&= -(r_m x H_m + c_c - r_m c_{\neg c}), && \text{(A3.3b)} \end{aligned}$$

where r_m is the life-for-life relatedness of mother to offspring. For simplicity, I will assume throughout that the mother is equally related to both her first- and second-brood offspring. r_m is defined as $\rho_m k_i / k_m$ for both first- and second-brood offspring (i.e., $i = 1, 2$), where $\rho_m = dz/dg_z$ is the regression relatedness of mother to first- and second-brood offspring. H_0, H and H_m are defined in the main text. I will make the simplifying assumption throughout that $c_c \approx r_m c_{\neg c}$. Hence, the system defined by (A3.3) has an equilibrium in $(x, z) = (0, z^*)$, where $z^* = H_0/H$. I also let $r \leq 1$; hence, $H_m > H$.

The dynamics are then determined by the signs of H_0, $H_0 - H$, and H_m. There are four cases:

- If $H_0 < 0$ and $H_0 - H < 0$, then spontaneous helping always decreases. The maternal care probability increases or decreases depending on the sign of H_m. In any case, the outcome is no spontaneous helping $[(x, z) = (0, z)]$.

- If $H_0 < 0$ and $H_0 - H > 0$, then spontaneous helping decreases for a small probability of maternal care, but increases for large probability of maternal care. There are two subcases: 1) if $H_m > 0$, then maternal care probability decreases and the outcome is no spontaneous helping $[(x, z) = (0, z)$ for $z < z^*]$. 2) If $H_m < 0$, then maternal care probability increases and the outcome is either no spontaneous helping $[(x, z) = (0, z)$ for $z < z^*]$ if maternal care probability is initially sufficiently small, or full spontaneous helping and full maternal care probability $[(x,z)=(1,1)]$ if maternal care probability is initially sufficiently large.

- If $H_0>0$ and $H_0-H<0$, then spontaneous helping increases for a small probability of maternal care and decreases for large probability of maternal care. Since necessarily $H>0$, then $H_m>0$. Therefore, maternal care probability decreases and the outcome is either no spontaneous helping $[(x,z)=(0,z)$ for $z>z^*]$ if maternal care probability is initially sufficiently large, or full spontaneous helping and zero maternal care probability $[(x,z)=(1,0)]$ if maternal care probability is initially sufficiently small.
- If $H_0>0$ and $H_0-H>0$, then spontaneous helping always increases. The outcome is full spontaneous helping and either full maternal care probability $[(x,z)=(1,1)]$ or zero maternal care probability $[(x,z)=(1,0)]$ depending on the sign of H_m.

I here am interested in the outcome of spontaneous helping with zero maternal care probability $[(x,z)=(1,0)]$. For reasons that become clear later, I refer to this outcome as queen specialization via spontaneous helping. This outcome can be obtained in the third case above or in the fourth case when $H_m>0$. The dynamics of the third case are in Fig. A3.1. The line in Fig. A3.1 that delimits the basin of attraction to the queen specialization outcome is given by the system's eigenvector with negative eigenvalue (this can be easily seen by solving for x and z in the system defined by (A3.3) and then determining the solutions that cross the equilibrium $(x,z)=(0,z^*)$). That is, the basin of attraction is specified by the line with positive slope with respect to spontaneous helping shown in Fig. A3.1. The eigenvectors of system (A3.3) are proportional to

$$\mathbf{v}=\left(\pm\sqrt{\frac{v_x k_1 H}{v_z k_m r_m H_m}},1\right)^T. \tag{A3.4}$$

Hence, the slopes of the lines defined by these eigenvectors are $\pm\sqrt{\frac{v_z k_m r_m H_m}{v_x k_1 H}}$. The intercept of these lines at $x=0$ is z^*. Because the basin of attraction (gray area in Fig.

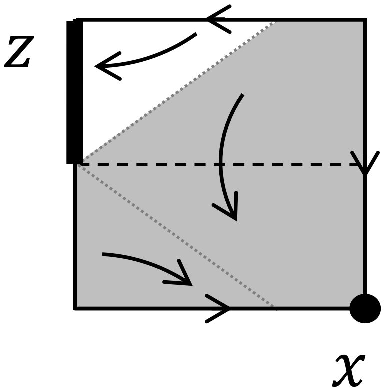

Figure A3.1: Dynamics of queen specialization via spontaneous helping. The dynamics shown are for the case in which $H_0 > 0$, $H_0 - H < 0$, and $H_m > 0$. The arrows indicate the direction of evolutionary change. The dashed line is the critical maternal care probability z^* at which selection for spontaneous helping changes. Thick strokes indicate stable equilibria. When the population starts in the gray area it evolves to queen specialization via spontaneous helping $[(x,z) = (1,0)]$.

A3.1) lies below the line with the positive slope with such an intercept, then convergence to queen specialization via spontaneous helping requires that the initial conditions satisfy

$$z < z^* + x\frac{E_z}{H}. \tag{A3.5}$$

where

$$E_z = \sqrt{\frac{v_z H^2}{v_x}\frac{k_m r_m H_m}{k_1 H}}. \tag{A3.6}$$

Since $z^* = H_0/H$, rearranging this inequality yields

$$br + xE_z > c. \tag{A3.7}$$

If initially the probability of spontaneous helping is small, inequality (A3.7) reduces to $br > c$.

Therefore, from the third and fourth cases above, queen specialization under spontaneous helping is obtained when

$$b_p r > c_p \tag{A3.8a}$$

$$b_p - b_g > c_p - c_g \tag{A3.8b}$$

$$br + xE_z > c. \tag{A3.8c}$$

If $H < 0$, then condition (A3.8c) is unnecessary. Inequality (A3.8a) states that Hamilton's rule for helping must be satisfied for poor-condition recipients. Inequality (A3.8b) states that mothers must be favored to decrease their probability of providing maternal care. The third condition (A3.8c) is a relaxed Hamilton's rule that reduces to Hamilton's rule for an initially small probability of spontaneous helping.

A3.2.2 Maternal care and maternal fertility

In this subsection, I express the maternal care probability in terms of the number of second-brood offspring, n (hereafter, maternal fertility), and the number of which the mother provides maternal care to, m (hereafter, maternal care). Hence, $z = m/n$. I assume that both maternal care m and maternal fertility n are under maternal control. This slight change will yield the same results as §A3.2.1, but the speed of evolutionary change is affected. This will only be of relevance for maternally manipulated helping and hence, this subsection is primarily to illustrate the method that will be used in the slightly more complex model of maternally manipulated helping.

Substituting $z = m/n$ in eq. (A3.2) yields a three-dimensional system $di/dt = v_i k_{\text{act}} h_i$ $(i = x, m, n)$ where

$$h_x = \quad br - c \quad = H_0 - zH \tag{A3.9a}$$

$$h_m = \quad -\frac{1}{n}\{r_m x[b_p - b_g - (c_p - c_g)] + c_c - r_m c_{\neg c}\} \quad = -\frac{1}{n}(r_m x H_m + c_c - r_m c_{\neg c}) \tag{A3.9b}$$

$$h_n = \quad \frac{m}{n^2}\{r_m x[b_p - b_g - (c_p - c_g)] + c_c - r_m c_{\neg c}\} \quad = \frac{m}{n^2}(r_m x H_m + c_c - r_m c_{\neg c}). \tag{A3.9c}$$

Here r_m is similarly $\rho_m k_i / k_m$ $(i = 1, 2)$ for $\rho_m = dz/dg_m = dz/dg_n$. Assuming that $c_c \approx r_m c_{\neg c}$, this system has an equilibrium line in $(x, m, n) = (0, m^*, n)$, where $m^* = nH_0/H$.

The same four cases as before are also obtained here:

- If $H_0 < 0$ and $H_0 - H < 0$, then spontaneous helping always decreases. Maternal care m and fertility n increase or decrease depending on the sign of H_m. The outcome is no spontaneous helping $[(x, m, n) = (0, m, n)]$.

- If $H_0 < 0$ and $H_0 - H > 0$, then spontaneous helping decreases for a small probability of maternal care, but increases for large probability of maternal care. There are two subcases: 1) if $H_m > 0$, then maternal care decreases and maternal fertility increases, so the outcome is no spontaneous helping $[(x, m, n) = (0, m, n)$ for $m < m^*]$. 2) If $H_m < 0$, then maternal care increases and maternal fertility decreases, so the outcome is either no spontaneous helping $[(x, m, n) = (0, m, n)$ for $m < m^*]$ if maternal care is initially sufficiently small, or full spontaneous helping, full maternal care and minimal fertility $[(x, m, n) = (1, 1, 1)]$ if maternal care is initially sufficiently large (I take minimal fertility to be one because benefits and costs of helping are not defined if there are no recipients).

- If $H_0 > 0$ and $H_0 - H < 0$, then spontaneous helping increases for a small probability of maternal care and decreases for large probability of maternal care. Since $H_m > 0$, then maternal care decreases and maternal fertility increases, so the outcome is either no spontaneous helping $[(x,m,n) = (0,m,n)$ for $m > m^*]$ if maternal care is initially sufficiently large, or full spontaneous helping, zero maternal care, and maximum fertility $[(x,m,n) = (1,0,n_{\max})]$ if maternal care is initially sufficiently small.

- If $H_0 > 0$ and $H_0 - H > 0$, then spontaneous helping always increases. The outcome is full spontaneous helping and either full maternal care and minimal fertility $[(x,m,n) = (1,1,1)]$ or zero maternal care and maximum fertility $[(x,m,n) = (1,0,n_{\max})]$ depending on the sign of H_m.

As in the previous section, queen specialization $[(x,m,n) = (1,0,n_{\max})]$ can be obtained in the third case or in the fourth case when $H_m > 0$. The dynamics of the third case are as in Fig. A3.1, replacing z by m and with the n axis projecting out of the page. The intercept of the dashed line in Fig. A3.1 increases with n in this three-dimensional extension. The line that delimits the basin of attraction toward queen specialization in the two-dimensional representation is a plane in the full three-dimensional system. This plane is defined by the dominant eigenvectors with origin along the equilibrium line $(x,m,n) = (0,m^*,n)$ defining lines with positive slope with respect to spontaneous helping x.

I obtain this plane as follows. The Jacobian of the system evaluated at the equilibrium line is

$$\mathbf{J}|_{x=0,m=m^*} = \begin{pmatrix} 0 & -v_x k_1 \frac{1}{n} H & v_x k_1 \frac{1}{n} H_0 \\ -v_m k_m r_m \frac{1}{n} H_m & 0 & 0 \\ v_n k_m r_m \frac{1}{n} \frac{H_0}{H} H_m & 0 & 0 \end{pmatrix}. \tag{A3.10}$$

Then, the dominant eigenvectors of the Jacobian matrix are proportional to

$$\mathbf{v}_1 = (U, -V, 1)^T, \tag{A3.11}$$

where

$$U = \mp\sqrt{\frac{v_x}{v_n}\frac{k_1 H}{k_m r_m H_m}\left[1+\frac{v_m}{v_n}\left(\frac{H}{H_0}\right)^2\right]} \tag{A3.12a}$$

$$V = \frac{v_m}{v_n}\frac{H}{H_0}. \tag{A3.12b}$$

These eigenvectors have origin along the equilibrium line $(x, m, n) = (0, m^*, n)$ which defines two planes that govern the dynamics around the equilibrium line. Equations for such planes can be obtained by determining another pair of vectors in the plane that are not parallel to $\mathbf{v}_1$; for example,

$$\mathbf{v}_2 = (U, \frac{H_0}{H} - V, 2)^T. \tag{A3.13}$$

$\mathbf{v}_2$ are found by shifting the origin of the eigenvectors defined by $\mathbf{v}_1$ by an amount of 1 along the n axis, which corresponds to an increment of $m^* \mid_{n=1} = H_0/H$ along the m axis. A normal vector to the planes containing $\mathbf{v}_1$ and $\mathbf{v}_2$ specifies the plane equation. The vectors

$$\mathbf{N} = \mathbf{v}_1 \times \mathbf{v}_2 = (-V - \frac{H_0}{H}, -U, U\frac{H_0}{H})^T \tag{A3.14}$$

are normal to the two planes governing the dynamics. Since the equilibrium line lies in the planes and crosses the point $(x, m, n) = (0, 0, 0)$, N_i being the i-th entry of $\mathbf{N}$, the equation for these planes is

$$N_1 x + N_2 m + N_3 n = 0. \tag{A3.15}$$

After rearrangement, this equation becomes

$$m = \pm x\frac{E}{H} + n\frac{H_0}{H}, \tag{A3.16}$$

where

$$E = \sqrt{\frac{v_m H^2 + v_n H_0^2}{v_x}\frac{k_m r_m H_m}{k_1 H}}. \tag{A3.17}$$

The plane with a positive slope with respect to x delimits the basins of attraction. The condition for convergence to spontaneous helping, no maternal care and maximum fertility $(x, m, n) = (1, 0, n_{\max})$ is that m is initially below such a plane. Rearrangement of this condition yields

$$br + x\frac{E}{n} > c. \tag{A3.18}$$

Although the magnitude of the relaxing term (the term proportional to x in eq. (A3.16)) is independent of n, condition (A3.7) indicates that the relative relaxation it confers decreases with n. Comparing this inequality to condition (A3.7) shows that

$$v_z = \frac{1}{n^2}\frac{v_m H^2 + v_n H_0^2}{H^2}. \tag{A3.19}$$

As obtained in §A3.2.1, condition (A3.7) reduces to $br > c$ for an initially small probability of spontaneous helping.

Therefore, as for §A3.2.1, queen specialization via spontaneous helping when maternal care and fertility are explicitly allowed to evolve is obtained when conditions (A3.8) hold (and $E_z = E/n$).

A3.3 Maternally manipulated helping

In this section I study the model of maternally manipulated helping described in the main text.

A3.3.1 Maternal care probability

In this subsection, I analyze the simpler version of the model where the components of the probability of maternal care z are not specified. That is, I study the coevolution of manipulation, resistance, and the probability of maternal care (p, q, z). The resulting inclusive fitness effects are

$$h_p = r_m(1-q)(b-c) = r_m(1-q)(H_{0m} - zH_m) \tag{A3.20a}$$

$$h_q = -p(br-c) = -p(H_0 - zH) \tag{A3.20b}$$

$$h_z = -\{r_m p(1-q)[b_p - b_g - (c_p - c_g)] + c_c - r_m c_{\neg c}\} = -[r_m p(1-q)H_m + c_c - r_m c_{\neg c}], \tag{A3.20c}$$

where $r_m = \rho_{1m}k_1/k_m = \rho_{2m}k_2/k_m$ is the life-for-life relatedness of mother to first- and second-brood offspring. The respective regression relatednesses are $\rho_{im} = dp/dg_p = dz/dg_z$ for $i = 1,2$ for first- and second-brood offspring. Similarly, $r = \rho_{21}k_2/k_1$ is the life-for-life relatedness of first- to second-brood offspring. The indicated regression relatedness is $\rho_{21} = dQ/dg_q$. Finally, direct life-for-life relatedness arises as $r_{ii} = \rho_{ii}k_i/k_i = 1$, with the corresponding regression relatedness of $\rho_{ii} = dq/dg_q = dz/dg_z$ for $i = m,1$ for mother and first-brood offspring. The quantities H, H_m, and H_0 are defined in the main text while $H_{0m} = b_p - c_p$. As before, I will assume that $c_c \approx r_m c_{\neg c}$.

Reduced system (p,z)

The dimensionality of the system (A3.20) can be reduced by dividing it by $1-q$. The resulting equations for p and z are independent of q:

$$\frac{dp}{d\tau_1} = v_p k_m r_m (H_{0m} - zH_m) \tag{A3.21a}$$

$$\frac{dz}{d\tau_1} = -v_z k_m r_m p H_m, \tag{A3.21b}$$

where $\tau_1 = (1-q)t$. This system has an equilibrium in $(p,z) = (p, z_p^*)$, where $z_p^* = H_{0m}/H_m$.

The dynamics of this system depend on the signs of H_{0m}, $H_{0m} - H_m$, and H_m. We have the analogous four cases as before:

- If $H_{0m} < 0$ and $H_{0m} - H_m < 0$, then manipulation always decreases. The probability of maternal care increases or decreases depending on the sign of H_m. In any case, the outcome is no manipulation $[(p, z) = (0, z)]$.

- $H_{0m} < 0$ and $H_{0m} - H_m > 0$, then manipulation decreases for a small probability of maternal care, but increases for large probability of maternal care. Since necessarily $H_m < 0$, then maternal care probability increases and the outcome is either no manipulation $[(p, z) = (0, z)$ for $z < z_p^*]$ if maternal care probability is initially sufficiently small, or full manipulation and full maternal care probability $[(p, z) = (1, 1)]$ if maternal care probability is initially sufficiently large.

- If $H_{0m} > 0$ and $H_{0m} - H_m < 0$, then manipulation increases for small maternal care probability but decreases for high maternal care probability. Since necessarily $H_m > 0$, then maternal care probability decreases. The outcome is either no manipulation $[(p, z) = (0, z)$ for $z > z_p^*]$ if maternal care probability is initially sufficiently large or full manipulation and zero maternal care probability $[(p, z) = (1, 0)]$ if maternal care probability is initially sufficiently small.

- If $H_{0m} > 0$ and $H_{0m} - H_m > 0$, then manipulation always increases. The outcome is full manipulation and either full maternal care probability $[(p, z) = (1, 1)]$ or zero maternal care probability $[(p, z) = (1, 0)]$ depending on the sign of H_m.

Therefore, full manipulation and zero maternal care probability $[(p, z) = (1, 0)]$ is obtained when

$$b_p > c_p \tag{A3.22a}$$

$$b_g - b_g > c_p - c_g \tag{A3.22b}$$

$$b + pM_z > c, \tag{A3.22c}$$

where

$$M_z = \sqrt{\frac{v_z H_m^2}{v_p}}. \tag{A3.23}$$

Condition (A3.22c) is obtained from the third case above using the method shown in §A3.2.1. Condition (A3.22a) states that maternal manipulation must be favored for poor-condition recipients of help. Condition (A3.22b) indicates that a decreased probability of maternal care must be favored once the mother has some help. Condition (A3.22c) is a relaxed Hamilton's rule for manipulation that converges to $b > c$ if manipulation is initially small.

Reduced system (q, z)

The dimensionality of system (A3.20) can also be reduced by dividing it by p. The resulting equations for q and z are independent of p:

$$\frac{dq}{d\tau_2} = -v_q k_1 (H_0 - zH) \tag{A3.24a}$$

$$\frac{dz}{d\tau_2} = -v_z k_m r_m (1-q) H_m, \tag{A3.24b}$$

where $\tau_2 = pt$. This system has an equilibrium in $(q, z) = (q, z^*)$, where $z^* = H_0/H$.

We have the four cases as in §A3.2.1:

- If $H_0 < 0$ and $H_0 - H < 0$, then resistance always increases. Maternal care probability increases or decreases depending on the sign of H_m. In any case, the outcome is full resistance $(q, z) = (1, z)$.

- If $H_0 < 0$ and $H_0 - H > 0$, then resistance increases for a small probability of maternal care, but decreases for large probability of maternal care. There are two subcases: 1) if $H_m > 0$, then maternal care probability decreases and the outcome is full resistance $[(q, z) = (1, z)$ for $z < z^*]$. 2) If $H_m < 0$, then maternal care probability increases and the outcome is either full resistance $[(q, z) = (1, z)$ for $z < z^*]$ if maternal care probability is initially sufficiently small, or no resistance and full maternal care probability $[(q, z) = (0, 1)]$ if maternal care probability is initially sufficiently large.

- If $H_0 > 0$ and $H_0 - H < 0$, then resistance decreases for a small probability of maternal care and increases for large probability of maternal care. Maternal care probability always decreases. The outcomes are either full resistance $[(q,z) = (1,z)$ for $z > z^*]$ or no resistance and no maternal care $[(q,z) = (0,0)]$ depending on the initial conditions.

- If $H_0 > 0$ and $H_0 - H > 0$, then resistance always decreases. The outcome is no resistance and either zero $[(q,z) = (0,0)]$ or full probability of maternal care $[(q,z) = (0,1)]$ depending on the sign of H_m.

Hence, full acquiescence and no maternal care is obtained

$$b_p r > c_p \tag{A3.25a}$$

$$b_p - b_g > c_p - c_g \tag{A3.25b}$$

$$br + (1-q)A_z > c, \tag{A3.25c}$$

where

$$A_z = \sqrt{\frac{v_z H^2}{v_q} \frac{k_m r_m H_m}{k_1 H}}. \tag{A3.26}$$

If $H < 0$, then condition (A3.25c) is unnecessary. Condition (A3.25c) is obtained as in §A3.2.1. The conditions (A3.25) for acquiescence are entirely analogous to those for spontaneous helping (A3.8). However, if initial absence of manipulation causes an initially small probability of resistance, then the relaxation term in condition (A3.25c) causes the condition for acquiescence to be a relaxed Hamilton's rule ($br + A_z > c$). This is similar to the effect caused by the evolution of social efficiency (González-Forero, 2013), but here the effect is caused by the evolution of maternal exploitation (i.e., decreased maternal care and increased maternal fertility).

Full system (p,q,z)

Bringing together conditions (A3.22) and (A3.25), queen specialization via manipulated helping $[(p,q,z)=(1,0,0)]$ is obtained when

$$b_p > c_p \tag{A3.27a}$$

$$b_p r > c_p \tag{A3.27b}$$

$$b_p - b_g > c_p - c_g \tag{A3.27c}$$

$$b + pM_z > c \tag{A3.27d}$$

$$br + (1-q)A_z > c. \tag{A3.27e}$$

If $H < 0$, then condition (A3.27e) is unnecessary. These conditions have simple interpretations given above.

A3.3.2 Maternal care and maternal fertility

In this subsection, I proceed as in §A3.2.2 and express the probability z of providing maternal care to the second brood in terms of the number of second brood offspring n and of those that receive maternal care m: $z = m/n$. As in §A3.2.2, this only changes the speed of evolutionary change. I study the coevolution of manipulation, resistance, maternal care, and maternal fertility (p,q,m,n). This produces a four-dimensional system $di/dt = v_i k_{\text{act}} h_i$ $(i = p, q, m, n)$ where the resulting inclusive fitness effects are

$$h_p = r_m(1-q)(b-c) = r_m(1-q)(H_{0m} - zH_m) \tag{A3.28a}$$

$$h_q = -p(br-c) = -p(H_0 - zH) \tag{A3.28b}$$

$$h_m = -r_m \frac{1}{n} p(1-q)[b_p - b_g - (c_p - c_g) + c_c - r_m c_{\neg c}] = -\frac{1}{n}[r_m p(1-q)H_m + c_c - r_m c_{\neg c}] \tag{A3.28c}$$

$$h_n = r_m \frac{m}{n^2} p(1-q)[b_p - b_g - (c_p - c_g) + c_c - r_m c_{\neg c}] = \frac{m}{n^2}[r_m p(1-q)H_m + c_c - r_m c_{\neg c}]. \tag{A3.28d}$$

H, H_m, H_0, and H_{0m} are defined as before. I continue to assume that $c_c \approx r_m c_{\neg c}$.

Reduced system (p, m, n)

The dimensionality of the system can be similarly reduced by dividing by $1-q$. The resulting equations for p, m and n are independent of q:

$$\frac{dp}{d\tau_1} = v_p k_m r_m (H_{0m} - \frac{m}{n} H_m) \tag{A3.29a}$$

$$\frac{dm}{d\tau_1} = -v_m k_m r_m \frac{1}{n} p H_m \tag{A3.29b}$$

$$\frac{dn}{d\tau_1} = v_n k_m r_m \frac{m}{n^2} p H_m, \tag{A3.29c}$$

where $\tau_1 = (1-q)t$. As before, the dynamics of this system depend on the signs of H_{0m}, $H_{0m} - H_m$, and H_m. This system has an equilibrium line in $(p, m, n) = (0, m_p^*, n)$, where $m_p^* = nH_{0m}/H_m$.

The same four dynamic cases as in §A3.3.1 are obtained with the same outcomes, replacing z_p^* by m_p^*/n. The basin of attraction toward queen specialization in the third case can be found as in §A3.2.2 by determining the dynamics of the system around the line of equilibria $(p, m, n) = (0, m_p^*, n)$. This is given by the Jacobian of the system evaluated at the equilibrium line:

$$\mathbf{J}|_{p=0,m=m_p^*} = \begin{pmatrix} 0 & -v_p k_m r_m \frac{1}{n} H_m & v_p k_m r_m \frac{1}{n} H_{0m} \\ -v_m k_m r_m \frac{1}{n} H_m & 0 & 0 \\ v_n k_m r_m \frac{1}{n} H_{0m} & 0 & 0 \end{pmatrix}. \tag{A3.30}$$

Using the same procedure as in §A3.2.2, the equations for the planes governing the dynamics are

$$N_1 p + N_2 m + N_3 n = 0. \tag{A3.31}$$

where N_i is the i-th entry of

$$\mathbf{N} = \mathbf{v}_1 \times \mathbf{v}_2 = (-V - \frac{H_{0m}}{H_m}, -U, U\frac{H_{0m}}{H_m})^T \tag{A3.32}$$

and

$$\mathbf{v}_1 = (U, -V, 1)^T \tag{A3.33a}$$

$$\mathbf{v}_2 = (U, \frac{H_{0m}}{H_m} - V, 2)^T \tag{A3.33b}$$

$$U = \pm\sqrt{\frac{v_p}{v_n}\left[1 + \frac{v_m}{v_n}\left(\frac{H_m}{H_{0m}}\right)^2\right]} \tag{A3.33c}$$

$$V = \frac{v_m}{v_n}\frac{H_m}{H_{0m}}. \tag{A3.33d}$$

Rearranging equation (A3.31), it becomes

$$m = \mp p\frac{M}{H_m} + n\frac{H_{0m}}{H_m}, \tag{A3.34}$$

where

$$M = \sqrt{\frac{v_m H_m^2 + v_n H_{0m}^2}{v_p}}. \tag{A3.35}$$

The plane with a positive slope with respect to p delimits the basins of attraction. The condition for convergence to manipulation, no maternal care and maximum fertility $(p, m, n) = (1, 0, n_{\max})$ is that m is initially below such a plane. Rearrangement of this condition yields

$$b + p\frac{M}{n} > c. \tag{A3.36}$$

As before, even though the magnitude of the relaxing term (the term proportional to p in eq. (A3.34)) is independent of n, condition (A3.36) indicates that the relative relaxation it confers decreases with n. Comparing this inequality to condition (A3.22c) shows that

$$v_z = \frac{1}{n^2}\frac{v_m H_m^2 + v_n H_{0m}^2}{H_m^2} \tag{A3.37}$$

regarding the evolution of manipulation.

Therefore, as for §A3.3.1, when maternal care and fertility are explicitly allowed to evolve, full manipulation with zero maternal care and maximum fertility $[(p, m, n) = (1, 0, n_{\max})]$ is obtained when conditions (A3.22) hold (and $M_z = M/n$).

Reduced system (q, m, n)

The dimensionality of system (A3.28) can similarly be reduced by dividing it by p. The resulting equations for q, m and n are independent of p:

$$\frac{dq}{d\tau_2} = -v_q k_1 (H_0 - \frac{m}{n} H) \tag{A3.38a}$$

$$\frac{dm}{d\tau_2} = -v_m k_m r_m \frac{1}{n}(1-q) H_m \tag{A3.38b}$$

$$\frac{dn}{d\tau_2} = v_n k_m r_m \frac{m}{n^2}(1-q) H_m, \tag{A3.38c}$$

where $\tau_2 = pt$. As before, the dynamics of this system depend on the signs of H_{0m}, $H_{0m} - H_m$, and H_m. The system has an equilibrium line in $(q, m, n) = (1, m^*, n)$, where $m^* = nH_0/H$.

The same four dynamic cases as in §A3.3.1 are obtained with the same outcomes, replacing z^* with m^*/n. The basin of attraction for the third case can be determined as before by determining the dynamics of the system around the line of equilibria

$(q, m, n) = (1, m^*, n)$. The Jacobian of the system evaluated at such equilibrium is

$$\mathbf{J}|_{q=1,m=m^*} = \begin{pmatrix} 0 & v_q k_1 \frac{1}{n} H & -v_q k_1 \frac{1}{n} H_0 \\ v_m k_m r_m \frac{1}{n} H_m & 0 & 0 \\ -v_n k_m r_m \frac{1}{n} \frac{H_0}{H} H_m & 0 & 0 \end{pmatrix}. \tag{A3.39}$$

Since the equilibrium line lies in the planes and it crosses the point $(q, m, n) = (1, 0, 0)$, the equation for the planes governing the dynamics is

$$N_1(q-1) + N_2 m + N_3 n = 0, \tag{A3.40}$$

where N_i is the i-th entry of

$$\mathbf{N} = \mathbf{v}_1 \times \mathbf{v}_2 = (-V - \frac{H_0}{H}, -U, U\frac{H_0}{H})^T \tag{A3.41}$$

and

$$\mathbf{v}_1 = (U, -V, 1)^T \tag{A3.42}$$

$$\mathbf{v}_2 = (U, \frac{H_0}{H} - V, 2)^T \tag{A3.43}$$

$$U = \mp\sqrt{\frac{v_q}{v_n}\frac{k_1 H}{k_m r_m H_m}\left[1 + \frac{v_m}{v_n}\left(\frac{H}{H_0}\right)^2\right]} \tag{A3.44}$$

$$V = \frac{v_m}{v_n}\frac{H}{H_0}. \tag{A3.45}$$

After rearrangement, equation (A3.40) becomes

$$m = \mp(1-q)\frac{A}{H} + n\frac{H_0}{H}, \tag{A3.46}$$

where

$$A = \sqrt{\frac{k_m r_m H_m}{k_1 H}\frac{v_m H^2 + v_n H_0^2}{v_q}}. \tag{A3.47}$$

The plane with a negative slope with respect to q delimits the basins of attraction. The condition for convergence to no resistance, no maternal care and maximum fertility $(1, m, n) = (0, 0, n_{\max})$ is that m is initially below such a plane. Rearrangement of this condition yields

$$br + (1 - q)\frac{A}{n} > c. \tag{A3.48}$$

Again, the magnitude of the relaxing term (the term proportional to $1 - q$ in eq. (A3.46)) is independent of n, but from condition (A3.48) it follows that the relative relaxation it confers decreases with n. Comparing this inequality to condition (A3.25c) shows that

$$v_z = \frac{1}{n^2}\frac{v_m H^2 + v_n H_0^2}{H^2}, \tag{A3.49}$$

regarding the evolution of resistance.

Hence, as for §A3.3.1, when maternal care and fertility are explicitly allowed to evolve, full acquiescence with zero maternal care and maximum fertility $[(q, m, n) = (0, 0, n_{\max})]$ is obtained when conditions (A3.25) hold ($A_z = A/n$).

Full system (p, q, m, n)

Substituting $M_z = M/n$ and $A_z = A/n$ in conditions (A3.27), queen specialization via manipulated helping $[(p, q, m, n) = (1, 0, 0, n_{\max})]$ is obtained when

$$b_p > c_p \tag{A3.50a}$$

$$b_p r > c_p \tag{A3.50b}$$

$$b_p - b_g > c_p - c_g \tag{A3.50c}$$

$$b + p\frac{M}{n} > c \tag{A3.50d}$$

$$br + (1 - q)\frac{A}{n} > c. \tag{A3.50e}$$

Assuming that $r \leq 1$, inequality (A3.50a) can be dropped as it is satisfied from inequality (A3.50b). If A is not real, then condition (A3.50e) can also be dropped. Letting $p, q \to 0$ yields conditions (3.3) in the main text.

Conclusion

Implications for evolutionary theory

The notion of the extended phenotype sought to expand evolutionary theory (Dawkins, 1982). The evolutionary dynamics of traits that are subject to the effects of extended phenotypes (indirect genetic effects) has previously received mathematical treatment (Kirkpatrick and Lande, 1989; Moore et al., 1997; McGlothlin et al., 2010). Such research has shown a variety of peculiarities in the evolutionary dynamics. However, that same work assumes that individuals allow others to influence their phenotype. In this dissertation, I have studied how such a tolerance may evolve. Chapter 1 addresses the effect of costs of resistance on the evolution of acquiescence to manipulation. Chapters 2 and 3 show that acquiescence can result from intrinsic processes created by manipulation itself.

These results show how indirect genetic effects can occur when manipulated individuals must consent to manipulation for the manipulated behavior to be expressed at all. Even with the stringent assumption that consent by manipulated individuals is required, these results show that, under a wide range of circumstances, a behavior can be more likely to stem from manipulation than being spontaneous. For Chapter 1, this finding was due to the fact that Hamilton's rule is more easily satisfied for manipulated behavior than for spontaneous behavior due to the occurrence of costs of resistance. In contrast, for Chapters 2 and 3, a behavior can be more likely to be the result of manipulation rather than being spontaneous because when the probability of resisting manipulation is initially small, induced behavior has a larger basin of attraction than spontaneous behavior. That is, to use an illustrative analogy (thanks to David McCandlish for pointing it out), Hamilton's rule can be seen as a black hole, and manipulation creates a larger event horizon within which any system evolves toward satisfaction of Hamilton's rule.

The processes described in Chapters 2 and 3 yield a final state where individuals are induced by partners to behave socially, yet the inducing and induced individuals are not in conflict anymore. At this point, it may appear that induced individuals are informed by partners that it is in their interest to express the behavior. In a sense, manipulation can produce a final state where individuals appear to communicate. This observation indicates that honest communication need not count as evidence against the relevance of manipulation.

Some guidelines to infer whether or not a behavior is the result of manipulation were offered in the chapters above, and are summarized in the next section.

Implications for empirical research

The results obtained here suggest that both primitive and advanced eusociality might often be better explained in terms of manipulation than of spontaneous behavior. First, manipulated behavior may be more likely than spontaneous behavior when conditional costs of resistance are present. Primitive eusociality often involves coercive caste determination that would imply costs of resistance: helpers appear to be usually induced through aggression, dominance hierarchies, or poor feeding (Weaver, 1966; Wheeler, 1986; O'Donnell, 1998; Hunt, 2007). Hence, primitive eusociality could be more likely to involve manipulated than spontaneous behavior. Estimation of the cost of resistance in specific systems is required to assess this possibility.

Second, manipulated behavior may be more likely than spontaneous behavior when there is genetic variation for social efficiency (i.e., the efficiency of manipulated individuals at giving a benefit or cost to social partners) and social inefficiency is costly. When this is the case, manipulation can yield specialized workers that are socially induced rather than spontaneous, yet that are not in conflict with their inducers. This is consistent with the worker specialization observed in advanced eusociality. Empirical assessment of this process requires the estimation of genetic variation of social efficiency and cost of inefficiency in extant, ancestral species (i.e., not in already advanced eusocial species). However, note that "genetic" here means heritable in a general, abstract sense, which may occur for example via learning. That is, increased efficiency through practice is also relevant to these observations.

Third, manipulated behavior may be more likely than spontaneous behavior when individuals in poor condition benefit greatly from receiving help. When this happens, the mother can become specialized into producing offspring, none of which she provides care to and all of which are cared for by maternally induced workers that are not in conflict with their inducing mother. This is consistent with queen specialization in advanced eusociality. Empirical test of this process similarly requires estimation of the benefit received by helped offspring that were or were not previously cared for by their mother and at least the genetic variation for maternal fertility, both in an extant, ancestral species (i.e., not an advanced eusocial one; by ancestral species I mean a species with the ancestral trait value of interest).

Phylogenetic analysis can then shed light on whether or not the queen or worker specialization in a currently advanced eusocial species is the result of manipulation: the occurrence of the conditions suggested above among ancestral species may be used to infer whether or not the relevant ancestor of the advanced eusocial species of interest had the required conditions. An affirmative answer would suggest that queen or worker specialization in this species may have been the result of manipulation. In contrast, the observation that queen signals are honest (Keller and Nonacs, 1993; Heinze and d'Ettorre, 2009) says little regarding this inference since the conflict over offspring help may have already been substantially reduced. Also, the assumption that the manipulated behavior is solely expressed by the manipulated individual substantially eliminates the possibility of perpetual arms races. Then, an observed absence of arms races (Keller, 2009) need not rule out manipulation as a driving factor.

Available empirical evidence

There is ample circumstantial evidence for costs of resistance in diverse systems. Dead female frogs (*Rhinella proboscidea*) release eggs after being forced by males to do so (Izzo et al., 2012). In principle, failure to release eggs after being killed would be more costly as there is no other reproductive option left. Cleaner fish (*Labroides dimidiatus*) are induced to feed against their preference by threats of early termination of the interaction with their hosts (Gingins et al., 2013). Keas (*Nestor notabilis*) coerce their partners into helping them (Tebbich et al., 1996). Human acquiescence is vivid in war events:

> Here is how a British general described the carnage of World War I: 'Not a man shirked going through the extremely heavy barrage, or facing the machine gun and rifle fire that finally wiped them out.... I have never seen, indeed could never have imagined, such a magnificent display of gallantry, discipline, and determination.' A sergeant described it differently: 'We knew it was pointless, even before we went over—crossing open ground like that. But you had to go. You were between the devil and the deep blue sea. If you go forward, you'll likely be shot. If you go back, you'll be court-martialed and shot. What can you do?' (Valentino, 2004). (Pinker, 2011, p. 354)

Educated circles are not exempt from manipulation tactics. Many journal editors appear to strategically pressure authors into citing the editors' journals (Wilhite and Fong, 2012).

However, socially triggered phenotypes often involve less obvious costs of resistance. Mothers determine offspring dispersal in great tits (*Parus major*) (Tschirren et al., 2007).

In zebra finches (*Taeniopygia guttata*), maternal state prior to breeding determines offspring's fecundity (Gorman and Nager, 2004). Male great bowerbirds (*Ptilonorhynchus nuchalis*) make use of visual illusions to persuade potential partners into choosing them (Kelley and Endler, 2012). Mud dauber wasps (*Sceliphron caementarium*) sting spiders which become paralyzed for later consumption by wasp larvae (Milne and Milne, 2003). Female guppies (*Poecilia reticulata*) can manipulate the aging of the sperm stored by them (Gasparini and Evans, 2013). In honeybees (*Apis mellifera*) and harvester ants (*Pogonomyrmex rugosus*), the queen controls the development of complex worker phenotypes by means of one or a few molecules (Kamakura, 2011; Libbrecht et al., 2013). In all these cases, direct costs of resisting social influence are either less obvious or seemingly negligible. Although the results in this dissertation cannot possibly identify the source of the apparent acquiescence in each of these cases, the results obtained here do suggest that the seeming acquiescence may have deeper causes than usually thought.

In particular, a key observation in eusociality is difficult to explain without manipulation. That is, the occurrence of queen pheromones. A simple explanation for the evolution of queen pheromones is the following. First, a mutation causing mothers to manipulate coercively her offspring into helping spreads due to costs of resistance. Second, the available help favors extra fertility in the mother. Thus, the mother becomes sufficiently fertile so that manipulated offspring become selected to help even if not coerced. However, offspring are not exceedingly numerous so that the mother can still coerce all of them. Third, a mutation cases the mother to manipulate non-coercively. Such a mutation can spread because coercion would be costlier for the mother than non-coercion. As a result, coercive caste determination disappears. In the end, non-coercive caste determination, for example via pheromones, is established. This explanation can be simplified further since coercion is not really necessary in the first place (large benefits to poor-condition offspring are instead sufficient; see chapter 3). In contrast, there is no available satisfactory explanation for queen pheromones without appealing to manipulation.

Implications for major evolutionary transitions

The results obtained here also inform the evolution of new levels of organization in a more conceptual way. A long-appreciated feature of living systems is that, key evolutionary events have involved the origin of new levels of organization (Mayr, 1982; Maynard Smith and Szathmáry, 1995). For instance, prokaryotic cells, eukaryotic cells, multicellular individuals, and advanced eusocial colonies are all thought to be upper-level individuals that originated from the association of lower-level individuals. In order to see how the findings of this dissertation shed light on the origins of new levels of organization, it is useful to consider a relatively recent definition of individual. In this definition, an individual is an entity whose parts display very *high* levels of cooperation and very *low* levels of conflict (Queller and Strassmann, 2009). Alternatively, an entity could be formed by parts with *low* levels of cooperation and *high* levels of conflict (competitors), *low* levels of cooperation and *low* levels of conflict (simple groups), or *high* levels of cooperation and *high* levels of conflict (societies) (Queller and Strassmann, 2009).

The evolutionary question posed by this scheme is how a group of competitors can become an individual. The results of Chapter 1 show that, when resistance is costly, manipulation can create high levels of cooperation. However, conflict remains in the form of what is sometimes called potential conflict (i.e., if the cost of resistance is not present, cooperation disappears). That is, in the light of the notions of Queller and Strassmann (2009), the cost of resistance may bring a group of competitors into society status. On the other hand, Chapters 2 and 3 show that the evolution of social efficiency and maternal exploitation may not only create high levels of cooperation, but also low levels of conflict. That is, manipulation could bring a group of competitors, through the evolution of social efficiency and maternal exploitation, into individual status.

Testing manipulation theory

A note of caution may be in order. The empirical tests suggested above are tests of the models developed from manipulation theory. Manipulation theory may be taken as considering that a phenotype is the result of partial or complete (either current or past) control of the phenotype by another individual. The models are necessarily much more specific than manipulation theory, so the rejection of a model does not reject manipulation theory as a whole. Other models can be devised for specific situations and a rejection of manipulation theory would involve a general failure of the models developed from it. This is not a peculiarity of manipulation theory. Natural selection theory may be taken as considering that a phenotype is the result of heritability and differential reproduction, and a myriad of models have been devised from this consideration. Only the general failure of models devised from the theory can speak against it.

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Appendices

Appendix I

Population genetics of maternally manipulated helping: exploration of favorable scenarios for manipulated helping

I.1 Introduction

The models developed in the previous chapters are general in the sense that they apply to arbitrary genetic (and non-genetic) systems with rather arbitrary life histories. Such general treatment is possible because the techniques that were used to derive the dynamic equations are based on the Price (1970) equation. A problem with that level of generality is that many details are hidden, and hence confusion may arise. Here we use population genetics models for the evolution in frequencies of genes controlling maternal manipulation and offspring resistance. These models give an explicit account of genetic systems and life histories, which brings clarity at the expense of complexity and lack of generality. We use these models to explore the evolution of maternally manipulated helping in 72 different biological scenarios.

I.2 Model

The models here build upon that of Charlesworth (1978). We consider an infinite, randomly mating population where manipulation and resistance are controlled by a single locus each. That is, one locus is expressed in the mother and controls maternal manipulation. The other locus is expressed in the offspring and controls offspring resistance. We consider resident alleles that cause no manipulation and no resistance respectively, and study the change in gene frequency of alleles that cause some manipulation and some resistance. Generations are quasi non-overlapping (the mother coexists with young offspring, but when counting gene frequencies we only count genes of the new generation). The life cycle consists of the following steps: a mated female produces offspring; young offspring receive maternal care; the mother dies, adult offspring disperse from the maternal site, and all mate singly and randomly; males die and each female starts the cycle again. A manipulating mother attempts to have a portion p of her manipulable offspring stay in the maternal site for a fraction of their adult life and help her raise further offspring. Manipulation may occur through poor feeding, zygotic effects, or behavioral coercion. Acquiescing (i.e., not resisting) individuals express maternal care while at the maternal site toward their siblings. Acquiescing individuals pay the cost of acquiescence c_a. Alternatively, a manipulated individual resists manipulation with probability q. A resisting individual disperses from the maternal site, mates, and starts a new site without paying the cost of acquiescence c_a. Instead, a resisting individual pays a cost of resistance c_r. One helper increases the fitness of a recipient up to an amount b; however, the helper distributes this amount b of allomaternal care uniformly among the recipients in the site. Thus, the fitness benefit received by an individual of a given genotype in a given brood is

$$B = b\frac{\text{\# of helpers}}{\text{\# of recipients}}.$$

We consider two alleles per locus. One allele has no phenotypic effect, while the other has either completely dominant or additive phenotypic effect. For the manipulation locus, allele **a** has no effect while allele **A** causes a mother to manipulate a fraction p of her offspring (or $p/2$ if the mother is heterozygous and allelic effects are additive). For the resistance locus, allele **b** has no effect, while allele **B** causes offspring to resist with probability q (or $q/2$ if offspring are heterozygous and allelic effects are additive). We study the change in gene frequencies numerically and analytically.

We assume the following possibilities. There are two kinds of manipulable individuals: both sexes (as would correspond to termites, eusocial thrips, and eusocial mole-rats) or females only (as would correspond to eusocial hymenoptera). We consider three possible recipients: only non-manipulated siblings (as would correspond to partially bivoltine life cycles, where a mother lays two subsequent broods; thus, the first brood can be constituted by helpers who raise the second brood formed by reproductives), only non-helpers (e.g., if manipulation is behavioral and the winner of a dominance contest still receives help, as may be the case in primitively eusocial taxa), or everyone in the maternal site (i.e., helpers also receive allomaternal care, as in advanced eusocial taxa). We consider two forms of cost of resistance: conditional, which is paid only if the individual resists (as would be the case with behavioral resistance) or constitutive, which is paid just by having a resistance allele (as would be the case with physiological resistance). The genetic system can either be haploid (either clonal or sexual), diploid or haplodiploid. For brevity, haploid below refers to the sexual case, as the description of the clonal case is rather trivial and is not included here. Allelic effects can be additive or dominant. Combinations of these considerations produce 72 different scenarios. We study the coevolution of the frequencies of the genes controlling manipulation and resistance. We refer to manipulated helping as the case when manipulation is fixed and resistance is lost. We seek to study scenarios that promote the evolution of manipulated helping.

Let x_i be the frequency of genotype i. Let R_{ijk} be the probability that genotype i is produced by a mother of genotype j and a father of genotype k. Hence, R_{ijk} depends on the genetic system (haploid, diploid, or haplodiploid), on the recombination frequency ρ between the two loci, and on the sex allocation s (the probability of male offspring produced by a female). Let w_{ijk} be the (viability) fitness of genotype i in a brood produced by the pair jk. Assuming random mating the frequency of i in the next generation is

$$x_i' = \frac{1}{\bar{w}} \sum_{jk} x_j x_k R_{ijk} w_{ijk}, \tag{I.1}$$

where $\bar{w} = \sum_{ijk} x_j x_k R_{ijk} w_{ijk}$ is the population-average fitness (counting genotypic frequencies is simpler than counting gamete frequencies; see §I.5.4). Let P_{ij} be the probability that a mother of genotype j manipulates offspring of genotype i, and Q_i be the probability that genotype i resists manipulation. A general fitness function that applies to all 12 scenarios mentioned above is

$$\begin{aligned} w_{ijk} = {} & P_{ij}(1-Q_i)(1-c_a)(1-C_{r,i1})(1+B_{jk1}) \\ & + P_{ij}Q_i(1-C_{r,i2})(1+B_{jk2}) \\ & + (1-P_{ij})(1-C_{r,i3})(1+B_{jk3}). \end{aligned}$$

The first line corresponds to the event in which i is manipulated and does not resist. Then, i pays the cost c_a of acquiescence and, depending on the scenario, it may also pay the resistance cost or get the benefit from being helped. The second line is for when i is manipulated but resists. The third line is when it is not manipulated. $C_{r,il}$ is the cost of resistance for genotype i at fitness position l. When the cost of resistance is constitutive, $C_{r,il} = c_r$ for all $l = 1,2,3$. When it is conditional, $C_{r,il} = c_r$ only for $l = 2$, otherwise it is zero. B_{jkl} is the fitness benefit at fitness position l for an individual in a brood produced by pair jk. The benefit B_{jkl} depends on the number of helpers and recipients, and hence B_{jkl} is defined as follows.

Let H_{jk} be the frequency of helpers produced by a jk mating. Supposing that selection occurs after dispersal, we count helpers before selection. Then,

$$H_{jk} = \sum_i R_{ijk} P_{ij} (1 - Q_i). \tag{I.2}$$

The frequency of helpers in the population is

$$h = \sum_{jk} x_j x_k H_{jk}.$$

Thus, the benefit from being helped is,

$$B_{jkl} = \begin{cases} b\frac{H_{jk}}{1-\sum_i R_{ijk} P_{ij}} & \text{for } l = 3, \text{ when recipients are only non-manipulated} \\ b\frac{H_{jk}}{1-H_{jk}} & \text{for } l = 2,3, \text{ when recipients are only non-helpers} \\ bH_{jk} & \text{for } l = 1,2,3, \text{ when recipients are everyone.} \end{cases}$$

I.3 Results

Numerical results

The initial conditions were specified as follows. We drew randomly sixteen initial frequencies for alleles **A** and **B** between 0 and 0.1, and calculated the initial genotypic frequencies from their linkage equilibrium distribution. We then iterated the recurrence equations (I.1) for $20,000$ generations ($30,000$ for the haploid case). We stopped iterations if genotypic frequencies reached quasi-equilibrium to an approximation of 10^{-10}. Parameter values evaluated were $b = 0.9, 1.1, 2.1$; $c_a = 1$; $p = 0.1, 0.5, 0.9$; $q = 0.1, 0.5, 1$; $c_r = 0, 0.1, 0.5$; $s = 0.25, 0.5, 0.75$; and $\rho = 0, 0.05, 0.5$. We evaluated the 72 scenarios. We did tests with no selection by setting $b = c_a = c_r = 0$ in which no change in gene frequency ever occurred. With selection, the quasi-equilibrium frequency of helpers in the expected region of conflict (i.e., when $b = 1.1$) in general was:

- larger when both sexes are manipulable than when only females are;

- usually zero when recipients are everyone, but can reach significant values when recipients are non-manipulated or non-helpers. It was subtly larger when recipients where non-manipulated compared to non-helpers;
- larger for constitutive costs than for conditional costs of resistance;
- similar for haploid and diploid, but substantially smaller for haplodiploid;
- similar for additive and completely dominant effects.

Some of the different dynamical regimes observed are in Fig. I1.1. Helper frequencies at quasi-equilibrium are given in Fig. I1.2 for different genetic systems and parameter values. Figures for all the results are available at

`http://neko.bio.utk.edu/~mgonzal7/Eusociality/Chapter_1/Numerically/`.

In haplodiploids, sex ratio evolves for several reasons, in decreasing order of influence: 1) if only females are manipulable, males have higher fitness; 2) if dominance is additive, males can only resist with half the ability of homozygous females; 3) if recombination rate is very small or resistance cost is large.

Analytical results

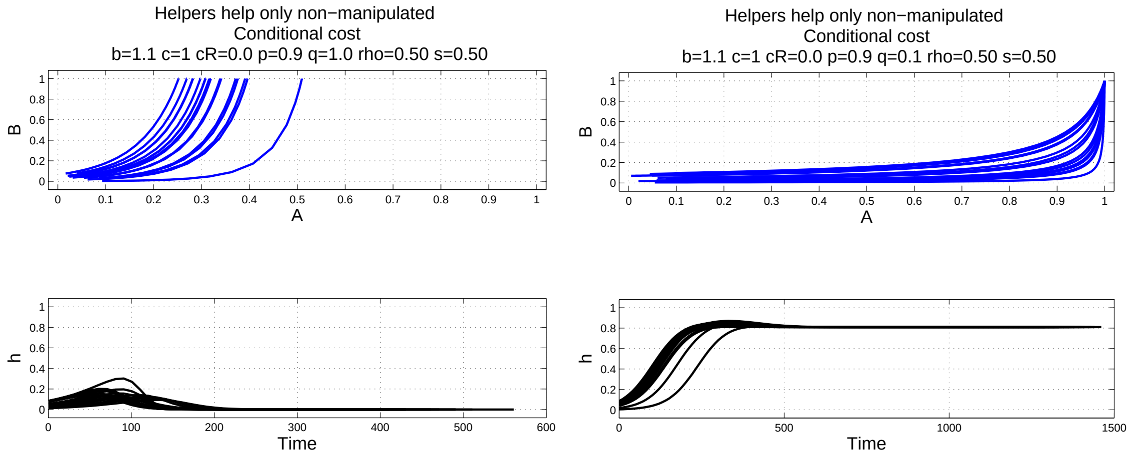
Here we focus on the scenarios in which only non-manipulated are recipients and resistance cost is conditional. We assume that $c_r < c_a$ and that the equilibrium genotypic frequencies are in linkage equilibrium, which implicitly assumes that selection is weak. Table I.1 gives equilibrium values for gene frequencies, helper behavior and sex ratio.

It can be shown that for haploids, the frequency of helpers for any gene frequency is

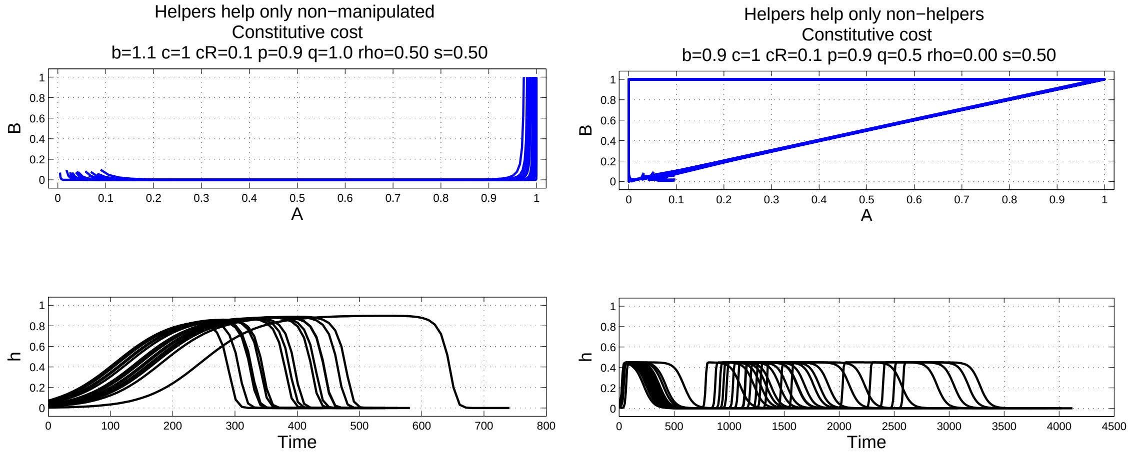
$$h = PX_{\mathbf{A}}\left(1 - \frac{1}{2}qX_{\mathbf{B}}\right) - \frac{1}{2}Pqx_{\mathbf{AB}},$$

which, under linkage equilibrium, reduces to

$$h = PX_{\mathbf{A}}\left(1 - qX_{\mathbf{B}}\right),$$

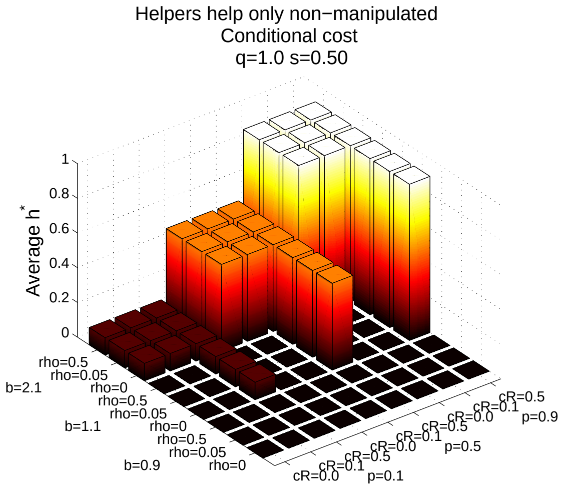


(a) Diploids; additive effects **(b)** Diploids; additive effects

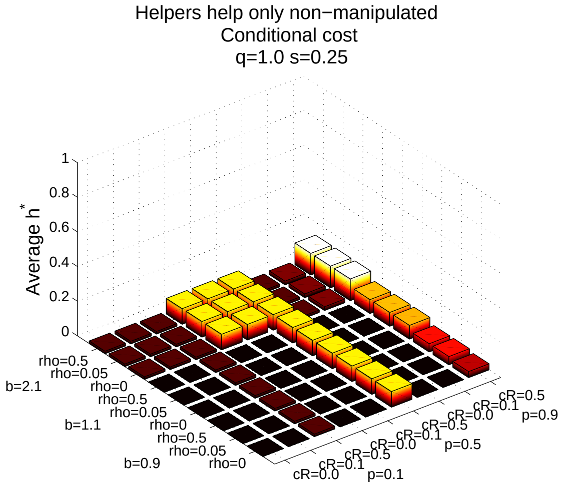


(c) Diploids; additive effects **(d)** Haploids

Figure I1.1: Typical dynamical regimes. The top plot in each panel (blue lines) shows the coevolution of gene frequencies of the manipulation allele (**A**) and the resistance allele (**B**). The bottom plot in each panel (black lines) shows the frequency of helpers (h) through time. In the four panels both sexes are manipulable. Regarding helper frequency, in (**a**) it initially increases but subsequently goes to zero; in (**b**) it is maintained; in (**c**) it is maintained for a number of generations but is subsequently lost; and in (**d**) it cycles. In (**a**) and (**b**) resistance cost is conditional while in (**c**) and (**d**) it is constitutive. In (**a**)-(**c**) recipients are non-manipulated while in (**d**) recipients are non-helpers.



(a) Haploids **(b)** Diploids



(c) Haplodiploids; only females are manipulable **(d)** Haplodiploids; both sexes are manipulable

Figure I1.2: A bar's height gives the helper frequency obtained either at quasi-equilibrium or at the end of the iteration, averaged over 16 random initial conditions. Notice that for haplodiploids, if only females are manipulable a female-skewed sex allocation produces a larger helper-equilibrium frequency while if both sexes are manipulable a larger male-skewed sex allocation produces a larger helper-equilibrium frequency.

Table I.1: Equilibrium values for manipulation allele frequency ($\hat{X}_{\mathbf{A}}$), resistance allele frequency ($\hat{X}_{\mathbf{B}}$), helper frequency ($\hat{h}$), and sex ratio ($\hat{z}$). Rows give the results for genetic system/manipulable sexes. We show only results for additive effects, even though analytical results are also possible for complete dominance. $P = p$ when both sexes are manipulable and $P = p(1-s)$ when only females are manipulable. $\sigma_1 = \frac{2+p\{2(b-c_a)+[(c_a-c_r)-(2-s)b]q\}}{2+p\{2(b-c_a)+(2-s)[(c_a-c_r)-b]q\}} < 1$. $\sigma_2 = \frac{1-p(1-s)(b-1)}{[1-p(1-s)][1-p(1-s)(b-c_a)]}$. $\sigma_3 = \frac{1-p(1-s)[1-b(1-q)]}{[1-p(1-s)]\{1-p(1-s)[(1-q)(c_a-b)+qc_r]\}} > 1$. $u^* = \frac{1}{2}\frac{1-p(1-s)}{bps(1-s)}\{b[2+(1-s)(4-3p)]-4[2-p(1-s)(c_a-c_r)]\}$, $v^* = \frac{b-c_a}{q(b-c_a+c_r)}$. $h^* = \frac{1}{2}\frac{c_r(1-s)(1-p(1-s))}{b(b-c_a+c_r)}\{[b-4(c_a-c_r)][2-p(1-s)]+2b(1-s)(2-p)\}$. For haplodiploids/both, fixation of full resistance cannot eliminate helper behavior because males can only resist halfway under the assumptions of the model.

	$(\hat{X}_{\mathbf{A}}, \hat{X}_{\mathbf{B}})$	$\hat{h}$
Haploids	$(0, X_{\mathbf{B}})$	0
	$(1, 0)$	P
	$(1, 1)$	$P(1-q)$

	$(\hat{X}_{\mathbf{A}}, \hat{X}_{\mathbf{B}})$	$\hat{h}$
Diploids	$(0, X_{\mathbf{B}})$	0
	$(\frac{1}{4}, 0)$	$\frac{1}{4}P$
	$(\frac{1}{4}, \frac{1}{4})$	$\frac{1}{4}P(1-\frac{1}{4}q)$
	$(\frac{1}{4}, 1)$	$\frac{1}{4}P(1-q)$
	$(1, 0)$	P
	$(1, \frac{1}{4})$	$P(1-\frac{1}{4}q)$
	$(1, 1)$	$P(1-q)$

	$(\hat{X}_{\mathbf{A}}, \hat{X}_{\mathbf{B}})$	$\hat{h}$	$\hat{z}$
Haplodiploids/both	$(0, X_{\mathbf{B}})$	0	s
	$(1, 0)$	$sp(1-s)$	s
	$(1, 1)$	$sp(1-s)\left[1-q\left(1-\frac{s}{2}\right)\right]$	$s\sigma_1$
Haplodiploids/female	$(0, X_{\mathbf{B}})$	0	s
	$(1, 0)$	$sp(1-s)^2$	$s\sigma_2$
	$(1, 1)$	$sp(1-s)^2(1-q)$	$s\sigma_3$
	(u^*, v^*)	h^*	s

where $P = p$ when both sexes are manipulable, $P = p(1-s)$ when only females are manipulable and $X_{\mathbf{i}}$ is the frequency of allele **i**.

Numerical iterations generally converge to points that appear to match those expected analytically, except in three detected cases: 1) For diploids, the polymorphic equilibria were not observed numerically. 2) For haplodiploids, the polymorphic equilibrium deviates somewhat from its expected analytical value, to the point of there being a polymorphic equilibrium in haplodiploids/both although none was expected analytically. 3) For haplodiploids/female, dynamics sometimes showed an elbow shape in which an equilibrium, polymorphic for manipulation and monomorphic for fixed resistance, was reached. A fourth discrepancy observed occasionally in all genetic systems is that a line of equilibria at $(X_{\mathbf{A}}, 1)$ was observed but this appears to occur when parameters are at the boundary of stability conditions. The reason for discrepancies 1-3 appears to be the strength of selection. Discrepancy 2 occurred only when $c_r = 0.5$ in numerical runs. Discrepancy 3 seems to suggest that the scenario haplodiploids/female is subject to stronger selection as it occurred even with $c_r = 0$. To avoid the linkage equilibrium assumption two alternatives were attempted: *i*) to look for equilibrium genotypic frequencies instead of equilibrium gene frequencies or *ii*) to look for equilibrium gamete frequencies. The first alternative is computationally prohibitive. The second alternative requires recurrence equations for gamete frequencies. Due to parental effects, these equations would be non-Markov since the next generation-gamete frequencies depend not only on the current generation frequencies, but also on frequencies at each past generation (see §I.5.4). Hence, it is to be kept in mind that the assumption of monomorphic equilibrium in invasion analyses below may not hold for haplodiploids/female.

Below we give local stability conditions for the haploid case.

Stability for haploids

For the equilibrium $(0, X_{\mathbf{B}})$:

If p^2 is much smaller than p, the line of equilibria $(0, X_{\mathbf{B}})$ is unstable if

$$\begin{aligned} b &> c_a + c_r \frac{X_{\mathbf{B}} q}{1 - X_{\mathbf{B}} q} && \text{for } c_r > K_1 \\ b &> 2\frac{2\rho + P(1-\rho)[c_a(1-q+X_{\mathbf{B}} q) + c_r q(1-X_{\mathbf{B}})]}{P(2-q)(1-\rho)} && \text{for } c_r < K_1, \end{aligned}$$

where $K_1 = (1 - X_{\mathbf{B}} q)\frac{c_a P q(1-\rho)(1-2X_{\mathbf{B}}) - 4\rho}{Pq(1-\rho)(1-2X_{\mathbf{B}})(2-X_{\mathbf{B}} q)}$ provided that $X_{\mathbf{B}} < 1/2$. If $X_{\mathbf{B}} > 1/2$ the inequalities for c_r are reverted. $P = p$ when both sexes are manipulable and $P = p(1-s)$

when only females are manipulable. If $\rho > \frac{1}{5}$, K_1 is negative and hence only the first inequality matters in that case.

For the equilibrium $(1,0)$**:**

The equilibrium $(1,0)$ is stable if

$$\begin{aligned} &b > 2(c_a - c_r) && \text{for } c_r < \frac{c_a}{2} \\ &b > c_a && \text{for } c_r > \frac{c_a}{2}. \end{aligned}$$

For the equilibrium $(1,1)$**:**

The equilibrium $(1,1)$ is stable if (the third inequality was not proved explicitly; only the equality was proved and the direction of the inequality was inferred from plots)

$$\begin{aligned} &b < 2(c_a - c_r) && \\ \text{and } &b > c_a + c_r \frac{q}{1-q} && \text{for } c_r > K_2 \\ \text{and } &b > 2\,(k_1 c_a - k_2 c_r + k_3) && \text{for } c_r < K_2, \end{aligned}$$

where $k_1 = \frac{1}{1+\frac{1-q}{1-2q/(1+\rho)}}$, $k_2 = \frac{2}{2-(1+\rho)(2-q)/q}$ and $k_3 = \frac{2\rho}{P[2q-(1+\rho)(2-q)]}$. $K_2 = \frac{1-q}{2-q}\left[c_a + \frac{4\rho}{Pq(1-\rho)}\right]$ provided that $\rho < \frac{3q-2}{2-q}$, which requires that $q > \frac{2}{3} \approx 0.66$. If $\rho > \frac{3q-2}{2-q}$, which requires that $q < \frac{6}{7} \approx 0.86$, the inequalities for c_r are reverted. Hence, if $q < \frac{2}{3}$, c_r needs to be greater than K_2 for the third inequality to apply. In such a case, from our assumption that $c_r < c_a$, K_2 needs to be smaller than c_a and then $\rho < \frac{3-\sqrt{5}}{1-3\sqrt{5}} \approx 0.13$. Therefore, if $q < \frac{2}{3}$ and $\rho \gtrsim 0.13$ then the third inequality can be ignored.

In summary for haploids, if p is small, $q < \frac{2}{3}$, $\rho > \frac{1}{5}$ and $c_r > \frac{c_a}{2}$, then for the manipulation allele to spread to fixation and the resistance allele to be lost it is sufficient that

$$b > c_a + c_r \frac{q}{1-q}.$$

The fact that $c_r > \frac{c_a}{2}$ makes this is a stringent condition in which case there is no conflict.

I.4 Discussion

The equilibrium frequency of helpers is larger when both sexes are manipulable. This is simply because males can also be helpers. When all siblings are recipients of help, the equilibrium frequency of helpers is close to zero because much of the helping effort is wasted into helping helpers who are unlikely to pass their genes to the future generation. Constitutive resistance costs caused larger equilibrium frequency of helpers than conditional costs because the resistance allele may be selected against even when it is not expressed, which causes stronger selection pressure against resistance. The substantially smaller equilibrium frequency of helpers in haplodiploids is seemingly an artifact of our definition of R_{ijk} for haplodiploids (eqs. (I.3)). We weighted the R_{ijk} for females by $1-s$ and that for males by s so that the sum of genotype frequencies is 1. However, this causes genotype frequencies to be weighted by sex frequencies, and thus the probability that genotypes i and j mate is $s(1-s)$. Consequently, worker frequencies are artificially weighted by the factor $s(1-s)$ for haplodiploids (see Table I.1). Therefore, our results for haplodiploids need to be corrected to account for this problem. In any case, the results for haploids and diploids, and presumably for haplodiploids once corrections are made, show that full resistance probability ($q = 1$) eliminates worker behavior, which contrasts with other approaches to model conflict in which contribution to trait expression by the conflicting parties is additive (e.g., Gavrilets, 2000; Frank and Crespi, 2011).

I.5 Calculation details

I.5.1 Definition of P_{ij} and Q_i

Haploid and diploid with complete dominance: If genotype j has the manipulation allele, $P_{ij} = p$ when both sexes are manipulable or $P_{ij} = (1-s)p$ when only females are manipulable, where s is the proportion of males produced by a mating. P_{ij} is constant over i in the haploid and diploid genetic systems. $Q_i = q$ when genotype i has the resistance allele.

Diploid with additive effects: If genotype j is homozygote for the manipulation allele, P_{ij} is defined as above. If j is heterozygote we let $P_{ij} = p/2$ when both sexes are manipulable or $P_{ij} = (1-s)p/2$ when only females are manipulable. Similarly, $Q_i = q/2$ for heterozygotes of the resistance allele.

Haplodiploid case: We arrange genotypes so that the first 16 genotypes are those of females, while genotypes from 17 to 20 are those of males. With complete dominance, $P_{ij} = p$ for $i = 1,\ldots,16$ when only females are manipulable, or for $i = 1,\ldots,20$ when both sexes are manipulable. With additive effects, $P_{ij} = p$ or $P_{ij} = p/2$ depending on whether j has two or one manipulation alleles. Notice that the weighting $(1-s)$ when only females are manipulable is not necessary in this account of the haplodiploid case. Q_i is defined as above, with $Q_i = q/2$ for males possessing the resistance allele.

I.5.2 Definition of R_{ijk}

Let ρ be the recombination frequency between the manipulation and resistance loci. Let s be the fraction of male offspring produced by a mating (sex allocation). Let δ_{ij} be the Kronecker delta, so $\delta_{ij} = 0$ if $i \neq j$ and $\delta_{ij} = 1$ if $i = j$. Let $i_l, j_l, k_l, I_l, J_l, K_l = 0, 1$ here denote the absence or presence of the allele **A** or **B** in locus l in haplotype i, j, k, I, J, K. Then, following Nagylaki (1992, eq. (8.9)), R_{ijk} is given by the following expressions.

For haploids:

$$\begin{aligned}R_{1+i_1+2i_2,1+j_1+2j_2,1+k_1+2k_2} = \; & \frac{1}{2}\delta_{i_1,j_1}[(1-\rho)\delta_{i_2,j_2}+\rho\delta_{i_2,k_2}] \\ & +\frac{1}{2}\delta_{i_1,k_1}[(1-\rho)\delta_{i_2,k_2}+\rho\delta_{i_2,j_2}].\end{aligned}$$

For diploids:

$$\begin{aligned}& R_{1+4(i_1+2i_2)+I_1+2I_2,1+4(j_1+2j_2)+k_1+2k_2,1+4(J_1+2J_2)+K_1+2K_2} = \\ & \quad \left\{\frac{1}{2}\delta_{i_1,j_1}[(1-\rho)\delta_{i_2,j_2}+\rho\delta_{i_2,k_2}]+\frac{1}{2}\delta_{i_1,k_1}[(1-\rho)\delta_{i_2,k_2}+\rho\delta_{i_2,j_2}]\right\} \\ & \quad \times\left\{\frac{1}{2}\delta_{I_1,J_1}[(1-\rho)\delta_{I_2,J_2}+\rho\delta_{I_2,K_2}]+\frac{1}{2}\delta_{I_1,K_1}[(1-\rho)\delta_{I_2,K_2}+\rho\delta_{I_2,J_2}]\right\}.\end{aligned}$$

For female offspring of haplodiploids:

$$\begin{aligned}& R_{1+4(i_1+2i_2)+I_1+2I_2,1+4(j_1+2j_2)+k_1+2k_2,17+K_1+2K_2} = \\ & \quad (1-s)\left\{\frac{1}{2}\delta_{i_1,j_1}[(1-\rho)\delta_{i_2,j_2}+\rho\delta_{i_2,k_2}]+\frac{1}{2}\delta_{i_1,k_1}[(1-\rho)\delta_{i_2,k_2}+\rho\delta_{i_2,j_2}]\right\} \\ & \quad \times(\delta_{I_1,K_1}\delta_{I_2,K_2}).\end{aligned} \tag{I.3a}$$

For male offspring of haplodiploids:

$$\begin{aligned}& R_{17+i_1+2i_2,1+4(j_1+2j_2)+k_1+2k_2,17\ldots20} = \\ & \quad s\left\{\frac{1}{2}\delta_{i_1,j_1}[(1-\rho)\delta_{i_2,j_2}+\rho\delta_{i_2,k_2}]+\frac{1}{2}\delta_{i_1,k_1}[(1-\rho)\delta_{i_2,k_2}+\rho\delta_{i_2,j_2}]\right\}.\end{aligned} \tag{I.3b}$$

I.5.3 Definition of H_{jk}

From the definition of H_{jk} in eq. (I.2) and the definitions of R_{ijk}, P_{ij}, and Q_i, we have that H_{jk} takes the following values.

For haploids:

$$H_{jk} = \begin{cases} P_{ij} & \text{when no one can resist} \\ P_{ij}(1-q/2) & \text{when half can resist} \\ P_{ij}(1-q) & \text{when all can resist.} \end{cases}$$

P_{ij} is constant over i for haploids and diploids, thus the subscript i can be dropped in H_{jk} for those genetic systems.

For diploids with complete dominance:

$$H_{jk} = \begin{cases} P_{ij} & \text{when no one can resist} \\ P_{ij}(1-q/2) & \text{when half can resist} \\ P_{ij}(1-3q/4) & \text{when 3/4 can resist} \\ P_{ij}(1-q) & \text{when all can resist.} \end{cases}$$

For diploids with additive allelic effects:

$$H_{jk} = \begin{cases} P_{ij} & \text{when no one can resist} \\ P_{ij}(1-q/4) & \text{when half can resist (with half ability)} \\ P_{ij}(1-q/2) & \text{when 3/4 can resist (1/4 with all ability, 1/2 with half ability)} \\ P_{ij}(1-q) & \text{when all can resist with all ability} \\ P_{ij}(1-q/2) & \text{when all can resist with half ability} \\ P_{ij}(1-3q/4) & \text{when all can resist; 1/2 with all ability, 1/2 with half ability.} \end{cases}$$

For haplodiploids with complete dominance where only females are manipulable:

$$H_{jk} = \begin{cases} (1-s)p & \text{when no one can resist} \\ (1-s)p(1-q/2) & \text{when half can resist} \\ (1-s)p(1-q) & \text{when all can resist} \\ (1-s)p(1-q) & \text{when all and only females can resist} \\ (1-s)p(1-q) & \text{when females and half of males can resist.} \end{cases}$$

For haplodiploids with complete dominance where both sexes are manipulable:

$$H_{jk} = \begin{cases} p & \text{when no one can resist} \\ p(1-q/2) & \text{when half can resist} \\ p(1-q) & \text{when all can resist} \\ p[(1-s)(1-q)+s] & \text{when all and only females can resist} \\ p[(1-s)(1-q)+s(1-q/2)] & \text{when females and half of males can resist.} \end{cases}$$

For haplodiploids with additive allelic effects where only females are manipulable:

$$H_{jk} = \begin{cases} (1-s)P_{1,j} & \text{when no one can resist} \\ (1-s)P_{1,j}(1-q/4) & \text{when half can resist (with half ability)} \\ (1-s)P_{1,j}(1-q/2) & \text{when all can resist (with half ability)} \\ (1-s)P_{1,j}(1-q/2) & \text{when females can resist (with half ability)} \\ (1-s)P_{1,j}(1-q/4) & \text{when all females and half males can resist} \\ & \text{(half females with full ability, half with half ability;} \\ & \text{males with half ability)} \\ (1-s)P_{1,j}(1-q) & \text{all can resist (females with full ability, males with half ability).} \end{cases}$$

For the haplodiploid case, P_{ij} is constant for $i = 1, \ldots, 16$ so we just picked 1 for the definition above.

I.5.4 Recurrence equations for gamete frequencies

Although the results in Appendix I were obtained using recurrence equations for genotype frequencies (eq. I.1), the dynamics can be equivalently described by recurrence equations for gamete (haplotype) frequencies. Here we illustrate that recurrence equations for gamete frequencies make the analysis more complicated. Let z_i^t be the frequency of gamete i at generation t. Let r_{ijk} be the probability that individual jk produces gamete i. Let $w_{jk\bullet\bullet}$ be the fitness of individual jk averaged over its possible mothers and fathers. The frequency of gamete i in the next generation is

$$z_i^{t+1} = \frac{1}{\bar{w}} \sum_{jk} z_j^t z_k^t w_{jk\bullet\bullet} r_{ijk}. \tag{I.4}$$

Let $w_{jk;lm,no}$ be the fitness of individual jk whose mother and father have genotype lm and no respectively. $R_{jk;lm,no}$ is the probability that genotype jk is produced by a mother lm and a father no. The average fitness of jk over mothers and fathers is

$$w_{jk\bullet\bullet} = \sum_{lmno} w_{jk;lm,no} (z_l^{t-1} z_m^{t-1} w_{lm\bullet\bullet})(z_n^{t-1} z_o^{t-1} w_{no\bullet\bullet}) R_{jk;lm,no}.$$

Hence, the recurrence equation (I.4) depends on the two previous time steps, which substantially complicates the analysis.

Appendix II

Invasion analysis of maternally manipulated helping: evolution of manipulated helping

II.1 Introduction

The population genetics models for the evolution of manipulated helping introduced in Appendix I make explicit many biologically relevant details that are hidden in the general accounts in chapters 1-3. However, the population genetics models in Appendix I only study the change in gene frequencies for fixed levels of manipulation and resistance. That is, manipulation and resistance themselves do not evolve. In this appendix, we introduce simplifying assumptions to the population genetics models of Appendix I to study the change in manipulation and resistance. We do this by studying the continuous invasion of mutants that differ slightly from resident genes (an approach often known as invasion analysis). This approach greatly simplifies the mathematics, which allows for analytical treatment for haploids, diploids, and haplodiploids. Expressions for relatedness and reproductive value arise from the algebra. We also consider arbitrary sex-differential manipulation: a mother can manipulate offspring of arbitrary sex composition. In addition to the coevolution of manipulation and resistance, we obtain results regarding the effect of sex-differential manipulation on the evolution of maternally manipulated helping.

II.2 Model

We focus on maternal rather than the broader parental manipulation because the relevant genetic variation may be particularly available for mothers (Linksvayer and Wade, 2005; Schwander et al., 2008; Russell and Lummaa, 2009; Uller et al., 2009; Maestripieri and Mateo, 2009). Our approach builds upon that of Charlesworth (1978) who developed a population genetics model for the evolution of parental manipulation in which offspring were not allowed to resist manipulation. We consider an infinite sexual population with a partially bivoltine life-cycle (figure II2.1). Partial bivoltinism causes altruism and manipulation to require smaller benefit-cost ratios to evolve than when helpers also receive help (Charlesworth, 1978, and Appendix I; see also Hunt and Amdam, 2005). In addition, partial bivoltinism has been found to yield high relatedness (Seger, 1983). We assume that parents of either or both sexes provide care to young. Adult offspring disperse from the maternal site to a common mating pool. Parents die after the second brood is raised. Individuals at the mating pool mate singly and randomly. This setting of dispersal before mating has been found to produce higher relatednesses than with dispersal after mating, thus favoring altruism (Taylor, 1988).

We assume that mothers can manipulate first-brood offspring into staying in the maternal site for a fraction of their adulthood. A mother manipulates a first-brood offspring of sex i with probability p_i. Manipulated offspring of sex i resist with probability q_i in which case they disperse without delay. Alternatively, manipulated offspring of sex i acquiesce with probability $1 - q_i$ and stay in the maternal site for a fraction of their adulthood. Acquiescing offspring express parental care (e.g., provisioning or defense) at the maternal site increasing fitness of the second-brood offspring.

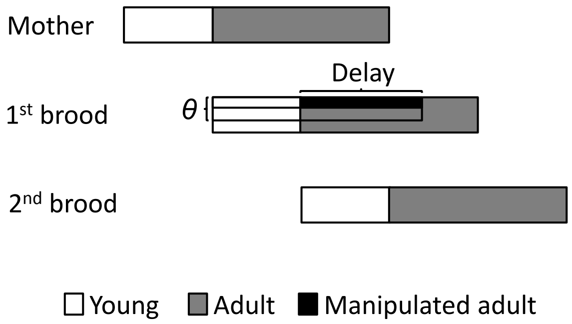


Figure II2.1: A mated female produces two subsequent, overlapping broods. A mother directs her manipulation effort toward a fraction θ of the first brood. A member of this target set of offspring is manipulated to stay with probability p. Acquiescing offspring remain in the maternal site for some fraction of their adulthood.

We simplify the study of sex-differential manipulation by proceeding as follows. Let p be a mother's manipulation effort ($0 \leq p \leq 1$) so that $p_i = \alpha_i p$ where α_i measures how much of a mother's manipulation effort translates into manipulation of a given sex. That is, α_i measures sex-differential manipulation. Rather than studying the independent evolution of p_i, we study the evolution of manipulation effort p. A normalized measure of sex-differential manipulation is $u_i = \alpha_i \gamma_{i1}/\theta$, where γ_{i1} is the probability that an individual of sex i is in the first brood and $\theta = \alpha_{♀}\gamma_{♀1} + \alpha_{♂}\gamma_{♂1}$ is the target set of manipulation (the fraction of the first brood that the mother intends to manipulate). That is, u_i is the fraction of manipulation effort p that goes toward sex i ($u_{♀} + u_{♂} = 1$). Sex-differential resistance can arise because of different ploidy levels between the sexes. We consider three genetic systems: sexual haploid, diploid and haplodiploid. For diploid individuals we let alleles have additive effects (i.e., the trait value is given by the sum of the contributions of alleles from the two chromosomes). Hence, for haploids and diploids, we let the resistance probability be equal between the sexes: $q_i = q$. However, for haploidiploids sexes have different ploidy levels. Although haplodiploid males are haploid in their germline, they may have a duplicate genome in some somatic tissues except in basal hymenoptera and non-hymenopteran haplodiploids (Aron et al., 2005).

Thus, we allow for the effect of dosage compensation in male haplodiploids which is relevant because if males do not compensate dosage, with additive allelic effects, males are half as likely to resist as females. Therefore, for haplodiploids, we let the probability of resistance of females be $q_{♀} = q$ while that of males be $q_{♂} = 1/2 d_{♂} q$. Here, $d_{♂}$ measures dosage compensation, so that $d_{♂} = 1$ if males do not compensate dosage or $d_{♂} = 2$ if they do. We study the coevolution of manipulation effort p, which we assume to be under maternal genetic control, and resistance probability q, which we assume to be under offspring genetic control.

A manipulating mother survives to produce the second brood with probability $1-c_m$, where c_m is the cost of manipulation (Bell et al., 2012). Acquiescing offspring have fitness $1-c_a$, where c_a is the cost of acquiescence which includes both the cost of helping and the cost being delayed at the maternal site. Resisting offspring disperse without paying the cost of acquiescence, but they may have reduced probabilities of completing dispersal and events thereafter (e.g., nest building and defense) depending on how manipulation is executed (Metcalfe and Monaghan, 2001). Thus, resisting offspring have fitness $1-c_r$, where c_r is the cost of resistance. The fitness benefit, if any, provided by an acquiescing individual is distributed uniformly among all second-brood offspring. We let the benefit depend on the sex of the helper. This intends to reflect relevant ancestral conditions: termite ancestors may have possessed biparental care (Korb, 2008) and hence both sexes would be similarly helpful if manipulated to stay, while ancestors to eusocial hymenoptera may have had predominantly maternal care (Hunt, 2007) and so females would be the primary helping sex. We thus denote by b_i the benefit to second-brood offspring provided by an acquiescing individual of sex i. The effective benefit received by a second-brood individual is therefore

$$B = \frac{b_{♀} \times \text{\# of female helpers} + b_{♂} \times \text{\# of male helpers}}{\text{\# of recipients}}. \tag{II.1}$$

We let manipulation effort p and resistance probability q be controlled by one locus each. For each locus, we consider a resident and a mutant allele, the latter of which slightly modifies manipulation or resistance probability. We make additional simplifying assumptions (rare mutation, small mutation effect and no overdominance or frequency dependent selection) so that we can study the invasion of one mutant allele at a time (Haldane, 1927; Eshel, 1983; Metz et al., 1996; Geritz et al., 1998; Waxman and Gavrilets, 2005). Manipulation effort p and resistance probability q can then be taken to evolve as continuous traits (see §II.5). These assumptions yield analogous simplifications to those of other approaches (e.g., Taylor and Frank, 1996).

The fitness of a mutant of sex i that has mother of genotype J and father of genotype K and belongs to the first or second brood respectively is

$$w_{i1,J\times K} = p_i(1-q_i)(1-c_a) + p_i q_i(1-c_r) + (1-p_i), \tag{II.2a}$$

$$w_{i2,J\times K} = 1 + B. \tag{II.2b}$$

In eq. (II.2a), the first term corresponds to the case where offspring are manipulated and acquiesce in which case they pay the cost of acquiescence c_a; the second term corresponds to when they are manipulated and resist in which case they pay the cost of resistance c_r; and the third term is when offspring are not manipulated in which case no fitness change occurs. Eq. (II.2b) gives fitness for second-brood individuals. The fitnesses of the two broods determine the average fitness of a mutant of sex i whose mother is J and father is K. Because a manipulating mother has a reduced probability of producing the second brood due to the cost of manipulation c_m, such average mutant fitness is

$$w_{i,J\times K} = g\gamma_{i1|i} w_{i1,J\times K} + (1-g)\gamma_{i2|i}(1-c_m) w_{i2,J\times K}, \tag{II.3}$$

where g is the fraction of offspring that belong to the first brood and $\gamma_{ij|i}$ is the probability that a mutant in brood j is of sex i given that a mutant of sex i is produced.

II.3 Results

The invasion analysis for the three genetic systems is shown in §II.5. Although the algebra is cumbersome especially for the haplodiploid case, final results can be described by simple expressions allowing for a straightforward interpretation.

Evolution of manipulation

For the three genetic systems, manipulation effort p increases if

$$\overline{b(1-q)}(1-c_m) > \overline{c}. \tag{II.4}$$

Throughout this Appendix, the overbar means averaging over sex-specific fractions u_i of manipulation effort. That is, $\overline{b(1-q)} = \sum_i u_i b_i (1-q_i)$ is the product of the benefit b_i and the probability of acquiescence $1-q_i$, averaged over manipulated offspring. The quantity $\overline{c} = \sum_i u_i c_i$ is the viability cost averaged over manipulated offspring, where the total viability cost to sex-i offspring $c_i = c_a(1-q_i) + c_r q_i$ depends on q and includes both the costs of acquiescence c_a and resistance c_r (see Table II.1 for the values of q_i in different genetic systems). Therefore, inequality (II.4) specifies how dosage compensation (implicit in $q_{\male}$) and sex-differential manipulation ($u_{\female}, u_{\male}$) influence the evolution of maternal manipulation for the three genetic systems.

The effect of sex-differential manipulation is specified by parameters u_i. Maximizing the ratio of the left-hand side of eq. (II.4) over its right-hand side with respect to u_i, we find that the inequality is easiest to satisfy when the entire manipulation effort goes toward the sex for which the quantity $(1-q_i)b_i/c_i$ is the largest. For haploids and diploids, q_i and c_i values are identical for both sexes so that manipulation increases the easiest if it is directed to the sex providing the largest benefit b_i.

Table II.1: Definition of several quantities for female and male offspring. The proportion of males in the population (sex ratio) is z and that of females is $\zeta = 1 - z$. The proportion of males produced by a mating (sex allocation) is s and that of females is $\sigma = 1 - s$. The proportion of brood j that is male is s_j (hence $s = gs_1 + (1-g)s_2$), and the proportion of brood j that is female is $\sigma_j = 1 - s_j$.

	Haploids and diploids	Haplodiploids	
	Females and males	Females	Males
q_i	q	q	$\frac{1}{2}d_{\male}q$
d_i	1	1	1 or 2
v_i	1	1	ζ
$\widehat{r}_i$	$\frac{1}{2}$	$\zeta\frac{1}{2} + z\sigma_2$	$\zeta\frac{1}{2}$

Evolution of acquiescence

For the three genetic systems, resistance probability q decreases (or acquiescence probability increases) if

$$\overline{b\widehat{r}d}(1 - c_m) > \overline{vd}(c_a - c_r), \tag{II.5}$$

where $\overline{b\widehat{r}d} = \sum_i u_i b_i \widehat{r}_i d_i$ and $\overline{vd} = \sum_i u_i v_i d_i$ (see Table II.1 for the values of d_i, v_i and $\widehat{r}_i$ in different genetic systems). The quantities $\widehat{r}_i$ give the probability that first-brood mutants of sex i share the mutant allele with second-brood individuals, averaged over the two mutant matings (Table II.1). The quantities v_i give the probability that mutant matings produce sex-i mutants (Table II.1). We show numerically in §II.5.2 that v_i matches the reproductive value of individuals of sex i, and that $\widehat{r}_i$ matches the regression relatedness of sex i toward the second brood times the reproductive value of recipients averaged over the two recipient sexes. We refer to $\widehat{r}_i$ as the reproductive-value-weighted relatedness of sex i toward the second brood. Thus, the ratio $r_i = \widehat{r}_i / v_i$ is the life-for-life relatedness of sex i toward the second brood (Hamilton, 1972; Bulmer, 1994).

Sex-differential manipulation, specified by $u_{\female}$ and $u_{\male}$, similarly affects whether inequality (II.5) can be satisfied. The inequality is easiest to satisfy when the entire manipulation effort goes toward the sex for which the quantity $b_i r_i$ is the largest.

For haploids and diploids, such a sex is simply determined by the largest b_i. In contrast to the evolution of manipulation, if only one sex is manipulated, the effect of dosage compensation cancels out. Hence, when only one sex is manipulated, dosage compensation is only relevant for manipulation but not for acquiescence.

Evolution of spontaneous helping

To compare the evolution of manipulated helping with that of spontaneous helping, we have also studied a model in which first-brood offspring stay at the maternal site and help second-brood offspring without being influenced by their mother (see §II.5.3). We refer to this as spontaneous helping. We show that the tendency of spontaneous helping increases if

$$\overline{b\hat{r}d}_s > \overline{vd}_s c_s. \tag{II.6}$$

Here the averages are given by the same expressions as in eq. (II.5) except that now all variables correspond to spontaneous helping (as indicated by the subscript s) and may thus be numerically different from those of acquiescence. The quantity c_s is the cost of spontaneous helping and plays an analogous role to that of the cost of acquiescence c_a. As with acquiescence, dosage compensation cancels out if only one sex helps spontaneously. Also, sex-differential expression of spontaneous helping causes inequality (II.6) to be most easily satisfied when spontaneous helping is only expressed by the sex with the largest value of $b_{i,s} r_i$.

Comparison of manipulated and spontaneous helping

Manipulated helping is favored but spontaneous helping is not if inequalities (II.4) and (II.5) are satisfied while inequality (II.6) is not. Figure II2.2 illustrates regions of parameter values where manipulated helping is favored under less stringent conditions (lower benefit-cost ratios) than spontaneous helping. The advantage is reduced as the resistance probability increases, but can still be observed with full resistance probability

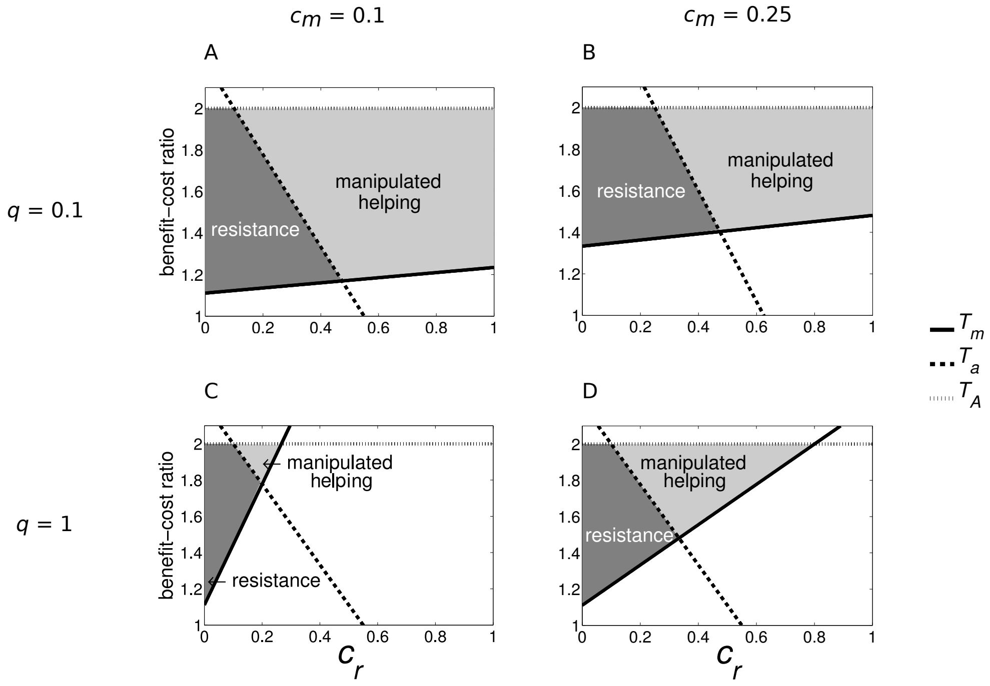


Figure II2.2: Region of advantage of manipulated helping. Let the benefit provided by helpers of sex i be $b_i = h_i a$, where h_i is the probability that an acquiescing individual of sex i provides help to the second brood and a is the amount of benefit. Manipulation, acquiescence, and spontaneous helping are favored when the benefit-cost ratio a/c_a is greater than the respective thresholds T_m, T_a, and T_A (as defined in expressions (II.12) in the online appendix). In the light gray area, manipulated helping is selected but spontaneous helping is not (in the wording of Ratnieks and Reeve 1992 and Ratnieks et al. 2006, potential but no actual conflict occurs). For A and B, only females are manipulated ($u_{♀} = 1$) and they are fully helpful ($h_{♀} = 1$). The thresholds for these two plots are the same for haploids, diploids and haplodiploids. For C and D, thresholds are shown for haplodiploids in which males are haploid in the tissue controlling resistance ($d_{♂} = 1$). For C, both sexes are equally manipulated ($u_{♀} = 1/2$) and both sexes are fully helpful ($h_{♀} = h_{♂} = 1$), while for D only males are manipulated ($u_{♂} = 1$) and they are fully helpful ($h_{♂} = 1$). The remaining parameter values are $c_a = 1$ and $z = s_1 = s_2 = 1/2$. Therefore, life-for-life relatedness is 1/2 in all cases.

in haplodiploids with helping males that do not compensate dosage ($d_{♂} = 1$). We illustrate the conditions for existence of the advantage in two simple examples: when resistance is absent ($q = 0$, which may be the case before a new form of manipulation starts evolving) and when it is complete ($q = 1$, which would be the case after the evolution of manipulation under conditions that favor resistance).

Example 1. Let resistance be absent ($q = 0$). While no other assumption is made for haploids and diploids, for haplodiploids suppose further that manipulation effort is entirely applied to female offspring ($u_{♀} = 1$) and that sex allocation to the second brood is even ($s_2 = 1/2$). This produces a life-for-life relatedness of $r = 1/2$. Under these conditions, the advantage of manipulated helping exists if the cost of manipulation c_m is smaller than the smallest value between c_r/c_a and $1/2$. Thus, the advantage may exist with substantial manipulation costs. With negligible manipulation costs ($c_m \to 0$) and substantial resistance costs ($c_r > c_a/2$), manipulated helping may be selected with benefit-cost ratios as low as one half of those necessary for spontaneous helping.

Example 2. Suppose instead that resistance is complete for haplodiploids ($q = 1$); for haploids and diploids complete resistance prevents manipulation from being favored at all. Suppose further that manipulation effort is entirely applied to male offspring ($u_{\male} = 1$) and that males are haploid in the tissue that controls their resistance ($d_{\male} = 1$, thus $\overline{q} = 1/2$). The relevant life-for-life relatedness is again $r_{\male} = 1/2$. In this situation, the advantage of manipulated helping exists if the cost of manipulation c_m is smaller than the smallest value among c_r/c_a, $(1 - c_r/c_a)/2$, and $1/3$. As illustrated in figure II2.2 (C-D), the advantage of manipulated helping may still exist when males are manipulated and resistance is complete, provided that males are haploid in the tissue controlling their resistance. This is because males are able to resist only half as much as females under our assumption of additive allelic effects.

Dynamics

The forms of inequalities (II.4) and (II.5) cause the dynamics of sex-differentially manipulated helping to be almost identical to those in Chapter 1 when relatednesses are positive. In particular, for the three genetic systems, there are two general dynamic outcomes: 1) complete disappearance of manipulation as a result of offspring resistance ($p = 0$) (offspring wins) and 2) evolution of maximum manipulation and complete acquiescence of offspring ($p = 1, q = 0$) (mother wins). However, in the haplodiploid case with no dosage compensation for resistance in males ($k_{\male} = 1$), there is a third dynamic outcome: 3) evolution to a state where manipulation is maximal, but resistance in female offspring is complete ($p = 1, q = 1$) with male offspring exhibiting partial acquiescence (mother partially wins over male offspring).

As in the general model of Chapter 1, for haploids and diploids and for haplodiploids with dosage compensation, the mother wins (outcome 2) if

$$\overline{b}(1 - c_m) > c_a \tag{II.7a}$$

$$q_0 < q^* + p_0\sqrt{\frac{-\mu_q R}{\mu_p \zeta M}} \tag{II.7b}$$

and acquiescence is favored (inequality II.5 holds). The subscript 0 in condition (II.7b) indicates that it is the initial value of the variable. As before, $q^* = M_0 - M$ is the resistance probability at which the direction of selection for manipulation changes, and R measures selection for resistance. They are

$$M_0 = \overline{b}(1 - c_m) - c_a \tag{II.8a}$$

$$M = \overline{D[b(1 - c_m) - c_a - c_r]} \tag{II.8b}$$

$$R = -[\overline{b\hat{r}d}(1 - c_m) - \overline{vd}(c_a - c_r)], \tag{II.8c}$$

where $D_i = 1$ for haploids, diploids, and haplodiploid females and $D_i = d_{\male}/2$ for haplodiploid males. The quantities μ_p and μ_q are functions of the mutation frequency and mutation effect of manipulation and resistance respectively. Comparison with the results of Chapter 1 suggests that the quantity ζ in inequality (II.7b) measures life-for-life relatedness of mother to offspring of either brood.

Figure II2.3 shows numerical solutions for two cases when the mother wins under benefit-cost ratios that are too low for spontaneous helping to be favored. Figure II2.3A illustrates a scenario that may correspond to termites in that both sexes are equally helpful. Figure II2.3B illustrates a scenario that may correspond to eusocial hymenoptera in that only females are helpful.

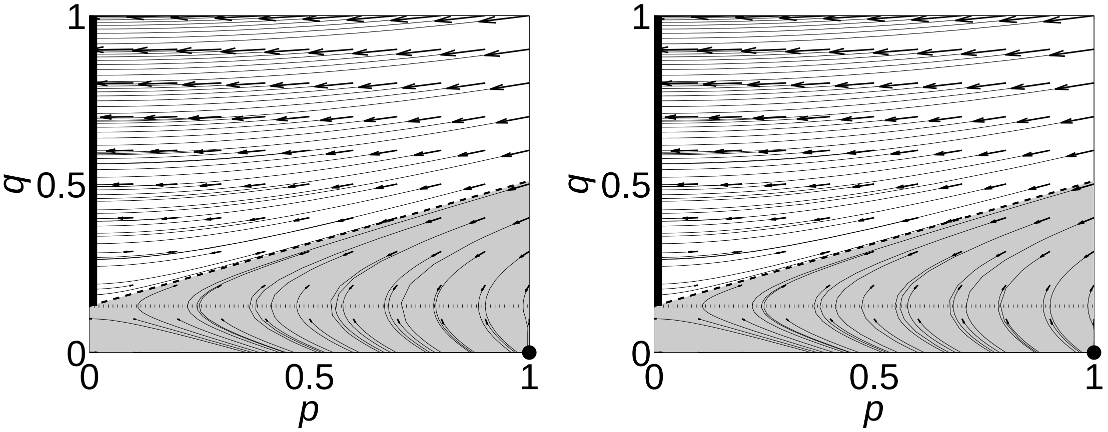


Figure II2.3: Numerical solutions for (A) diploids and (B) haplodiploids. For A, both sexes are equally helpful ($b_♀ = b_♂ = 1.2$) and equally manipulated ($u_♀ = 0.5$). For B, only females are helpful ($b_♀ = 1.2$, $b_♂ = 0$) and manipulated ($u_♀ = 1$). The remaining parameter values are: $r = 1/2$, $c_a = 1$, $c_r = 0.5$, $c_m = 0.1$, and $g = s_1 = s_2 = z = 0.5$. The mother wins when manipulation effort and resistance probability fall within the gray region. Spontaneous helping requires a benefit greater than 2 to be selected in these conditions so it is not favored.

II.4 Discussion

Inequalities (II.5) and (II.6) show that sex-differentially manipulated helping can be obtained under less stringent conditions than spontaneous helping. The possibility of this advantage does not necessarily mean that manipulated helping should be observed more frequently than spontaneous helping. Capitalizing on this advantage may require that the mother is able to preferentially manipulate the more helping sex. This requirement imposes biologically informative constraints on the evolution of maternally manipulated helping. In particular, if the mother manipulates her offspring indiscriminately, but only one sex provides help, then maternal manipulation is less likely to be selected than if she had the ability to direct her manipulation effort toward the helping sex. This restriction is not relevant to spontaneous helping, and it may offer a possibility to distinguish between manipulated helping and spontaneous helping. If mechanisms for preferential manipulation are not available even though helpers tend to be of a particular sex, this would suggest that manipulation is an unlikely source of the behavior. Inversely, if mechanisms for preferential manipulation are available, but offspring can deceive the mother into believing that they are of the sex she chooses not to manipulate, manipulation would also be an unlikely cause. The sex determination mechanism in haplodiploids gives mothers substantial control of the sex of her offspring (Bull, 1983; Heimpel and de Boer, 2008; Verhulst et al., 2010), yet such an ability may be common across taxa (Thogerson et al., 2013). This may reduce the possibility that offspring can deceive their mother regarding their sex, which may allow for manipulated helping given an ancestral state with primarily only one helping sex. If the ancestral state involves biparental care, as would be the case for termite ancestors (Korb, 2008), indiscriminate manipulation does not make manipulated helping less likely.

II.5 Calculation details

The proportion of males in the population (sex ratio) is z and that of females is $\zeta = 1 - z$. Assuming that mutation is rare, the average fitness of a mutant individual is

$$w_M = \zeta w_{M,M\times R} + z w_{M,R\times M},$$

where $w_{M,J\times K}$ is the fitness of mutant M whose mother is J and father is K. The letters M and R denote mutant carrier and resident, respectively. That is, the first term above corresponds to the mutant's fitness when its mother is a carrier and the second when its father is a carrier. The fitness of a mutant whose mother is J and father is K is

$$w_{M,J\times K} = \gamma_{♀} w_{♀,I\times K} + \gamma_{♂} w_{♂,I\times K},$$

where γ_i is the probability that mutant M is of sex i. We let s be the proportion of males produced by a mating (sex allocation) and that of females be $\sigma = 1 - s$. Thus, $\gamma_{♀} = \sigma$ and $\gamma_{♂} = s$ in all cases except for haplodiploids when the father is mutant in whose case $\gamma_{♂} = 0$.

The proportion of offspring that belong to the first brood is g ($0 < g < 1$). The proportion of males in brood j is s_j (hence $s = gs_1 + (1-g)s_2$), and the proportion of females in brood j is $\sigma_j = 1 - s_j$. The probability that a mutant of sex i is in brood j is γ_{ij} (thus, $\gamma_{♀j} = \sigma_j$ and $\gamma_{♂j} = s_j$ in all cases except for haplodiploids when the father is mutant in whose case $\gamma_{♂j} = 0$). Considering the conditional probability of being of a given sex, the fitness of a mutant of sex i whose mother is J and father is K is

$$w_{i,J\times K} = g\frac{\gamma_{i1}}{\gamma_i} w_{i1,J\times K} + (1-g)\frac{\gamma_{i2}}{\gamma_i}(1-c_m)w_{i2,J\times K},$$

where $w_{ij,J\times K}$ is the fitness of sex-i mutant in brood j whose parents are $J \times K$, as indicated by eq. II.3 in the main text. The fitness of a first- and second-brood individual are respectively given by eqs. II.2 in the main text.

To define a mother's total manipulation effort p, a fraction of which is directed to each sex, we write manipulation effort toward sex-i offspring as $p_i = \alpha_i p$. The quantities α_i ($0 \leq \alpha_i \leq 1$) give the fraction of first-brood offspring of sex i toward which manipulation effort is targeted (e.g., $\alpha_♀ = 1$ means that all first-brood females are target of manipulation). Thus, α_i's do not necessarily add up to 1. It can be seen that the fraction of manipulation effort toward sex i is thus $u_i = \alpha_i\gamma_{i1}/\theta$, where the target set of manipulation is $\theta = \sum \alpha_i\gamma_{i1}$, and then $\sum u_i = 1$. Now, let q_{ik} denote the resistance probability of sex i of genotype k. Denote by $q_{i\bullet}$ the average resistance probability among sex-i offspring resulting from mating $J \times K$. Thus, the effective benefit is

$$\begin{aligned} B &= \frac{b_♀ g\sigma_1 p_♀(1-q_{♀\bullet}) + b_♂ g s_1 p_♂(1-q_{♂\bullet})}{1-g} \\ &= \frac{gp\theta}{1-g}\left[u_♀ b_♀(1-q_{♀\bullet}) + u_♂ b_♂(1-q_{♂\bullet})\right] \\ &= \frac{gp\theta}{1-g}\overline{b(1-q_\bullet)}, \end{aligned}$$

where the overbar denotes the average over manipulated offspring (i.e., $\overline{x} = \sum u_i x_i$).

II.5.1 Haploids and diploids

Here we build the model for diploids, and the results extend to sexual haploids except that for the latter evolutionary change is twice as fast. Consider an infinite diploid, sexual population with a resident manipulation allele **a** and a resident resistance allele **b**, each in a separate locus. A mother with genotype **aa** manipulates with probability p a fraction θ of her first brood. Offspring with genotype **bb** resist with probability q. Assuming additive allelic effects, we let each resident manipulation allele code for $p/2$ and each resident resistance allele code for $q/2$. A rare manipulation allele **A** codes for a slightly different probability $p'/2$, and a rare resistance allele **B** codes a slightly different probability $q'/2$. Thus, a manipulation-mutant mother, with genotype **Aa**, manipulates with probability $P' = (p' + p)/2$, while a resistance-mutant offspring, with genotype **Bb**, resists with probability $Q' = (q' + q)/2$. We study the spread of these mutant alleles.

We assume that mutation is rare enough so that when a mutant allele arises, there is enough time for it to approach an equilibrium frequency before another mutant allele arises (see e.g., Metz et al., 1996; Geritz et al., 1998; Waxman and Gavrilets, 2005). No evolutionary forces maintaining polymorphism will be considered (e.g., overdominance or frequency-dependent selection), so that each allele is either lost or fixed. This allows one to consider separately the spread of mutant alleles in each of the two loci, without any assumption about linkage between them.

Consider first the spread of a rare manipulation allele **A**. Because the sex ratio is z (and $\zeta = 1 - z$), the rare allele is involved in matings **Aa** × **aa** (females on the left) with a probability approximately equal to ζ, and in matings **aa** × **Aa** with a probability approximately equal to z. The viability of genotype **Aa** given that its mother and father are **Aa** and **aa**, respectively, is $w_{\mathbf{Aa},\mathbf{Aa}\times\mathbf{aa}}$. Hence, the average viability of carriers of the mutant allele is

$$w_{\mathbf{Aa}} = \zeta\, w_{\mathbf{Aa},\mathbf{Aa}\times\mathbf{aa}} + z\, w_{\mathbf{Aa},\mathbf{aa}\times\mathbf{Aa}}.$$

Assuming that mutation is of small effect and that the mother produces a very large number of offspring, the evolutionary change in manipulation effort Δp between the time of mutation and the time of fixation is approximately given by the product between the mutational process μ_p which measures the mutation frequency and mutation effect, and the selection gradient $\partial w_{\mathbf{Aa}}/\partial p'|_{p'=p}$ (Kimura, 1965; Lande, 1979; Iwasa et al., 1991; Dieckmann and Law, 1996).

Denoting mutant manipulation effort toward sex i as $P'_i = \alpha_i P'$, the mutant's viability when the mother is also mutant reduces to

$$
\begin{aligned}
w_{\mathbf{Aa},\mathbf{Aa}\times\mathbf{aa}} = {} & g\sigma_1 P'_{\text{♀}}(1-q)(1-c_a) + g\sigma_1 P'_{\text{♀}} q(1-c_r) + g\sigma_1(1-P'_{\text{♀}}) \\
& \qquad + (1-g)\sigma_2(1-c_m)(1+B') \\
& + g s_1 P'_{\text{♂}}(1-q)(1-c_a) + g s_1 P'_{\text{♂}} q(1-c_r) + g s_1(1-P'_{\text{♂}}) \\
& \qquad + (1-g)s_2(1-c_m)(1+B') \\
= {} & 1-(1-g)c_m + gP'\theta[\overline{b}(1-q)(1-c_m)-c],
\end{aligned}
$$

where the effective benefit is $B' = gP'\theta/(1-g)\overline{b}(1-q)$, the average benefit provided is $\overline{b} = u_{\text{♀}}b_{\text{♀}} + u_{\text{♂}}b_{\text{♂}}$, and the overall viability cost to offspring is $c = c_a(1-q) + c_r q$. For the reciprocal mating, the viability $w_{\mathbf{Aa},\mathbf{aa}\times\mathbf{Aa}}$ is constant with respect to p'. Hence, with a constant cost of manipulation with respect to manipulation effort, the fitness gradient for manipulation is

$$
\left.\frac{\partial w_{\mathbf{Aa}}}{\partial p'}\right|_{p'=p} = \frac{1}{2}\zeta g\theta\left[\overline{b}(1-q)(1-c_m)-c\right]. \tag{II.9}
$$

The rate of change depends on the proportion of females, ζ, as only mothers express the mutant allele. It is also weighted by 1/2 because of our treatment of additive allelic effects, and depends on the size of the available workforce given by the size of the first brood, g, and the target set, θ. Manipulation probability increases if

$$
\overline{b}(1-q)(1-c_m) > c.
$$

To determine how the direction of selection is affected by sex-differential manipulation, notice that in this inequality only $\overline{b}$ depends on u_i. Differentiating $\overline{b}$ with respect to $u_♀ = 1 - u_♂$, we obtain that $\overline{b}$ is maximized when the mother allocates her entire manipulation effort to the sex that provides the largest benefit. When both sexes provide the same benefit, the inequality is constant with respect to $u_♀$.

We can now look at the evolution of resistance. The average viability of mutant carriers is

$$w_{\mathbf{Bb}} = \zeta w_{\mathbf{Bb},\mathbf{Bb}\times\mathbf{bb}} + z w_{\mathbf{Bb},\mathbf{bb}\times\mathbf{Bb}}.$$

Mothers are all of genotype **aa**, so first-brood offspring are manipulated with probability p. Offspring from a **Bb** × **bb** mating have genotype **Bb** or **bb** with equal probability, assuming no meiotic drive. Thus, manipulated offspring from this mating resist on average with probability $(Q' + q)/2$, and hence the effective benefit is $B' = gp\theta/(1 - g)\overline{b}[1 - (Q' + q)/2]$. Therefore, the viability of a mutant carrier when its mother is a mutant reduces to

$$\begin{aligned}
w_{\mathbf{Bb},\mathbf{Bb}\times\mathbf{bb}} = g\sigma_1 p_♀(1 - Q')(1 - c_a) + g\sigma_1 p_♀ Q'(1 - c_r) + g\sigma_1(1 - p_♀)&\\
+ (1 - g)\sigma_2(1 - c_m)(1 + B')&\\
+ g s_1 p_♂(1 - Q')(1 - c_a) + g s_1 p_♂ Q'(1 - c_r) + g s_1(1 - p_♂)&\\
+ (1 - g)s_2(1 - c_m)(1 + B')&\\
= 1 - (1 - g)c_m + gp\theta\left\{\overline{b}\left[1 - \frac{1}{2}(Q' + q)\right](1 - c_m) - c'\right\},&
\end{aligned}$$

where the overall viability cost to offspring is $c' = c_a(1 - Q') + c_r Q'$. The viability is the same in the reciprocal mating. The fitness gradient for resistance is thus

$$\left.\frac{\partial w_{\mathbf{Bb}}}{\partial q'}\right|_{q'=q} = -\frac{1}{2}gp\theta\left[\frac{1}{2}\overline{b}(1 - c_m) - (c_a - c_r)\right]. \tag{II.10}$$

The rate of change is also weighted by 1/2 from our treatment of additive allelic effects, and depends on the total probability of being manipulated, given by $gp\theta$. Resistance probability decreases if

$$\frac{1}{2}\overline{b}(1-c_m) > c_a - c_r.$$

As for manipulation, only $\overline{b}$ depends on sex-differential manipulation, u_i, in this inequality. Thus, when sexes are differentially helping, this inequality is of easier satisfaction when the mother only manipulates the sex that provides the greatest benefit.

To study the sexual haploid case, the only modification needed above is to replace $P' = p'$ and $Q' = q'$ (so now each allele codes for the full trait, not just half of it). The only effect of this is that it eliminates the $1/2$ from the fitness gradients, doubling the rate of evolutionary change for both manipulation and resistance. Thus, the haploid and diploid case are qualitatively identical.

II.5.2 Haplodiploids

Let each resident manipulation and resistance allele code for a manipulation effort $p/2$ and resistance probability $q/2$, respectively. Allow males, which are haploid, to compensate dosage (Aron et al., 2005) so that the resistance probability for a resident male is $dq/2$, where $d = 1$ without dosage compensation, or $d = 2$ with dosage compensation (indeed, dosage compensation can also be thought of as switching from adding to averaging gene effects in males; Gardner, 2012). A mutant female for the respective locus has a manipulation effort of $P' = (p' + p)/2$ or a resistance probability of $Q' = (q' + q)/2$. A mutant male has a resistance probability of $dq'/2$.

First, consider the evolution of manipulation effort. The average viability of a mutant is

$$w_{\mathbf{A\_}} = \zeta w_{\mathbf{A\_},\mathbf{Aa}\times\mathbf{a}} + z w_{\mathbf{A\_},\mathbf{aa}\times\mathbf{A}}$$

where $w_{\mathbf{A\_},J\times K} = \gamma_{♀} w_{\mathbf{Aa},J\times K} + \gamma_{♂} w_{\mathbf{A},J\times K}$. For the mating $\mathbf{Aa} \times \mathbf{a}$, we have that $\gamma_{♀} = \sigma$ and $\gamma_{♂} = s$, while for the reciprocal mating $\mathbf{aa} \times \mathbf{A}$, $\gamma_{♀} = \sigma$ and $\gamma_{♂} = 0$ because no mutant males are produced. Thus, offspring viabilities for the first mating are

$$
\begin{aligned}
w_{\mathbf{Aa},\mathbf{Aa}\times\mathbf{a}} &= g\frac{\sigma_1}{\sigma}P'_{\text{♀}}(1-q)(1-c_a) + g\frac{\sigma_1}{\sigma}P'_{\text{♀}}q(1-c_r) + g\frac{\sigma_1}{\sigma}(1-P'_{\text{♀}}) \\
&\qquad + (1-g)\frac{\sigma_2}{\sigma}(1-c_m)(1+B') \\
&= \frac{\sigma_2}{\sigma} + g\left(\frac{\sigma_1}{\sigma}-\frac{\sigma_2}{\sigma}\right) - c_m\frac{\sigma_2}{\sigma}(1-g) + gP'\theta\left[\frac{\sigma_2}{\sigma}\overline{b(1-q)}(1-c_m) - \frac{u_{\text{♀}}}{\sigma}c_{\text{♀}}\right] \\
w_{\mathbf{A},\mathbf{Aa}\times\mathbf{a}} &= g\frac{s_1}{s}P'_{\text{♂}}\left(1-d\frac{q}{2}\right)(1-c_a) + g\frac{s_1}{s}P'_{\text{♂}}d\frac{q}{2}(1-c_r) + g\frac{s_1}{s}(1-P'_{\text{♂}}) \\
&\qquad + (1-g)\frac{s_2}{s}(1-c_m)(1+B') \\
&= \frac{s_2}{s} + g\left(\frac{s_1}{s}-\frac{s_2}{s}\right) - c_m\frac{s_2}{s}(1-g) + gP'\theta\left[\frac{s_2}{s}\overline{b(1-q)}(1-c_m) - \frac{u_{\text{♂}}}{s}c_{\text{♂}}\right],
\end{aligned}
$$

where the effective benefit for this mating is

$$
\begin{aligned}
B' &= \frac{gP'\theta}{1-g}\left[u_{\text{♀}}b_{\text{♀}}(1-q) + u_{\text{♂}}b_{\text{♂}}\left(1-d\frac{q}{2}\right)\right] \\
&= \frac{gP'\theta}{1-g}\overline{b(1-q)},
\end{aligned}
$$

the overall cost paid by female offspring is $c_{\text{♀}} = c_a(1-q) + c_r q$, and by male offspring is $c_{\text{♂}} = c_a\left(1-dq/2\right) + c_r dq/2$. Adding these two viabilities with their corresponding weights as specified by the definition of $w_{\mathbf{A\_},\mathbf{Aa}\times\mathbf{a}}$, we obtain

$$
w_{\mathbf{A\_},\mathbf{Aa}\times\mathbf{a}} = 1 - c_m(1-g) + gP'\theta\left[\overline{b(1-q)}(1-c_m) - \overline{c}\right],
$$

where the average cost to offspring viability is $\overline{c} = u_{\text{♂}}c_{\text{♂}} + u_{\text{♀}}c_{\text{♀}}$. The mutant viability from the reciprocal mating is constant with respect to p'. With a constant cost of manipulation with respect to manipulation effort, the fitness gradient is

$$
\left.\frac{\partial w_{\mathbf{A\_}}}{\partial p'}\right|_{p'=p} = \frac{1}{2}\zeta g\theta\left[\overline{b(1-q)}(1-c_m) - \overline{c}\right], \tag{II.11}
$$

which is analogous to that for haploids and diploids. Manipulation probability increases if

$$\overline{b(1-q)}(1-c_m) > \overline{c}.$$

To determine how the direction of selection is affected by sex-differential manipulation, we notice that now both $\overline{b(1-q)}$ and $\overline{c}$ depend on u_i. Differentiating with respect to $u_♀$, we find that $\overline{b(1-q)}/\overline{c}$ is maximized when manipulation effort goes entirely to the sex determined by the larger side of the inequalities

$$\frac{b_♀}{c_♀}(1-q) \gtrless \frac{b_♂}{c_♂}\left(1-d\frac{q}{2}\right).$$

Regarding the evolution of resistance, the average mutant viability for the resistance allele is as before

$$w_{\mathbf{B\_}} = \zeta w_{\mathbf{B\_,Bb\times b}} + z w_{\mathbf{B\_,bb\times B}},$$

where $w_{\mathbf{B\_},J\times K} = \gamma_♀ w_{\mathbf{Bb},J\times K} + \gamma_♂ w_{\mathbf{B},J\times K}$, with $\gamma_♀ = \sigma$ and $\gamma_♂ = s$ except for the mating **bb** × **B** where $\gamma_♂ = 0$. The viabilities for mutant offspring from the first mating are

$$\begin{aligned}
w_{\mathbf{Bb,Bb\times b}} &= g\frac{\sigma_1}{\sigma}p_♀(1-Q')(1-c_a) + g\frac{\sigma_1}{\sigma}p_♀ Q'(1-c_r) + g\frac{\sigma_1}{\sigma}(1-p_♀) \\
&\qquad + (1-g)\frac{\sigma_2}{\sigma}(1-c_m)(1+B') \\
&= \frac{\sigma_2}{\sigma} + g\left(\frac{\sigma_1}{\sigma} - \frac{\sigma_2}{\sigma}\right) - c_m\frac{\sigma_2}{\sigma}(1-g) + gp\theta\left[\frac{\sigma_2}{\sigma}\overline{b(1-q'_\bullet)}(1-c_m) - \frac{u_♀}{\sigma}c'_♀\right] \\
w_{\mathbf{B,Bb\times b}} &= g\frac{s_1}{s}p_♂\left(1-d\frac{q'}{2}\right)(1-c_a) + g\frac{s_1}{s}p_♂ d\frac{q'}{2}(1-c_r) + g\frac{s_1}{s}(1-p_♂) \\
&\qquad + (1-g)\frac{s_2}{s}(1-c_m)(1+B') \\
&= \frac{s_2}{s} + g\left(\frac{s_1}{s} - \frac{s_2}{s}\right) - c_m\frac{s_2}{s}(1-g) + gp\theta\left[\frac{s_2}{s}\overline{b(1-q'_\bullet)}(1-c_m) - \frac{u_♂}{s}c'_♂\right],
\end{aligned}$$

where the effective benefit is

$$\begin{aligned}B' &= \frac{gp\theta}{1-g}\left\{u_{♀}b_{♀}\left[1-\frac{1}{2}\left(Q'+q\right)\right]+u_{♂}b_{♂}\left[1-\frac{1}{2}\left(d\frac{q'}{2}+d\frac{q}{2}\right)\right]\right\}\\ &= \frac{gp\theta}{1-g}\overline{b(1-q'_{\bullet})},\end{aligned}$$

the average cost to females is $c'_{♀} = c_a(1-Q')+c_rQ'$, and the average viability cost to males is $c'_{♂} = c_a(1-dq'/2)+c_rdq'/2$. Adding these two viabilities with their corresponding weights we obtain

$$w_{\mathbf{B\_,Bb\times b}} = 1-c_m(1-g)+gp\theta\left[\overline{b(1-q'_{\bullet})}(1-c_m)-\overline{c}'\right],$$

where the average cost to offspring viability is $\overline{c}' = u_{♂}c'_{♂}+u_{♀}c'_{♀}$. The viability for the reciprocal mating $w_{\mathbf{Bb,bb\times B}}$ is almost the same as that obtained for the first mating except that B' is replaced by

$$\begin{aligned}B'' &= \frac{gp\theta}{1-g}[u_{♀}b_{♀}(1-Q')+u_{♂}b_{♂}\left(1-d\frac{q}{2}\right)]\\ &= \frac{gp\theta}{1-g}\overline{b(1-q''_{\bullet})}\end{aligned}$$

because now all female offspring are mutant, while no male offspring are:

$$\begin{aligned}w_{\mathbf{Bb,bb\times B}} &= g\frac{\sigma_1}{\sigma}p_{♀}(1-Q')(1-c_a)+g\frac{\sigma_1}{\sigma}p_{♀}Q'(1-c_r)+g\frac{\sigma_1}{\sigma}(1-p_{♀})\\ &\qquad +(1-g)\frac{\sigma_2}{\sigma}(1-c_m)(1+B'')\\ &= \frac{\sigma_2}{\sigma}+g\left(\frac{\sigma_1}{\sigma}-\frac{\sigma_2}{\sigma}\right)-c_m\frac{\sigma_2}{\sigma}(1-g)+gp\theta\left[\frac{\sigma_2}{\sigma}\overline{b(1-q''_{\bullet})}(1-c_m)-\frac{u_{♀}}{\sigma}c'_{♀}\right].\end{aligned}$$

Performing the necessary computations, the selection gradient now takes the form

$$\left.\frac{\partial w_{\mathbf{B\_}}}{\partial q'}\right|_{q'=q} = -\frac{1}{2}gp\theta\left[\overline{b\hat{r}d}(1-c_m)-\overline{vd}(c_a-c_r)\right],$$

where $\overline{b\hat{r}d} = u_♀ b_♀ \hat{r}_♀ d_♀ + u_♂ b_♂ \hat{r}_♂ d_♂$ and $\overline{vd} = u_♀ v_♀ d_♀ + u_♂ v_♂ d_♂$, where in turn $d_♀ = 1$ and $d_♂ = d$. The quantities $\hat{r}_i$ give the probability that first-brood mutants of sex i share the mutant allele with second brood individuals, averaged over the two mutant matings. The quantities v_i give the probability that mutant matings produce sex-i mutants. They are

$$\begin{aligned} \hat{r}_♀ &= \zeta\frac{1}{2} + z\sigma_2, & v_♀ &= 1 \\ \hat{r}_♂ &= \zeta\frac{1}{2}, & v_♂ &= \zeta. \end{aligned}$$

Resistance probability decreases if

$$\overline{b\hat{r}d}(1 - c_m) > \overline{vd}(c_a - c_r).$$

To determine how sex-differential manipulation affects the direction of selection, we maximize the ratio $\overline{b\hat{r}d}/\overline{vd}$. This ratio is maximized when manipulation effort is directed only to the sex determined by the larger side of the inequalities

$$b_♀ r_♀ \gtrless b_♂ r_♂,$$

where $r_i = \hat{r}_i / v_i$.

The quantities $\hat{r}_i$ and v_i can be interpreted in standard kin selection terms. We check this numerically for a few cases. Let sex ratio be even ($z = 1/2$). With even sex allocation to the second brood ($s_2 = 1/2$), we have that $\hat{r}_♀ = 1/2$ and $\hat{r}_♂ = 1/4$ (this corresponds to the case of females and males helping both sexes in equal proportion). If sex allocation to the second brood is completely female-skewed ($s_2 = 0$), then $\hat{r}_♀ = 3/4$ (this corresponds to the case of females helping full sisters). If sex allocation to the second brood is completely male-skewed ($s_2 = 1$), then $\hat{r}_♀ = 1/4$ (this corresponds to females helping full brothers). Quantities v_i match the reproductive value of individuals of sex i ($v_♀ = 1$ and $v_♂ = 1/2$; Price, 1970). These values indicate that $\hat{r}_i$ refers to the

Table II.2: Numerical comparison of $\widehat{r}_i$ with standard relatedness coefficients for haplodiploids under single mating and outbreeding. Regression relatedness times the reproductive value of the recipient matches $\widehat{r}_i$. Life-for-life relatedness matches $\widehat{r}_i/v_i$.

	Regression relatedness	Regression relatedness $\times\, v_{\text{recipient}}$	$\widehat{r}_i$	Life-for-life relatedness	$\widehat{r}_i/v_i$
Female to sister	3/4	3/4	3/4	3/4	3/4
Female to brother	1/2	1/4	1/4	1/4	1/4
Male to sister	1/4	1/4	1/4	1/2	1/2
Male to brother	1/2	1/4	1/4	1/2	1/2

regression definition of relatedness times the reproductive value of the recipient, while $\widehat{r}_i/v_i$ refers to the life-for-life definition of relatedness (Hamilton, 1972; Bulmer, 1994, Table II.2). Indeed, let

$$\rho = \begin{pmatrix} \zeta\frac{1}{2} + z & \frac{1}{2} \\ \zeta\frac{1}{2} & \frac{1}{2} \end{pmatrix}.$$

The entries ρ_{ij} match numerically the regression relatedness of first-brood sex i toward second-brood sex j (females are in row and column 1). It can be checked that $\widehat{r}_i = \sum_j f_j v_j \rho_{ij}$, where f_j gives the frequency of recipients of sex j. In our model, $f_{♀} = \sigma_2$ and $f_{♂} = s_2$.

II.5.3 Spontaneous helping

Consider the same scenario but now first-brood individuals may opt to stay a fraction of their adulthood in the maternal site, without any influence from their mother. Let π_i be the probability that a first-brood offspring of sex i spontaneously stays in the maternal site. Let c_s be the cost of spontaneously staying in the maternal site ($0 \leq c_s \leq 1$). Let $b_{i,s}$ be the benefit provided by spontaneously staying individuals of sex i. The reasoning closely follows that of acquiescence. As before, rather than studying independently the evolution of female and male spontaneous helping, we consider a spontaneously staying tendency, π ($0 \leq \pi \leq 1$), a fraction of which is expressed by each sex. Thus, we write $\pi_i = \beta_i \pi$, where β_i measures the tendency of first-brood offspring of sex i to stay spontaneously (e.g., $\beta_{♀} = 1, \beta_{♂} = 0$ means that females stay but males do not). The fraction of the tendency to stay spontaneously corresponding to sex i is $U_i = \beta_i \gamma_{i1}/\Theta$ where $\Theta = \sum \beta_i \gamma_{i1}$ is the fraction of first-brood offspring who have a tendency to stay, so $\sum U_i = 1$. Let **c** be a resident allele for the tendency of staying π, and let **C** be a mutant allele. For diploids, the staying tendency of a mutant of sex i is $\Pi'_i = (\pi'_i + \pi_i)/2$. For haplodiploids, the staying tendency of a mutant female is $\Pi'_{♀} = (\pi'_{♀} + \pi_{♀})/2$ and that of a mutant male is $d\pi'_{♂}/2$. Here, $\pi'_i = \beta_i \pi'$.

Denote by π_{ik} the probability of staying of sex i of genotype k, and by $\pi_{i\bullet}$ the probability of staying of sex-i offspring averaged over the sex-i genotypes arising from a $J \times K$ mating. Denote by $\pi_{ik,T}$ the staying tendency in sex i of genotype k; for instance, for resident females $\pi_{♀R,T} = \pi$ and for resident haplodiploid males $\pi_{♂R,T} = d\pi/2$. Thus, $\pi_{ik} = \beta_i \pi_{ik,T}$, and $\pi_{i\bullet,T}$ is the average $\pi_{ik,T}$ over the genotypes of sex i arising from a $J \times K$ mating. Hence, the effective benefit corresponding to spontaneous helping is

$$\begin{aligned} B_s &= \frac{b_{♀,s} g \sigma_1 \pi_{♀\bullet} + b_{♂,s} g s_1 \pi_{♂\bullet}}{1-g} \\ &= \frac{g\Theta}{1-g}(U_{♀} b_{♀,s} \pi_{♀\bullet,T} + U_{♂} b_{♂,s} \pi_{♂\bullet,T}) \\ &= \frac{g\Theta}{1-g} \overline{b_s \pi_{\bullet,T}}. \end{aligned}$$

For haploids and diploids we have:

$$\begin{aligned} w_{\mathbf{Cc},\mathbf{Cc}\times\mathbf{cc}} &= g\sigma_1 \Pi'_{♀}(1-c_s) + g\sigma_1(1-\Pi'_{♀}) + (1-g)\sigma_2(1+B'_s) \\ &\quad + g s_1 \Pi'_{♂}(1-c_s) + g s_1(1-\Pi'_{♂}) + (1-g)s_2(1+B'_s) \\ &= 1 + g\Theta\left\{\overline{b_s}\left[\frac{1}{2}(\Pi' + \pi)\right] - \Pi' c_s\right\}, \end{aligned}$$

where

$$B'_s = \frac{gR}{1-g}\overline{b_s}\left[\frac{1}{2}(\Pi' + \pi)\right].$$

Since $w_{\mathbf{Cc,cc\times Cc}} = w_{\mathbf{Cc,Cc\times cc}}$, the fitness gradient is

$$\left.\frac{\partial w_{\mathbf{Cc}}}{\partial \pi'}\right|_{\pi'=\pi} = \frac{1}{2} g\Theta\left(\frac{1}{2}\overline{b_s} - c_s\right).$$

The haploid case is identical, except that the 1/2 affecting the rate of selection for diploids disappears.

For haplodiploids we have:

$$\begin{aligned}
w_{\mathbf{Cc,Cc\times c}} &= g\frac{\sigma_1}{\sigma}\Pi'_{\text{♀}}(1-c_s) + g\frac{\sigma_1}{\sigma}(1-\Pi'_{\text{♀}}) + (1-g)\frac{\sigma_2}{\sigma}(1+B'_s) \\
&= \frac{\sigma_2}{\sigma} + g\left(\frac{\sigma_1}{\sigma} - \frac{\sigma_2}{\sigma}\right) + g\left(\frac{\sigma_2}{\sigma}\Theta\overline{b_s\pi'_{\bullet}} - \frac{\sigma_1}{\sigma}\beta_{\text{♀}}\Pi' c_s\right) \\
w_{\mathbf{C,Cc\times c}} &= g\frac{s_1}{s} d\frac{\pi'_{\text{♂}}}{2}(1-c_s) + g\frac{s_1}{s}\left(1 - d\frac{\pi'_{\text{♂}}}{2}\right) + (1-g)\frac{s_2}{s}(1+B'_s) \\
&= \frac{s_2}{s} + g\left(\frac{s_1}{s} - \frac{s_2}{s}\right) + g\left(\frac{s_2}{s}\Theta\overline{b_s\pi'_{\bullet}} - \frac{s_1}{s}\beta_{\text{♂}} d\frac{\pi'}{2}c_s\right),
\end{aligned}$$

where

$$\begin{aligned}
B'_s &= \frac{g\Theta}{1-g}\left[U_{\text{♀}} b_{\text{♀},s}\frac{1}{2}(\Pi' + \pi) + U_{\text{♂}} b_{\text{♂},s}\frac{1}{2}\left(d\frac{\pi'}{2} + d\frac{\pi}{2}\right)\right] \\
&= \frac{g\Theta}{1-g}\overline{b_s\pi'_{\bullet}}.
\end{aligned}$$

Adding these two viabilities with their corresponding weights we obtain

$$w_{\mathbf{C\_,Cc\times c}} = 1 + g\Theta\left(\overline{b_s\pi'_{\bullet}} - \overline{\pi}' c_s\right),$$

where $\overline{\pi}' = U_{\text{♀}}\Pi' + U_{\text{♂}} d\pi'/2$. For the reciprocal mating,

$$\begin{aligned}
w_{\mathbf{Cc,cc\times C}} &= g\frac{\sigma_1}{\sigma}\Pi'_{\text{♀}}(1-c_s) + g\frac{\sigma_1}{\sigma}(1-\Pi'_{\text{♀}}) + (1-g)\frac{\sigma_2}{\sigma}(1+B''_s) \\
&= \frac{\sigma_2}{\sigma} + g\left(\frac{\sigma_1}{\sigma} - \frac{\sigma_2}{\sigma}\right) + g\left[\frac{\sigma_2}{\sigma}\Theta\overline{b_s\pi''_{\bullet}} - \frac{\sigma_1}{\sigma}\beta_{\text{♀}}\Pi' c_s\right],
\end{aligned}$$

where

$$\begin{aligned}B''_s &= \frac{g\Theta}{1-g}\left(U_{♀} b_{♀,s}\Pi' + U_{♂} b_{♂,s} d\frac{\pi}{2}\right)\\ &= \frac{g\Theta}{1-g}\overline{b_s\pi''_{\bullet}}.\end{aligned}$$

Performing the indicated computations, the selection gradient is now

$$\left.\frac{\partial w_{\mathbf{C}_-}}{\partial \pi'}\right|_{\pi'=\pi} = \frac{1}{2}g\Theta\left(\overline{b_s\hat{r}d} - \overline{vd}c_s\right),$$

where $\overline{b_s\hat{r}d}$ and $\overline{vd}$ are defined as for resistance with terms accordingly reinterpreted.

II.5.4 Comparison of manipulated and spontaneous helping

We first write the benefit provided by helpers of sex i as $b_i = h_i a$, where h_i is the probability that an acquiescing individual of sex i provides help to the second brood (helping probability). The quantity a gives the amount of benefit. Assume that sex-differential manipulation and spontaneous helping, the benefit from acquiescence and spontaneous helping, and the costs of acquiescence and spontaneous helping are correspondingly approximately the same (i.e., $u_i \approx U_i$, $b_i \approx b_{i,s}$, and $c_a \approx c_s$). Then, from inequalities (II.4), (II.5) and (II.6), manipulation and acquiescence are selected while spontaneous helping is not if the benefit-cost ratio satisfies the following conditions:

$$\frac{a}{c_a} > \frac{1}{\overline{h(1-q)}}\frac{\overline{c}}{c_a(1-c_m)} = T_m \tag{II.12a}$$

$$\frac{a}{c_a} > \frac{\overline{vd}}{\overline{hrd}}\frac{1-c_r/c_a}{1-c_m} = T_a \tag{II.12b}$$

$$\frac{a}{c_a} < \frac{\overline{vd}}{\overline{hrd}} = T_A. \tag{II.12c}$$

Following our notation, here $\overline{h(1-q)} = \sum u_i h_i(1-q_i)$, $\overline{vd} = \sum u_i v_i d_i$ and $\overline{hrd} = \sum u_i h_i r_i d_i$. For inequalities (II.12) to be satisfied simultaneously, it is required that $T_A > T_m, T_a$. We thus define the ratio of thresholds for selection of spontaneous helping relative to manipulated helping as

$$H = \begin{cases} T_A/T_a & \text{if } T_m < T_a \\ T_A/T_m & \text{otherwise.} \end{cases} \tag{II.13}$$

The quantity H measures the extent to which spontaneous helping is “harder” to select than manipulated helping. Manipulated helping requires smaller benefit-cost ratios than spontaneous helping if $H > 1$, in which case we say that the advantage of manipulated helping occurs. Substituting (II.12) into (II.13), we obtain

$$H = \begin{cases} \frac{1-c_m}{1-c_r/c_a} & \text{if } c_r < c_a(1-A_1) \\ A_2\frac{1-c_m}{1-\overline{q}+\overline{q}c_r/c_a} & \text{otherwise,} \end{cases}$$

where

$$A_1 = \frac{\overline{hrd}}{\overline{vd}\;\overline{h(1-q)}+\overline{hrk}\;\overline{q}}$$

$$A_2 = \frac{\overline{vd}\;\overline{h(1-q)}}{\overline{hrd}}.$$

Therefore, if acquiescence is harder to select than manipulation ($T_m < T_a$), the advantage of manipulated helping exists when

$$c_a c_m < c_r < c_a(1-A_1) \tag{II.14a}$$

$$\text{and } c_m < 1-A_1. \tag{II.14b}$$

If manipulation is harder to select than acquiescence ($T_m > T_a$), the advantage of manipulated helping exists when

$$c_a(1-A_1) < c_r < c_a\frac{1}{\overline{q}}\left[(1-c_m)A_2-(1-\overline{q})\right] \tag{II.15a}$$

$$\text{and } c_m < 1-\frac{1}{A_2}\left(1-\overline{q}A_1\right). \tag{II.15b}$$

As expected, inequalities (II.14) and (II.15) show that the advantage of manipulated helping is more likely to exist as the cost of manipulation c_m decreases and the cost of resistance c_r increases up to a limit.

II.5.4.1 Example 1

Suppose that resistance is absent ($q = 0$). For haplodiploids, suppose further that manipulation effort is entirely applied to female offspring ($u_{♀} = 1$), and that sex allocation to the second brood is even ($s_2 = 1/2$). These conditions lead to $r_{♀} = 1/2$, $\overline{vd} = 1$ and $\overline{hrd} = \overline{h}/2$. Then, $A_1 = 1/2$ and $A_2 = 2$. Hence, the ratio of thresholds for selection of spontaneous helping relative to manipulated helping reduces to

$$H = \begin{cases} \frac{1-c_m}{1-c_r/c_a} & \text{if } c_r < \frac{1}{2}c_a \\ 2(1-c_m) & \text{otherwise.} \end{cases}$$

Hence, the advantage of manipulated helping exists if $c_m < 1/2$ and

$$\begin{aligned} c_a c_m < c_r &< \frac{1}{2}c_a \\ \text{or} \quad c_r &> \frac{1}{2}c_a. \end{aligned}$$

The top line corresponds to the case in which acquiescence is “harder” to select (requires larger benefit cost ratios) than manipulation. The bottom line corresponds to that in which manipulation is harder to select than acquiescence. From this, it follows that a sufficient condition for the advantage to exist in this case is that the cost of manipulation c_m is smaller than the smallest value between c_r/c_a and 1/2.

II.5.4.2 Example 2

Suppose instead that resistance is complete for haplodiploids ($q = 1$). Suppose further that manipulation effort is entirely applied to male offspring ($u_{♂} = 1$) and that males are haploid in the tissue that controls their resistance ($d_{♂} = 1$, thus $\overline{q} = 1/2$). It follows that $\overline{vd} = \zeta$ and that the relevant relatedness is $r_{♂} = \zeta/2$. Then, $A_1 = 2/3$ and $A_2 = 1$. Hence, the ratio of thresholds in this case is

$$H = \begin{cases} \frac{1-c_m}{1-c_r/c_a} & \text{if } c_r < \frac{1}{3}c_a \\ 2\frac{1-c_m}{1+c_r/c_a} & \text{otherwise.} \end{cases}$$

Hence, the advantage of manipulated helping exists if $c_m < 1/3$ and

$$\begin{aligned} & c_a c_m < c_r < \frac{1}{3}c_a \\ \text{or} \quad & \frac{1}{3}c_a < c_r < c_a(1-2c_m). \end{aligned}$$

Again, the top line corresponds to the case in which acquiescence is harder to select than manipulation, while the bottom line corresponds to the reverse case. A sufficient condition for the advantage to exist is that the cost of manipulation c_m is smaller than the smallest value among c_r/c_a, $(1-c_r/c_a)/2$, and 1/3.

II.5.5 Dynamics

The expressions for fitness gradients for haploids and diploids (II.9) and (II.10) are generalized by those for haplodiploids (II.11) and (II.5.2), so it is sufficient to look at the haplodiploid case. We rewrite the condition for the evolution of manipulation (II.4) as $M_0 - qM > 0$, where both terms M_0 and M are independent of the resistance probability q. These terms are defined in eqs. (II.8). The term M_0 measures selection for manipulation when there is no resistance. The term $M_1 = M_0 - M$ measures selection for manipulation when there is full resistance. The term $M = M_0 - M_1$ measures the effect of acquiescence on selection for manipulation. The direction of selection of manipulation changes at the resistance probability $q^* = M_0/M$. The term R measures selection for resistance.

Manipulation effort remains constant on the line $q = q^* = M_0/M$. Resistance probability remains constant on the line $p = 0$. There is thus a single equilibrium point $(0, q^*)$. The eigenvalues of the Jacobian evaluated at the equilibrium point specify the global dynamics because the system is linear. They are

$$\lambda = \pm \frac{1}{2} g\theta \sqrt{-\mu_p \mu_q \zeta M R}$$

dropping 1/2 for haploids. The corresponding eigenvectors are

$$\left(\mp \sqrt{\frac{\mu_p \zeta M}{-\mu_q R}}, 1 \right)^T$$

The separatrixes are thus

$$q = q^* \pm p \sqrt{\frac{-\mu_q R}{\mu_p \zeta M}}. \qquad \text{(II.16)}$$

Figure II2.4 illustrates qualitatively the different dynamic regimes for haploids and diploids while Figure II2.5 shows possible dynamics for haplodiploids.

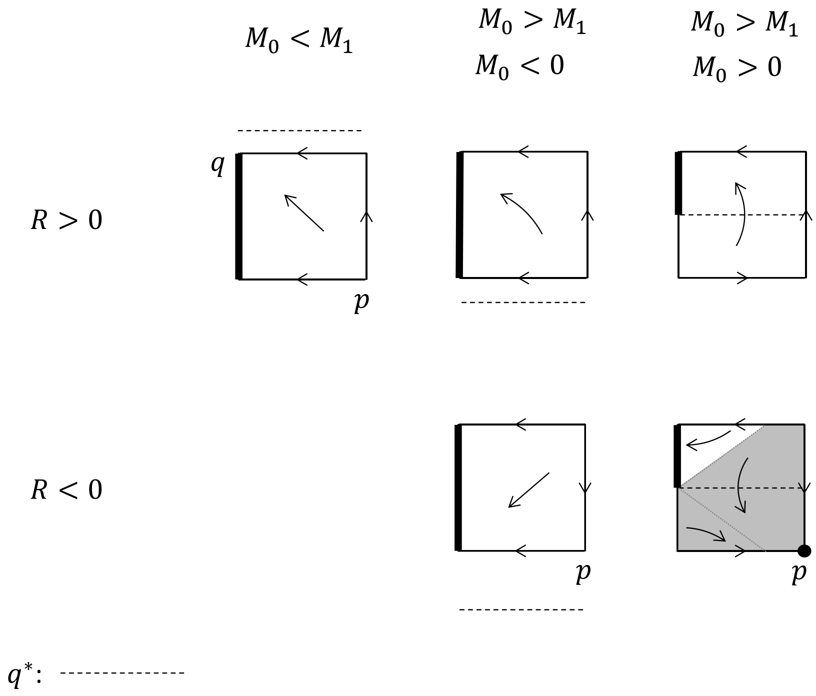


Figure II2.4: Coevolutionary dynamics for haploids and diploids. The legend of figure 1.2 applies. The case $M_0 < M_1$ and $R < 0$ is not possible since $M > -R$ for haploids and diploids. For these genetic systems, $M_1 < 0$. The mother wins when manipulation effort and resistance probability fall within the gray region.

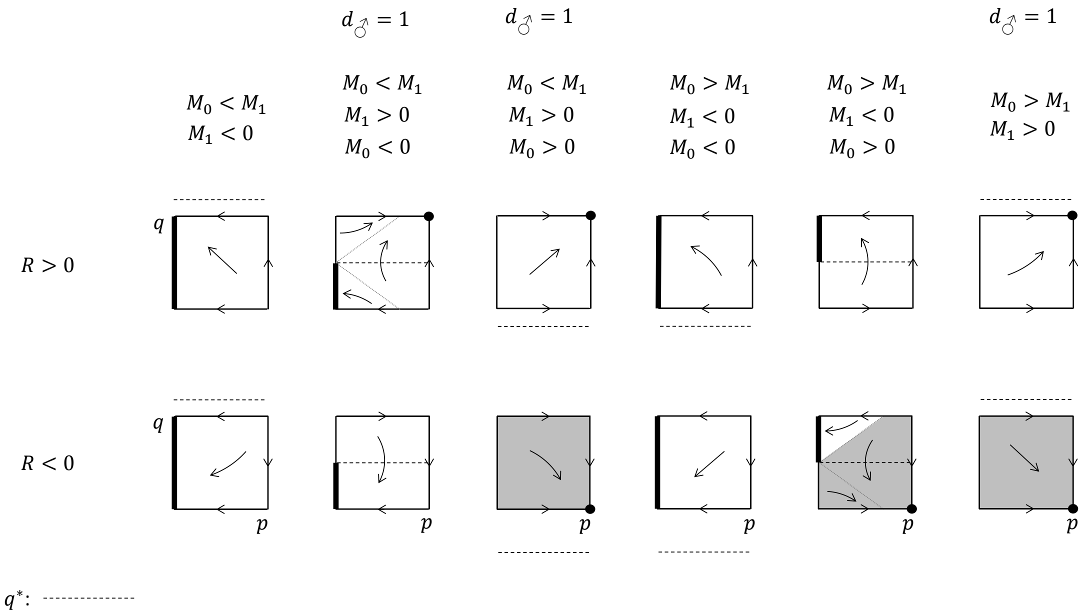


Figure II2.5: Coevolutionary dynamics for haplodiploids. There are three additional columns with respect to haploids and diploids that occur only if $d_♂ = 1$ as required by $M_1 > 0$. The mother wins when manipulation effort and resistance probability fall within the gray region. Numerical values satisfying the phase portraits in the second row with second and third column have not been found.

Appendix III

Invasion analysis of maternally manipulated helping: evolution of the benefit

III.1 Introduction

In this appendix, I give an invasion analysis treatment to the evolution of the benefits and costs as considered in chapters 2 and 3. The invasion analysis approach yields the same results with the clarity yet less generality brought by complete genetic treatment. I consider the simultaneous evolution of the offspring-controlled benefit (Chapter 2) and of the maternally-controlled benefit (Chapter 3). This consideration generates more complicated mathematics which prevents one from reaching many of the analytical results of chapters 2 and 3. Consequently, I use numerical explorations in this appendix.

III.2 Model

I extend the model in Appendix II. The model considers a population where mothers produce two subsequent broods and one or both parents provide parental care. A mother manipulates some of her first-brood offspring to delay dispersal (for instance, by feeding them poorly, or by disrupting their development physiologically or psychologically). Manipulated offspring may or may not resist manipulation. If they resist they disperse without delay, or if they acquiesce they stay for a fraction of their adulthood. Acquiescing offspring may or may not help raise the second brood while they are delayed. I thus consider the evolution of three traits: offspring dispersal, helping, and the extent of the delay. Mother and offspring influence the expression of each trait.

A mother directs her manipulation effort toward a fraction θ of her first brood. This target set may be constituted by females, males or some combination of them. Manipulation effort is the fraction p of the target set that the mother manipulates to stay. Manipulating mothers pay an manipulation cost c_m measuring their reduced probability to survive to produce the second brood. Manipulated offspring may resist by dispersing without delay with probability q in which case they pay the resistance cost c_r. Alternatively, manipulated offspring may acquiesce by staying with probability $1-q$, and thus pay the acquiescence cost c_a. Acquiescing offspring stay in the maternal site for a fraction δ of their adulthood, and may express parental care, providing the second brood with a viability benefit b. The benefit b depends on the condition in which the mother leaves second-brood offspring and on the extent in which acquiescing offspring help.

The help provided by an acquiescing individual increases the viability of members of the second brood by an amount b. This fitness benefit is distributed uniformly among all second brood individuals. I allow the sexes to have different helping probabilities. Let $b_♀$ and $b_♂$ be the benefit provided by females and males, respectively. The effective benefit received by second-brood offspring of a given genotype is thus

$$b_E = \frac{b_♀ \times \text{\# of female helpers} + b_♂ \times \text{\# of male helpers}}{\text{\# of recipients}}. \tag{III.1}$$

The benefit provided by sex i is $b_i = a_i h_i$, where h_i is the helping probability of sex i which gives the probability that an acquiescing individual of sex i provides help to the second brood. The quantity a_i is the amount of benefit provided, which includes ecological factors and factors that may be under maternal or offspring control: for example, a_i may be a function of the number of offspring that a mother does not fully raise herself, and of the fraction of adulthood that she attempts to delay her manipulated offspring. I write $a_i = \delta_i(a_0 + e)$ where e is a part of the benefit under maternal control relating to the condition in which the mother leaves the offspring (I let $0 \leq e \leq e_{\max}$), and a_0 is the baseline amount of benefit which includes any remaining components of a_i.

The benefit provided b_i may also affect the cost of acquiescence c_a because helping effort may affect reproductive success. I thus expand c_a in terms of b. The effect of helping may be different before dispersal and after dispersal. For example, a helping individual may have reduced reproductive output before dispersal since it allocates time and energy to alloparenting, but after dispersal it may have enhanced reproductive output if it learned parenting skills as a former alloparent. I thus split the cost of acquiescence to offspring of sex i into the cost of acquiescence before dispersal (c_δ) and after dispersal ($c_{\to\delta}$):

$$c_{ai} = \delta_i c_{\delta i} + (1 - \delta_i) c_{\to\delta i}. \tag{III.2}$$

Before dispersal, the cost to an acquiescing offspring that helps is $\kappa_{\delta h}$ and the cost to one that does not help is $\kappa_{\delta\neg h}$. For example, if by not helping an acquiescing individual can exploit resources and reproduce at the maternal site, $\kappa_{\delta\neg h}$ would be negative reflecting a fitness gain. After dispersal, the cost to a previously acquiescing offspring that helped is $\kappa_{\to\delta h}$ and the cost to one that did not is $\kappa_{\to\delta\neg h}$. So, if by helping, an acquiescing individual learns useful parenting skills, $\kappa_{\to\delta h}$ would also be negative. Since I am interested in cases of permanent sterility, I will consider $0 \leq \kappa_{ij} \leq 1$. Finally, I normalize the amount of benefit provided as $b_i/b_{\max}$, where $b_{\max}$ is the maximum benefit that offspring can provide, and will be referred to as offspring helping efficiency. Then, the cost of acquiescence before dispersal and after dispersal are

$$c_{\delta i} = \frac{b_i}{b_{\max}} \kappa_{\delta h} + \left(1 - \frac{b_i}{b_{\max}}\right) \kappa_{\delta \neg h} \tag{III.3a}$$

$$c_{\rightarrow \delta i} = \frac{b_i}{b_{\max}} \kappa_{\rightarrow \delta h} + \left(1 - \frac{b_i}{b_{\max}}\right) \kappa_{\rightarrow \delta \neg h}. \tag{III.3b}$$

Rearranging, the cost of acquiescence becomes

$$c_{ai} = \frac{b_i}{b_{\max}} c_{hi} + \left(1 - \frac{b_i}{b_{\max}}\right) c_{\neg hi}, \tag{III.4}$$

where the costs for helping and for not helping are

$$c_{hi} = \delta_i \kappa_{\delta h} + (1 - \delta_i) \kappa_{\rightarrow \delta h} \tag{III.5a}$$

$$c_{\neg hi} = \delta_i \kappa_{\delta \neg h} + (1 - \delta_i) \kappa_{\rightarrow \delta \neg h}. \tag{III.5b}$$

The cost of acquiescence thus depends on the amount of benefit provided and on costs ($\kappa_{\delta h}, \kappa_{\delta \neg h}, \kappa_{\rightarrow \delta h}, \kappa_{\rightarrow \delta \neg h}$) that depend on the ecology. The extent of delay δ is under shared control: $\delta = \delta_m - \delta_o$ where δ_m is under maternal control and δ_o is under offspring control (Frank and Crespi, 2011). Therefore, each trait is under the influence of mother and offspring: dispersal (whose maternal effect is p and offspring effect is q), helping (maternal effect is e, offspring effect is h) and delay (maternal effect is δ_m, offspring effect is δ_o). Finally, I let the helping probability evolve independently for each sex: the helping probability of sex i is h_i. This produces 7 coevolving subtraits (p, q, e, $h_♀$, $h_♂$, δ_m, and δ_o). The population is assumed to be either sexual haploid, diploid, or haplodiploid. Further details of the model are described in §III.5.

III.3 Results

Each subtrait is assumed to be controlled by a separate locus with a continuum of alleles and I study the invasion of mutant alleles. This yields the selection gradient for each subtrait (§III.5.1–III.5.3). Numerical solutions of the system produce evolutionary dynamics of the kind illustrated in Figs. III3.1A,B. Fig. III3.1B shows that the evolution of resistance can be reverted by the evolution of maternally induced benefits. I refer to such a phenomenon as a rescue of eusociality by maternally induced benefits. Therefore, under initial conditions in which altruism is not favored, maternal manipulation can produce altruism due to the evolution of the benefit.

To illustrate how maternally induced benefits relate to specific features controlled by the mother, let e refer to a part of the benefit that depends on the condition in which offspring are left by the mother (West Eberhard, 1975). I model this in a simple way by assuming that the mother provisions her second-brood offspring with full maternal care up to an offspring after which she provides no maternal care (§III.5.7). This results in $e = e_0(n - j_0)$, where e_0 is the benefit that a minimal-condition (i.e., when provisioned with no maternal care) individual obtains when helped, n is the number of second-brood offspring, and j_0 is the second-brood offspring at which the mother stops providing care. Both n and j_0 are assumed to be under maternal control. Substituting this form of e in the system produces rescues with dynamics as in Fig. III3.1C–E. As a result, maternally induced benefits can arise if the mother stops caring for some of her offspring (i.e., if she reduces j_0; Figs. III3.1C and D), or if she produces additional offspring some of which she will not raise herself (i.e., if she increases n; Figs. 2D and 2E). Which of these regimes is observed depends on how close a mother is from reaching her maximum fertility. Extreme division of reproductive labor is obtained as in Fig. III3.1E, where the mother becomes highly fertile and refrains from providing any maternal care to the second brood, which is cared for by her acquiescing offspring.

To disentangle the reasons for the rescue, I obtain analytical conditions for the increase in each variable (Fig. III3.2). Three different Alexander-Trivers (Alexander, 1974; Trivers, 1974) rules are obtained for the maternally controlled subtraits, and three different Hamilton's rules (Hamilton, 1964b) for the offspring controlled subtraits. The inequalities for maternal manipulation p and offspring resistance q recover previous results (González-Forero and Gavrilets, 2012). The maternally induced benefits e are

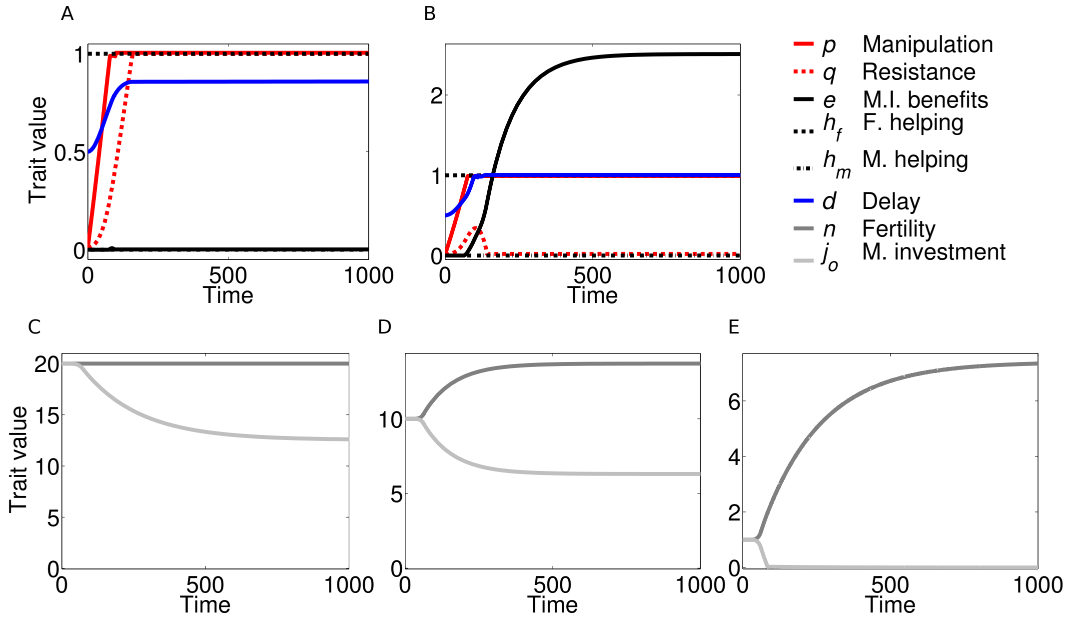


Figure III3.1: Rescue of eusociality by the maternally induced benefit. Numerical solutions for haplodiploids are shown. Dispersal is in red, helping in black and delay in blue. Offspring controlled subtraits are in dashed lines. (*A*) Resistance evolves and eliminates manipulated helping since all offspring leave without delay (in this panel, $e_{\max} = 9$). (*B*) Resistance is eliminated by the evolution of maternally induced benefits once the Hamilton's rule for dispersal is satisfied (in this panel $e_{\max} = 10$). (*C*–*E*) Three regimes of rescues depending on initial conditions. The number of second-brood offspring, n (dark grey), and the offspring at which the mother stops provisioning, j_0 (light grey), start (*C*) at their maximum, (*D*) at an intermediate value and (*E*) at a low value. For *C*–*E* the same scenario of *A* and *B* is used except that $e_{\max} = 20$ for illustration. Life-for-life relatedness of actors toward recipients is 1/2 throughout numerical solutions. The timescale is rescaled, and the original timescale is to be obtained by dividing the x-axis by the magnitude of the mutational process (i.e., mutation rate and mutation effect).

favored if manipulation effort p is favored and the maximum maternally induced benefit $e_{\max}$ is large. A large $e_{\max}$ does not refer to large actual benefits, but to the lack of constraints in the mother to evolve them. For the evolution of offspring helping h_i the difference between the cost of helping c_h and the cost of not helping $c_{\neg h}$ is weighted by offspring helping efficiency $b_{\max}$. That is, increasing helping efficiency, reduces selection against helping. As for maternally induced benefits, selection for helping does not depend on actual benefits, but on offspring's efficiency to provide them. The evolution of delay (δ_m and δ_o) depends on the difference between the cost of acquiescence and its component after dispersal ($c_a - c_{\to\delta}$), and on the former and its component from not helping ($c_a - c_{\neg h}$). Such differences between costs allow for offspring controlled subtraits to evolve with zero relatedness, despite positive costs: acquiescence evolves with zero relatedness if resistance is costlier than acquiescing ($c_a < c_r$) (González-Forero and Gavrilets, 2012); helping does if not helping is costlier than helping ($c_h < c_{\neg h}$); and delay does if both not helping is costlier than helping ($c_h < c_{\neg h}$) and the cost after dispersal is greater than before dispersal ($c_\delta < c_{\to\delta}$). In consequence, maternally induced helping does not require relatedness to be stable, despite positive costs, if it is costlier to rebel against manipulation. However, relatedness does facilitate the evolution of maternally induced helping. Finally, the occurrence of three different Hamilton's rules suggests a reason for the rescue to happen: even if the Hamilton's rule for dispersal is not satisfied, the Hamilton's rule for helping or delay may be satisfied and thus allow for the benefit to increase.

In order to determine if any of the subtraits is a particular facilitator of rescues, I determined whether it was necessary that a given subtrait be favored at the start of the process for there to be a rescue. This was done numerically for a set of parameter combinations (§III.5.5-III.5.6). I find that for rescues to occur, the offspring helping subtrait $\overline{h}$ must be initially selected for (Fig. III3.3A). In addition, maternal manipulation p, offspring helping $\overline{h}$, and the maternal effect on delay δ_m had to be initially easier to select for (i.e., require lower benefits) than offspring resistance q (Fig. III3.3B). If manipulation effort is directed entirely to sex-i offspring, the latter necessary conditions

Dispersal	maternal effect (p)	$\overline{b(1-q)}(1-c_m) > \bar{c}$
	offspring effect ($-q$)	$\overline{brd}(1-c_m) > \overline{vd(c_a-c_r)}$
Helping	maternal effect (e)	$e < \frac{1}{2}\left(e_{\max} - a_0 - \frac{1-C_m}{\Delta e_\infty}\right)$
	offspring effect (h_i)	$r_i(1-c_m) > v_i \frac{c_{hi}-c_{\neg hi}}{b_{\max}}$
Delay	maternal effect (δ_m)	$\overline{\frac{b}{\delta}(1-q)}(1-c_m) > \overline{\frac{1}{\delta}(1-q)(c_a - c_{\to\delta} + c_a - c_{\neg h})}$
	offspring effect ($-\delta_o$)	$\overline{\frac{brd}{\delta}(1-q)}(1-c_m) > \overline{\frac{vd}{\delta}(1-q)(c_a - c_{\to\delta} + c_a - c_{\neg h})}$

Figure III3.2: Conditions for increase in each of the subtraits considered. The overbars indicate averages taken over the manipulated offspring of a mother (i.e., $\overline{x} = \sum_i u_i x_i$, where u_i is the fraction of manipulation effort that goes toward sex-i offspring). $c_m = (1-g)c_m + gp\theta\left[\overline{c_{\neg h}(1-q)} + c_r\overline{q}\right]$ is the reduction in mother's fertility due to wasted effort and $\Delta e_\infty = gp\theta\overline{\delta h(1-q)\,[1-c_m-(c_h-c_{\neg h})/b_{\max}]}$ is proportional to the selection gradient for e when $e_{\max} \to \infty$ (§III.5.2.2.1). r_i is the reproductive-value-weighted relatedness of sex i toward the second brood, v_i is the reproductive value of sex i, r_i/v_i is the life-for-life relatedness of sex i toward the second brood (Hamilton, 1972), k_i is the dosage compensation of sex i (§III.5.3), and g is the fraction of offspring that belong to the first brood.

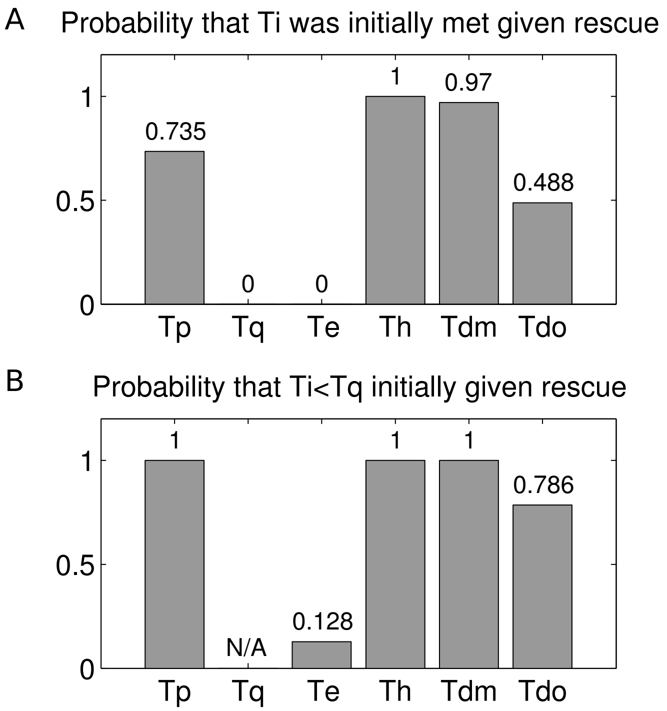


Figure III3.3: Tests for necessary conditions. Inequalities in Fig. III3.2 define thresholds, T_i, so that the condition for subtrait i to be selected for is $a_0 + e > T_i$ (section 4 in SI Appendix). The histograms give the probability that the threshold for a given subtrait at the start of a run is (*A*) greater than $a_0 + e$ and (*B*) smaller than T_q. Total runs: 310,692. Total rescues: 11,354. For a rescue to occur, a condition had to be necessarily met at the start of numerical solutions if the bar height is 1.

(i.e., that initially $T_p, T_h, T_{\delta m} < T_q$) reduce to $c_r < c_{ai} A_1, c_{\neg hi}, c_{ai} - A_2$ for some quantities A_1 and A_2 (§III.5.6). That is, the cost of resistance must be sufficiently small for rescues to occur, otherwise resistance would not be favored in the first place (González-Forero and Gavrilets, 2012). As a result, a driving force for the rescue is not a cost of resistance, but the selection for helping even though resistance is favored. This indicates that it is the lack of conflict over helping that allows for the conflict over dispersal to be eliminated. The mother can thus capitalize on the helping available, opening the possibility that the rescue proceeds. On the other hand, no sufficient conditions could be identified in terms of the initial values of the thresholds (Fig. III3.6).

III.4 Discussion

Advanced eusociality evolves here in the following steps: 1) mothers cause delayed dispersal; 2) when a mother-offspring conflict over dispersal occurs and offspring are still favored to help, maternally induced benefits can be favored; 3) maternally induced benefits can evolve to a point where offspring are selected to stay voluntarily; 4) when the mother is not constrained to small fertility, extreme fertility is produced. The evolution of helping produces division of reproductive labor and eliminates any incentive to disperse if manipulated. Maternal manipulation can therefore produce two major features of advanced eusociality: non-conflictive social determination of reproductive status and extreme fertility in reproductives.

Even though the winner of a conflict is often expected to be the party that pays smaller costs (Clutton-Brock, 1998), the rescue can still occur when maternal manipulation is costlier than offspring resistance (Fig. III3.1B). In addition, maternally manipulated behavior that would otherwise be unstable can be rescued by maternally induced benefits. For example, if a mother disrupts psychologically some of her offspring, disrupted offspring may initially acquiesce and stay. If the cost of resistance to psychological disruption is small, resistance to disruption would be favored. However, if disrupted offspring express sufficient help, maternally induced benefits may win the race eliminating resistance to disruption. Eusociality via maternally induced disruption would thus be a feasible possibility, which otherwise would have been too subtle to be stable.

The capacity to be hyperfertile is present in non-eusocial insects (Kamakura, 2011), and thus it is not sufficient to produce eusociality. This is consistent with the present model in that it is also necessary that there is parental care and the ability of mothers to direct manipulation effort to helping offspring (González-Forero and Gavrilets, 2012). Hyperfertility would only be beneficial if help is available. Maternal manipulation makes help available, allowing hyperfertility to evolve. In this light, social determination of reproductive status would act as inducing some offspring to develop into workers, while inducing others (queens) to take advantage of the help made available. Regarding polyandry, with the evolution of maternally induced benefits, delayed dispersal can be selected for with increasingly smaller relatedness. Thus, if polyandry is favored (Mattila and Seeley, 2007), already advanced eusocial colonies can evolve polyandry without reverting to subsociality. In such a case, polyandry would be an effect rather than a cause of advanced eusociality. Yet, as polyandry evolves, policing would also be favored in hymenopterans (Ratnieks, 1988).

Advanced eusociality is often considered to be a maximal expression of sociality (Hölldobler and Wilson, 2009). Here advanced eusociality evolves via socially manipulated behavior. The inequalities found for trait evolution offer insights into the evolutionary dynamics, illustrating for example how relatedness may not be necessary even if it is favorable. These results offer a distinct form of conflict resolution with applicability to settings other than mother-offspring interactions, for instance when relatedness arises as a phenotypic correlation (Frank, 1998).

III.5 Calculation details

III.5.1 Model

The model extends that in Appendix II. I consider a very large sexual population where mated females produce two subsequent, overlapping broods. Young offspring receive parental care. Parents die after the second brood is raised. Adult offspring disperse from the maternal site to a common mating pool. Individuals at the mating pool mate singly and randomly. A mother manipulates a fraction p of a target set θ of the first brood to stay as adults. p is referred to as manipulation effort. Manipulated offspring may acquiesce by staying in the maternal site or alternatively, they may resist and disperse without delay. The probability that a manipulated offspring disperses without delay is q. Acquiescing offspring stay for a fraction δ of their adulthood during which they express some form of helping with some probability.

A manipulating mother pays the cost of manipulation c_m which measures her reduced probability of surviving to produce the second brood. Acquiescing offspring pay the cost of acquiescence c_a that measures their diminished reproductive success because of delayed dispersal and helping effort. A resisting individual disperses without paying the cost of acquiescence, but pays the cost of resistance c_r which measures its reduced probability to complete dispersal and events thereafter (e.g., nest founding).

I seek to study the coevolution of maternal manipulation p, offspring resistance q, and the maternally induced benefit e. As seen above, the evolution of e affects the benefit of helping as well as the cost of acquiescence. Such benefit and cost also depend on the evolution of helping probabilities h_i, and on the extent of delay δ. Thus, an adequate dynamical study of the coevolution of manipulation, resistance, and maternally induced benefits should consider the evolution of helping probabilities and delay. Therefore, I study the coevolution of p, q, e, h_i, and δ. I consider p and e to be under maternal control, q and h_i under offspring control, and δ under shared control. Thus, I express the delay of sex i as $\delta_i = \delta_m - \delta_{oi}$ where δ_m is under maternal control while δ_{oi} is under offspring control. This produces 7 coevolving subtraits (p, q, e, $h_♀$, $h_♂$, δ_m, and δ_o).

I consider each subtrait to be controlled by a separate locus. I assume that mutation is rare enough so that when a mutant allele arises, there is enough time for it to approach an equilibrium frequency before another mutant allele arises (see e.g., Metz et al., 1996; Geritz et al., 1998; Waxman and Gavrilets, 2005). This allows one to consider separately the spread of mutant alleles in each of the loci, without any specific assumption about linkage among them. I do not consider mechanisms that produce polymorphism (such as overdominance or frequency dependent selection), so the allelic equilibrium frequency is always either zero or one. I denote by $\mathbf{a}_i$ and $\mathbf{A}_i$ the resident and mutant alleles for the locus i respectively. For a resident subtrait value x, I denote by x' the mutant subtrait value.

The proportion of males produced by a mating is s (sex allocation) and that of females is $\sigma = 1 - s$. The proportion of offspring that belong to the first brood is g. I allow for a different sex allocation to each brood, with s_i being the sex allocation to brood i, so that $s = gs_1 + (1-g)s_2$. The allocation into females for brood i is $\sigma_i = 1 - s_i$. A resident mother manipulates first brood female- and male offspring with effort $p_{♀} = \alpha p$ and $p_{♂} = \beta p$ (where $0 \le p, \alpha, \beta \le 1$). The quantities α and β are proportionality constants of the manipulation effort p that goes toward males or females respectively. A resident mother directs her manipulation effort toward a fraction of the first brood $\theta = \sigma_1\alpha + s_1\beta$. Thus, the fraction of manipulation effort that goes to females and males is respectively $u_{♀} = \sigma_1\alpha/\theta$ and $u_{♂} = s_1\beta/\theta$ (so $u_{♀} + u_{♂} = 1$). I now write a general definition of the effective benefit in the model. Let x_{ij} denote the subtrait value of sex i of genotype j. Denote by $x_{i\bullet}$ the average over the offspring genotypes of sex i that arise from a given mating. Then, the effective benefit takes the form

$$\begin{aligned}
b_E &= \frac{b_{♀\bullet} g \sigma_1 p_{♀}(1-q_{♀\bullet}) + b_{♂\bullet} g s_1 p_{♂}(1-q_{♂\bullet})}{1-g} \\
&= \frac{gp\theta}{1-g}\left[u_{♀} b_{♀\bullet}(1-q_{♀\bullet}) + u_{♂} b_{♂\bullet}(1-q_{♂\bullet})\right] \\
&= \frac{gp\theta}{1-g}\overline{b_{\bullet}(1-q_{\bullet})}.
\end{aligned}$$

Because mutation is rare, the mutant allele is involved only in matings $M \times R$ (where M is a mutant carrier, and R is a resident; females on the left) or in matings $R \times M$. Denote by $w_{I,J\times K}$ the viability of a mutant individual I given that its mother and father are J and K, respectively. Hence, the average viability of mutants is

$$w_M = \zeta w_{M,M\times R}\left(1 - \frac{e_M}{e_{\max}}\right) + z w_{M,R\times M}\left(1 - \frac{e_R}{e_{\max}}\right), \tag{III.6}$$

where $\zeta = 1 - z$ and z are the respective frequencies of females and males (sex ratio) in the population, corresponding to the frequency of mutant parents of a given sex. The factor $1 - e/e_{\max}$ captures the reduction of mother's fertility as the number of offspring that she does not raise herself increases. Assuming that mutation is of small effect and that the mother produces a very large number of offspring, the evolutionary change in subtrait x is proportional to its selection gradient given by $\partial w_M / \partial x'|_{x'=x}$ (Kimura, 1965; Lande, 1979; Iwasa et al., 1991; Dieckmann and Law, 1996).

As indicated, acquiescing individuals of sex i pay the cost of acquiescing c_{ai} and provide second-brood individuals with a viability benefit b_E. Resisting individuals pay the cost of resistance c_r. Then, the viability of a mutant individual I given that its mother and father are J and K is

$$w_{I,J\times K} = g\sigma_1 p_{\female}(1-q_{\female})(1-c_{a\female}) + g\sigma_1 p_{\female} q_{\female}(1-c_r) + g\sigma_1(1-p_{\female}) \tag{III.7a}$$

$$+ (1-g)\sigma_2(1-c_m)(1+b_E) \tag{III.7b}$$

$$+ g s_1 p_{\male}(1-q_{\male})(1-c_{a\male}) + g s_1 p_{\male} q_{\male}(1-c_r) + g s_1(1-p_{\male}) \tag{III.7c}$$

$$+ (1-g)s_2(1-c_m)(1+b_E). \tag{III.7d}$$

Lines (III.7a) and (III.7b) correspond to when I is a female, while lines (III.7c) and (III.7d) correspond to when I is a male. The first term in (III.7a) and (III.7c) gives the fitness payoff $1-c_{ai}$ when the mutant offspring belongs to the first brood (with probability g), it is of sex i (σ_1 or s_1 for females and males), it is manipulated (with probability p_i) and it does not resist (with probability $1-q_i$). The second term gives the fitness payoff $1-c_r$ in the same situation, but when the mutant resists. The third term gives the fitness payoff 1 when such an offspring is in the first brood but it is not manipulated. The term in (III.7b) and (III.7d) gives the payoff $1+b_E$ when the mutant offspring is in the second brood, weighted by the probability $1-c_m$ that the mother survives to produce the second brood. Rearranging yields

$$w_{I,J\times K} = 1-(1-g)c_m + gp\theta\left[\overline{b_\bullet(1-q_\bullet)}(1-c_m) - \overline{c}\right], \tag{III.7e}$$

where $\overline{c} = \overline{c_a(1-q)} + c_r\overline{q}$, or equivalently $\overline{c} = \sum_i u_i c_i$ where $c_i = c_{ai}(1-q_i) + c_r q_i$. Special considerations need to be made for haplodiploids since in the second mating (when the father is mutant) no mutant males are produced.

III.5.2 Haploids and diploids

III.5.2.1 Evolution of dispersal

III.5.2.1.1 Maternal effect (maternal manipulation) In this section I study the evolution of manipulation effort p. Consider for now a sexual haploid genetic system. The average viability for manipulation mutants $w_{\mathbf{A}_p}$ is obtained from equation (III.6). Female and male mutants occur in proportion to ζ and z. Since I am considering mutants for the manipulation subtrait only, then $e_{\mathbf{A}_p} = e_{\mathbf{a}_p} = e$. The mutant's viability for the first mating $w_{\mathbf{A}_p,\mathbf{A}_p \times \mathbf{a}_p}$ is obtained from equation (III.7e) by replacing p for p'. For the reciprocal mating, the mother is resident and thus the viability is constant with respect to p'. The evolutionary change in manipulation effort between the time of mutation and the time of fixation Δp is then proportional to the selection gradient

$$\frac{\partial w_{\mathbf{A}_p}}{\partial p'}\bigg|_{p'=p} = \zeta g \theta \left[\overline{b}(1-q)(1-c_m) - \overline{c}\right]\left(1 - \frac{e}{e_{\max}}\right).$$

The rate of change depends on the proportion of females ζ as only mothers express the mutant allele. It also depends on the size of the first brood g, the fraction of offspring subject to manipulation θ, the probability of acquiescing $1-q$ (which means that complete resistance will prevent any change in manipulation), and the maternally induced benefit e. The direction of change can only be modified by the term within square brackets. Thus, manipulation effort increases if

$$\overline{b}(1-q)(1-c_m) > \overline{c}, \tag{III.8}$$

which recovers previous results (Alexander, 1974; Trivers, 1974; Charlesworth, 1978; González-Forero and Gavrilets, 2012). As long as the inequality holds, manipulation effort p increases to 1; otherwise it decreases to 0. These bounds occur because the mutation rate for a larger or smaller p is zero. When $p = 1$, the entire proportion θ of the first brood is manipulated to stay.

III.5.2.1.2 Offspring effect (offspring resistance) I now look at the evolution of resistance probability q. Consider a resident resistance allele, $\mathbf{a}_q$. A rare resistance allele $\mathbf{A}_q$ causes offspring to resist with a slightly different probability q'. Again, $e_{\mathbf{A}_q} = e_{\mathbf{a}_q} = e$. Mothers are all of genotype $\mathbf{a}_p$, so first-brood offspring are manipulated with effort p. The mutant's viability for the first mating $w_{\mathbf{A}_q,\mathbf{A}_q\times\mathbf{a}_q}$ is obtained from equation (III.7e) by replacing $q_{\bullet}$ for the average resistance probability in offspring from this mating: $\frac{1}{2}(q' + q)$, assuming no meiotic drive. Also, for the average cost $\overline{c}$ in equation (III.7e), the resistance probability q is replaced by q'. The mutant's viability for the reciprocal mating is the same.

Thus, the evolutionary change in resistance probability Δq is proportional to the selection gradient

$$\left.\frac{\partial w_{\mathbf{A}_q}}{\partial q'}\right|_{q'=q} = -gp\theta\left[\frac{1}{2}\overline{b} - \left(\overline{c}_a - c_r\right)\right]\left(1 - \frac{e}{e_{\max}}\right),$$

where $\overline{c}_a = u_{♀}c_{a♀} + u_{♂}c_{a♂}$. This gradient shows that there is selection pressure for resistance as long as there is some manipulation ($p \neq 0$) and the more manipulation the faster the change in resistance. Resistance probability decreases if

$$\frac{1}{2}\overline{b} > \overline{c}_a - c_r, \tag{III.9}$$

which recovers a form of Hamilton's rule.

III.5.2.2 Evolution of help

III.5.2.2.1 Maternal effect I now look at the maternally induced benefit e. Consider a resident maternally controlled allele $\mathbf{a}_e$ that causes a maternally induced benefit e. A rare maternally-controlled allele $\mathbf{A}_e$ causes a mother to produce a slightly different benefit e'. Thus, the mutant's viability $w_{\mathbf{A}_e}$ is obtained from equation (III.6) by replacing e_M with e' and e_R with e, and by replacing e with e' in the first-mating viability $w_{\mathbf{A}_e,\mathbf{A}_e\times\mathbf{a}_e}$.

Since the mother for the reciprocal mating is not a carrier of the mutant allele, the fitness $w_{\mathbf{A}_e,\mathbf{a}_e\times\mathbf{A}_e}$ is constant with respect to e'.

Hence, the evolutionary change in extra fertility Δe is proportional to the selection gradient

$$\frac{\partial w_{\mathbf{A}_e}}{\partial e'}\bigg|_{e'=e} = \zeta\left[\Delta e_\infty\left(1-\frac{a_0}{e_{\max}}-2\frac{e}{e_{\max}}\right)-\frac{1-C_m}{e_{\max}}\right],$$

where

$$\Delta e_\infty = gp\theta\delta\overline{h}(1-q)\left(1-c_m-\frac{c_h-c_{\neg h}}{b_{\max}}\right) \tag{III.10}$$

is the selection gradient of e (divided by ζ) as $e_{\max}\to\infty$ and $C_m = c_m(1-g)+gp\theta[c_{\neg h}(1-q)+c_r q]$ is the reduction of mother's fertility due to wasted effort (wasted effort due to offspring not produced as a result of the cost of manipulation, and of acquiescing offspring that pay the cost of not helping or resisting offspring that pay the cost of resisting). The number 2 in front of e arises from the quadratic fitness form with respect to e' that results from the linear expense of e in equation (III.6) (an expense of degree γ would replace 2 by $1+\gamma$ plus terms of lower degree). Since $C_m \leq 1$, a zero manipulation effort makes the selection gradient negative. This shows that without help, maternally induced benefits are selected against. Manipulation effort introduces a selection pressure for maternally induced benefits, which increase if

$$e < \frac{1}{2}\left(e_{\max}-a_0-\frac{1-C_m}{\Delta e_\infty}\right) \tag{III.11}$$

when $\Delta e_\infty > 0$, otherwise the inequality is reversed. We have that $\Delta e_\infty > 0$ when $c_m < 1-(c_h-c_{\neg h})/b_{\max}$. The condition (III.8) for increase of maternal manipulation p can be rewritten as $c_m < 1-\overline{c}/[\overline{b}(1-q)]$ and it can be checked that $\overline{c}/[\overline{b}(1-q)] \geq (c_h-c_{\neg h})/b_{\max}$. Therefore, if maternal manipulation is favored, inequality (III.11) gives the condition for increase of maternally induced benefits e. We have that $\partial^2 w_{\mathbf{A}_e}/\partial e'^2|_{e'=e} = -2\zeta\Delta e_\infty/e_{\max}$, so the equilibrium e^* defined by inequality (III.11) is stable if $\Delta e_\infty > 0$.

III.5.2.2.2 Female-offspring effect Now I evaluate the evolution of female helping probability $h_\female$. The resident allele $\mathbf{a}_{h_\female}$ codes for female helping probability $h_\female$ while the mutant allele $\mathbf{A}_{h_\female}$ causes a female to have a slightly different helping probability $h'_\female$. The mutant's viability from the first mating $w_{\mathbf{A}_{h_\female},\mathbf{A}_{h_\female}\times\mathbf{a}_{h_\female}}$ is obtained from equation (III.7e) replacing $b_{\female\bullet}$ by the average benefit provided by female offspring from this mating: $a(h'_\female + h_\female)/2$. The cost of acquiescence to female offspring is thus

$$c_{a\female} = \frac{1}{2}(h'_\female + h_\female)\frac{a}{b_{\max}}c_h + \left(1 - \frac{1}{2}(h'_\female + h_\female)\frac{a}{b_{\max}}\right)c_{\neg h}.$$

The evolutionary change of female-helping probability $\Delta h_\female$ is proportional to the selection gradient

$$\left.\frac{\partial w_{\mathbf{A}_{h_\female}}}{\partial h'_\female}\right|_{h'_\female = h_\female} = u_\female a g p \theta(1-q)\left(\frac{1}{2}(1-c_m) - \frac{c_h - c_{\neg h}}{b_{\max}}\right)\left(1 - \frac{e}{e_{\max}}\right).$$

Female-helping probability increases if

$$\frac{1}{2}(1-c_m) > \frac{c_h - c_{\neg h}}{b_{\max}}. \tag{III.12}$$

The benefit does not appear in this Hamilton's rule as it only affects the rate and not the direction of selection. Instead, it is the maximum benefit $b_{\max}$ or maximum helping efficiency that appears. A large maximum helping efficiency reduces the strength of selection against helping by scaling down the cost of helping relative to the cost of not helping $(c_h - c_{\neg h})$.

III.5.2.2.3 Male-offspring effect Now I evaluate the evolution of male helping probability $h_\male$. The resident allele $\mathbf{a}_{h_\male}$ codes for male helping probability $h_\male$ while the mutant allele $\mathbf{A}_{h_\male}$ causes a male to have a slightly different helping probability $h'_\male$. The mutant's viability from the first mating $w_{\mathbf{A}_{h_\male},\mathbf{A}_{h_\male}\times\mathbf{a}_{h_\male}}$ is obtained from equation (III.7e) replacing $b_{\male\bullet}$ by the average benefit provided by male offspring from this mating:

$a(h'_{\male} + h_{\male})/2$. The cost of acquiescence to male offspring is

$$c_{a\male} = \frac{1}{2}(h'_{\male} + h_{\male})\frac{a}{b_{\max}}c_h + \left(1 - \frac{1}{2}(h'_{\male} + h_{\male})\frac{a}{b_{\max}}\right)c_{\neg h}. \tag{III.13}$$

The evolutionary change of female-helping probability $\Delta h_{\male}$ is proportional to the selection gradient

$$\frac{\partial w_{\mathbf{A}_{h_{\male}}}}{\partial h'_{\male}}\Big|_{h'_{\male} = h_{\male}} = u_{\male}\, a g p \theta (1-q)\left(\frac{1}{2}(1-c_m) - \frac{c_h - c_{\neg h}}{b_{\max}}\right)\left(1 - \frac{e}{e_{\max}}\right),$$

as for females.

III.5.2.3 Evolution of delay

III.5.2.3.1 Maternal effect I now look at the evolution of the maternal effect on offspring's delay δ_m. Consider a resident allele $\mathbf{a}_{\delta_m}$ that causes a mother to push for delay with effort δ_m. A rare allele $\mathbf{A}_{\delta_m}$ that causes a mother to push with a slightly different effort δ'_m. Thus, the mutant's viability from the first-mating viability $w_{\mathbf{A}_{\delta_m},\mathbf{A}_{\delta_m}\times\mathbf{a}_{\delta_m}}$ is obtained from equation (III.6) by setting $b_{i\bullet} = b_i$, $q_{\bullet} = q$, and $\delta = \delta'_m - \delta_o$. Since the mother for the reciprocal mating is not a carrier of the mutant allele, fitness $w_{\mathbf{A}_{\delta_m},\mathbf{a}_{\delta_m}\times\mathbf{A}_{\delta_m}}$ is constant with respect to δ'_m.

Hence, the evolutionary change in the maternal effect on delay $\Delta\delta_m$ is proportional to the selection gradient

$$\frac{\partial w_{\mathbf{A}_{\delta_m}}}{\partial \delta'_m}\Big|_{\delta'_m = \delta_m} = \zeta g p \theta (1-q)\left[\frac{\overline{b}}{\delta}(1-c_m) - \frac{1}{\delta}\left(\overline{c_a - c_{\to\delta}} + \overline{c_a} - c_{\neg h}\right)\right]\left(1 - \frac{e}{e_{\max}}\right).$$

The maternal effect on delay increases if

$$\overline{b}(1-c_m) > \overline{c_a - c_{\to\delta}} + \overline{c_a} - c_{\neg h}.$$

III.5.2.3.2 Offspring effect I now look at the evolution of the offspring effect on delay δ_o. Consider a resident allele $\mathbf{a}_{\delta_o}$ that causes an offspring to oppose the maternally caused delay with effort δ_o. A rare allele $\mathbf{A}_{\delta_o}$ causes an offspring to oppose delay with a slightly different effort δ'_o. The mutant's viability from the first-mating viability $w_{\mathbf{A}_{\delta_o},\mathbf{A}_{\delta_o}\times\mathbf{a}_{\delta_o}}$ is obtained from equation (III.6) by setting $b_{i\bullet} = h_i(a'+a)/2$ and $a' = (\delta_m - \delta'_o)(a_0 + e)$. The benefit provided a is replaced by a' in the expression (III.4) for the cost of acquiescence. The mutant's viability for the reciprocal mating is the same.

The evolutionary change in the offspring effect on delay $\Delta\delta_o$ is proportional to the selection gradient

$$\frac{\partial w_{\mathbf{A}_{\delta_o}}}{\partial \delta'_o}\Big|_{\delta'_o=\delta_o} = -gp\theta(1-q)\left[\frac{1}{2}\frac{\overline{b}}{\delta}(1-c_m) - \frac{1}{\delta}\left(\overline{c_a - c_{\to\delta}} + \overline{c_a} - c_{\neg h}\right)\right]\left(1-\frac{e}{e_{\max}}\right).$$

In contrast to the maternal effect on delay, this gradient is not multiplied by ζ and hence the offspring effect on delay evolves faster. Offspring controlled delay decreases if

$$\frac{1}{2}\overline{b}(1-c_m) > \overline{c_a - c_{\to\delta}} + \overline{c_a} - c_{\neg h}.$$

The analysis for diploids is entirely analogous and only requires replacing x' by $X' = (x'+x)/2$ assuming additive genetic effects. The only effect of this change is to reduce by half the rate of evolutionary dynamics for each subtrait.

III.5.3 Haplodiploids

The average mutant's viability (equation (III.6)) now takes the form

$$w_{\mathbf{A\_}} = \zeta w_{\mathbf{A\_},\mathbf{Aa}\times\mathbf{a}} + z w_{\mathbf{A\_},\mathbf{aa}\times\mathbf{A}}, \tag{III.14}$$

where $w_{\mathbf{A\_},i\times j} = \sigma w_{\mathbf{Aa},i\times j} + s w_{\mathbf{A},i\times j}$. Since no mutant males are produced from the second mating, we have that $w_{\mathbf{A\_},\mathbf{aa}\times\mathbf{A}} = \sigma w_{\mathbf{Aa},\mathbf{aa}\times\mathbf{A}}$. Because now sexes differ in genotypes, the viabilities are conditional on the probability of being of the given sex.

Let d be the dosage compensation in males. Thus, $d = 1$ if males are haploid in the tissue controlling their resistance or delay, or $d = 2$ if males are diploid in such a tissue. Hence, including these modifications, the viabilities for the first mating are as before:

$$\begin{aligned}
w_{\mathbf{Aa,Aa}\times\mathbf{a}} = {} & g\frac{\sigma_1}{\sigma}p_{\female}(1-q_{\female})(1-c_{a\female}) + g\frac{\sigma_1}{\sigma}p_{\female}q_{\female}(1-c_r) + g\frac{\sigma_1}{\sigma}(1-p_{\female}) \\
& + (1-g)\frac{\sigma_2}{\sigma}(1-c_m)(1+b_E) \\
w_{\mathbf{A,Aa}\times\mathbf{a}} = {} & g\frac{s_1}{s}p_{\male}\left(1-q_{\male}\right)(1-c_{a\male}) + g\frac{s_1}{s}p_{\male}q_{\male}(1-c_r) + g\frac{s_1}{s}(1-p_{\male}) \\
& + (1-g)\frac{s_2}{s}(1-c_m)(1+b_E).
\end{aligned}$$

After rearranging, the viability from the first mating $w_{\mathbf{A\_,Aa}\times\mathbf{a}}$ equals that in equation (III.7e). However, male-offspring-controlled subtrait values are now $q_{\male} = dq/2$ and $\delta_{o\male} = d\delta_o/2$ (and I let $q_{\female} = q$ and $\delta_{o\female} = \delta_o$). I thus now make use of the notation of delay for sex i as $\delta_i = \delta_m - \delta_{oi}$ and the amount of benefit provided by it as $a_i = \delta_i(a0+e)$. For a resident subtrait value x for females and $dx/2$ for males, the mutant subtrait value for females is $X' = (x'+x)/2$ and for males is $dx'/2$, assuming additive genetic effects.

For maternal effect subtraits, the viability from the reciprocal mating $w_{\mathbf{Aa,aa}\times\mathbf{A}}$ is constant with respect to the mutant subtrait value x'. However, in contrast to haploids and diploids, such viability is not equal to that of the reciprocal mating for offspring effect subtraits. It differs in that the viability applies only to female offspring and that the effective benefit is different. The mutant viability for females from this mating is

$$\begin{aligned}
w_{\mathbf{Aa,aa}\times\mathbf{A}} = {} & g\frac{\sigma_1}{\sigma}p_{\female}(1-q_{\female})(1-c_{a\female}) + g\frac{\sigma_1}{\sigma}p_{\female}q_{\female}(1-c_r) + g\frac{\sigma_1}{\sigma}(1-p_{\female}) \\
& + (1-g)\frac{\sigma_2}{\sigma}(1-c_m)(1+b''_E), \qquad \text{(III.15a)}
\end{aligned}$$

which differs only by the effective benefit b''_E. The different form of b''_E is seen for each subtrait below. Rearranging yields

$$w_{\mathbf{Aa,aa\times A}} = \frac{\sigma_2}{\sigma} + g\left(\frac{\sigma_1}{\sigma} - \frac{\sigma_2}{\sigma}\right) - (1-g)c_m\frac{\sigma_2}{\sigma} + gp\theta\left[\frac{\sigma_2}{\sigma}\overline{b_\bullet(1-q_\bullet)}''(1-c_m) - \frac{u_♀}{\sigma}c_♀\right], \tag{III.15b}$$

where $c_♀ = c_{a♀}(1-q) + c_r q$ and " $''$ " indicates that this corresponds to the second mutant mating.

III.5.3.1 Evolution of dispersal

III.5.3.1.1 Maternal effect (maternal manipulation) Proceeding as before, we have that the evolutionary change in manipulation effort Δp is proportional to the selection gradient

$$\left.\frac{\partial w_{\mathbf{A}_p}}{\partial p'}\right|_{p'=p} = \frac{1}{2}\zeta g\theta\left[\overline{b(1-q)}(1-c_m) - \overline{c}\right]\left(1 - \frac{e}{e_{\max}}\right).$$

The $1/2$ comes from the additive allelic effects and diploid mothers. Manipulation effort increases if

$$\overline{b(1-q)}(1-c_m) > \overline{c}. \tag{III.16}$$

III.5.3.1.2 Offspring effect (offspring resistance) For the first mating, wee have that $q_{♀\bullet} = (Q'+q)/2$, where $Q' = (q'+q)/2$, and that $q_{♂\bullet} = (dq'/2 + dq/2)/2$. This is used to obtain

$$b_E = \frac{gp\theta}{1-g}\overline{b(1-q_\bullet)}.$$

In contrast, for the reciprocal mating we have that $q_{♀\bullet} = Q'$ and that $q_{♂\bullet} = dq/2$. This produces a different

$$b''_E = \frac{gp\theta}{1-g}\overline{b(1-q''_\bullet)}.$$

Then, the evolutionary change in resistance probability Δq is proportional to the selection gradient

$$\frac{\partial w_{\mathbf{A}_q}}{\partial q'}\bigg|_{q'=q} = -\frac{1}{2} g p \theta \left[\overline{brd} - \overline{vd\,(c_a - c_r)}\right]\left(1 - \frac{e}{e_{\max}}\right).$$

where $\overline{brd} = u_{♀} b_{♀} r_{♀} d_{♀} + u_{♂} b_{♂} r_{♂} d_{♂}$. The quantities r_i give the probability that manipulated individuals of sex i share the mutant allele with individuals in the second brood. The quantities v_i give the probability that mutant matings produce sex-i mutants. They are

$$r_{♀} = \zeta \frac{1}{2} + z\sigma_2, \qquad v_{♀} = 1 \tag{III.17}$$

$$r_{♂} = \zeta \frac{1}{2}, \qquad v_{♂} = \zeta. \tag{III.18}$$

The quantities d_i give the dosage compensation of sex i: $d_{♀} = 1$ and $d_{♂} = d$. It can be checked that v_i gives the reproductive value of sex i individuals and that r_i is the regression relatedness toward sex i averaged over first-brood offspring, weighted by first-brood offspring's reproductive value (González-Forero and Gavrilets, 2012). Thus, r_i / v_i is the life-for-life relatedness of first brood offspring toward second brood offspring of sex i (Hamilton, 1972; Bulmer, 1994). Resistance probability decreases if

$$\overline{brd} > \overline{vd\,(c_a - c_r)}. \tag{III.19}$$

For haploids and diploids, we had that $r_i = 1/2$, $d_i = 1$ and $v_i = 1$ for sex i offspring.

III.5.3.2 Evolution of help

III.5.3.2.1 Maternal effect The evolutionary change in extra fertility Δe is proportional to the selection gradient

$$\frac{\partial w_{\mathbf{A}_e}}{\partial e'}\bigg|_{e'=e} = \frac{1}{2}\zeta \left[\Delta e_{\infty}\left(1 - \frac{a_0}{e_{\max}} - 2\frac{e}{e_{\max}}\right) - \frac{1 - C_m}{e_{\max}}\right],$$

where again

$$\Delta e_\infty = gp\theta\overline{\delta h(1-q)\left(1-c_m-\frac{c_h-c_{\neg h}}{b_{\max}}\right)} \tag{III.20}$$

gives the selection gradient of e (divided by ζ) as $e_{\max} \to \infty$, and $C_m = c_m(1-g) + gp\theta\left[\overline{c_{\neg h}(1-q)} + c_r\overline{q}\right]$ gives the loss of maternal fertility due to wasted effort. As before, since $C_m \leq 1$, a zero manipulation effort makes this selection gradient negative. Therefore, manipulation effort introduces a selection pressure for maternally induced benefits which increase if

$$e < \frac{1}{2}\left(e_{\max} - a_0 - \frac{1-C_m}{\Delta e_\infty}\right), \tag{III.21}$$

if $\Delta e_\infty > 0$; otherwise the inequality is reversed. Similarly, $\Delta e_\infty > 0$ when

$$c_m < 1 - \frac{\overline{dh(1-q)\frac{c_h-c_{\neg h}}{b_{\max}}}}{\overline{dh(1-q)}}.$$

The condition for increase in maternal manipulation p can be rewritten as $c_m < 1 - \overline{c}/[\overline{b(1-q)}]$ and it can be checked that

$$\frac{\overline{c}}{\overline{b(1-q)}} \geq \frac{\overline{dh(1-q)\frac{c_h-c_{\neg h}}{b_{\max}}}}{\overline{dh(1-q)}}.$$

Therefore, if maternal manipulation is favored, inequality (III.21) gives the condition for increase in maternally induced benefits e. We have that $\partial^2 w_{\mathbf{A}_e}/\partial e'^2|_{e'=e} = -2\zeta\Delta e_\infty/e_{\max}$, so the equilibrium e^* defined by inequality (III.21) is stable if $\Delta e_\infty > 0$.

III.5.3.2.2 Female-offspring effect For the first mating, we have that $b_{\text{♀}\bullet} = a_{\text{♀}}(H'_{\text{♀}} + h_{\text{♀}})/2$, where $H'_{\text{♀}} = (h'_{\text{♀}} + h_{\text{♀}})/2$. This is used to obtain $b_E = gp\theta\overline{b_\bullet(1-q)}/(1-g)$. In contrast, for the reciprocal mating we have that $b_{\text{♀}\bullet} = a_{\text{♀}}H'_{\text{♀}}$. This produces a different $b''_E = gp\theta\overline{b''_\bullet(1-q)}/(1-g)$.

Thus, the evolutionary change of female-helping probability $\Delta h_{♀}$ is proportional to the selection gradient

$$\left.\frac{\partial w_{\mathbf{A}_{h_{♀}}}}{\partial h'_{♀}}\right|_{h'_{♀}=h_{♀}} = \frac{1}{2} u_{♀} a_{♀} g p \theta (1-q) \left(r_{♀}(1-c_m) - \frac{c_{h♀} - c_{\neg h♀}}{b_{\max}} \right) \left(1 - \frac{e}{e_{\max}}\right).$$

Female-helping probability increases if

$$r_{♀}(1-c_m) > \frac{c_{h♀} - c_{\neg h♀}}{b_{\max}}. \tag{III.22}$$

III.5.3.2.3 Male-offspring effect For the first mating, we have that $b_{♂\bullet} = a_{♂}(h'_{♂} + h_{♂})/2$. For the reciprocal mating, we have that $b_{♂\bullet} = a_{♂} h_{♂}$. This produces an effective benefit $b''_E = g p \theta \overline{b''_{\bullet}(1-q)}/(1-g)$ that is constant with respect to $h'_{♂}$.

Hence, the evolutionary change of male-helping probability $\Delta h_{♂}$ is proportional to the selection gradient

$$\left.\frac{\partial w_{\mathbf{A}_{h_{♂}}}}{\partial h'_{♂}}\right|_{h'_{♂}=h_{♂}} = u_{♂} a_{♂} g p \theta \left(1 - \frac{q}{2}\right) \left(r_{♂}(1-c_m) - v_{♂} \frac{c_{h♂} - c_{\neg h♂}}{b_{\max}} \right) \left(1 - \frac{e}{e_{\max}}\right),$$

which is the analogous to that for females. Male-helping probability increases if

$$r_{♂}(1-c_m) > v_{♂} \frac{c_{h♂} - c_{\neg h♂}}{b_{\max}}. \tag{III.23}$$

III.5.3.3 Evolution of delay

III.5.3.3.1 Maternal effect I replace δ'_m in equation (III.7e) by $D'_m = (\delta'_m + \delta_m)/2$. Then, the evolutionary change in the maternally effect on offspring delay $\Delta\delta_m$ is proportional to the selection gradient

$$\left.\frac{\partial w_{\mathbf{A}_{\delta_m}}}{\partial \delta'_m}\right|_{\delta'_m=\delta_m} = \frac{1}{2} \zeta g p \theta \overline{(1-q) \left[\frac{b}{\delta}(1-c_m) - \frac{1}{\delta}\left(c_a - c_{\to\delta} + c_a - c_{\neg h}\right) \right]} \left(1 - \frac{e}{e_{\max}}\right).$$

Then, maternally effect on delay increases if

$$\overline{\frac{b}{\delta}(1-q)}(1-c_m) > \overline{\frac{1}{\delta}(1-q)\left(c_a - c_{\to\delta} + c_a - c_{\neg h}\right)}. \tag{III.24}$$

III.5.3.3.2 Offspring effect I replace in equation (III.7e) $\delta'_{o\female} = (\delta'_o + \delta_o)/2$ and $\delta'_{o\male} = \delta'_o/2$. I thus denote $\delta'_i = \delta_m - \delta'_{oi}$ and $a'_i = \delta'_i(a_o + e)$. Hence, for the first mating, we have that $b_{i\bullet} = h_i(a'_i + a_i)/2$. For the reciprocal mating, we have that $b_{\female\bullet} = a'_{\female} h_{\female}$ and $b_{\male\bullet}$ is constant with respect to δ'_o.

The evolutionary change in the offspring controlled delay $\Delta\delta_o$ is hence proportional to the selection gradient

$$\left.\frac{\partial w_{\mathbf{A}_{\delta_o}}}{\partial \delta'_o}\right|_{\delta'_o=\delta_o} = -\frac{1}{2} g p \theta \overline{(1-q)\left[\frac{brd}{\delta}(1-c_m) - \frac{vd}{\delta}\left(c_a - c_{\to\delta} + c_a - c_{\neg h}\right)\right]}\left(1 - \frac{e}{e_{\max}}\right).$$

Therefore, offspring controlled delay decreases if

$$\overline{\frac{brd}{\delta}(1-q)}(1-c_m) > \overline{\frac{vd}{\delta}(1-q)\left(c_a - c_{\to\delta} + c_a - c_{\neg h}\right)}.$$

III.5.4 Thresholds

The inequalities for increase of subtrait i define thresholds, T_i, such that if $a_0 + e > T_i$ then subtrait i increases. They are given in Table III.1.

III.5.5 Numerical solutions

In long time scales, the change in population subtrait value Δx between the time of mutation and the time of fixation is approximately given by dx/dt. Thus, the selection gradients found above specify systems of differential equations of the form (Kimura, 1965; Lande, 1979; Iwasa et al., 1991; Dieckmann and Law, 1996)

$$\frac{dx}{dt} = \mu_x \left.\frac{\partial w_{\mathbf{A}_x}}{\partial x'}\right|_{x'=x},$$

Table III.1: For the corresponding subtrait to evolve, $a_0 + e$ is required to be greater than the above quantities. T_h gives the threshold for increase of $\overline{h}$. $A = (1 - C_m)/\Delta e_\infty$.

T_p	$\frac{\overline{c}}{\overline{\delta h(1-q)}(1-c_m)}$
T_q	$\frac{\overline{vd(c_a-c_r)}}{\overline{\delta hrd}(1-c_m)}$
T_e	$2(a_0 + e) - \frac{1}{2}(e_{\max} + a_0 - A)$
T_h	$\frac{a_0+e}{b_{\max}} \frac{\overline{v(c_h-c_{\neg h})}}{\overline{r}(1-c_m)}$
$T_{\delta m}$	$\frac{\overline{\frac{1}{\delta}(1-q)(c_a-c_{\to\delta}+c_a-c_{\neg h})}}{\overline{h(1-q)}(1-c_m)}$
$T_{\delta o}$	$\frac{\overline{\frac{vd}{\delta}(1-q)(c_a-c_{\to\delta}+c_a-c_{\neg h})}}{\overline{hrd(1-q)}(1-c_m)}$

where μ_x is a function of the mutation rate and the mutation effect. Each subtrait x was defined to be bounded (e.g., $0 \leq p \leq 1$ and $0 \leq e \leq e_{\max}$). For numerical solutions, μ_x is thus set equal to zero when the next time step $x(t+1)$ is out of bounds. In such a case, $x(t+1) = x(t)$. Within bounds, I assume μ_x to be equal among all subtraits. I thus solve numerically the system

$$\frac{dx}{d\tau} = \frac{\partial w_{\mathbf{A}_x}}{\partial x'}\bigg|_{x'=x},$$

where $\tau = t\mu_x$. I define a rescue to occur when at the first time step both manipulation effort and resistance increase ($p(1) > p(0)$ and $q(1) > q(0)$) and at the last time step both manipulation effort and maternally induced benefits are substantial but resistance is not ($p(\text{end}) > 0.1$, $e(\text{end}) > 0.1$, and $q(\text{end}) < 0.1$). The solver was let run for 10^6 time steps.

A necessarily restrictive set of parameter values was chosen, on the basis that rescues would be expected to happen (Table III.2). This produced a number of runs and rescues (Fig. III3.4). Rescues occurred only in a narrow zone of the parameter space (Fig. III3.5). Sufficiency tests failed to suggest sufficient conditions for the rescue in

Table III.2: Initial conditions and parameter values. The values shown in the table were implemented for the three genetic systems. For Fig. III3.1, the values are the following. Initial conditions: $h_{♀}(0) = 1$, $h_{♂}(0) = 0$, $\delta_m(0) = 0.5$, $\delta_o(0) = 0$. Parameter values: for differential manipulation: $\alpha = 1$, $\beta = 0$; for costs: $c_r = 0$, $c_m = 0.1$, $\kappa_{\delta h} = 1$, $\kappa_{\delta\neg h} = 0.5$, $\kappa_{\to\delta h} = 0$, $\kappa_{\to\delta\neg h} = 0$; and for dosage compensation: $d = 2$.

$p(0)$	0.1	a_0	1	α	0, 1
$q(0)$	0.1	s_1	0.5	β	1, if $\alpha = 0$
$e(0)$	0	g	0.5		0, 1, otherwise
$h_{♀}(0)$	0, 0.5, 1	s_2	0.5	$\kappa_{\delta h}$	0.5, 1
$h_{♂}(0)$	0.5, 1, if $h_{♀}(0) = 0$	s	$gs_1 + (1-g)s_2$	$\kappa_{\delta\neg h}$	0, 0.5, 1
	0, 0.5, 1, otherwise	z	s	$\kappa_{\to\delta h}$	0, 0.5, 1
$\delta_m(0)$	0.5, 1	$e_{\max}$	1, 10, 20	$\kappa_{\to\delta\neg h}$	0, 0.5
$\delta_o(0)$	0, 0.5, if $\delta_m(0) = 0.5$	c_r	0, 0.1	d	1, 2
	0, 0.5, 1, otherwise	c_m	0, 0.1	$b_{\max}$	$a_0 + e_{\max}$

terms of the initial values of the thresholds (Fig. III3.6). Out of the 66 different initial threshold arrangements evaluated (Fig. III3.5; 47 occurring in haploids and diploids, and 66 occurring in haplodiploids), only 9 of them produced rescues (Figs. III3.7 and III3.8). As only even relatedness was considered, even though haplodiploids showed a larger number of rescues (Fig. III3.4), outcomes of advanced eusociality unique to haplodiploids only occurred when there was no dosage compensation in males (Fig. III3.9). Absence of dosage compensation makes males half as able as females to resist and to oppose delay.

III.5.6 Necessary conditions

For the numerical solutions evaluated, it was necessary for rescue that initially $T_p, T_h, T_{\delta m} < T_q$ (Fig. III3.3B). When manipulation effort goes only to sex i, these conditions

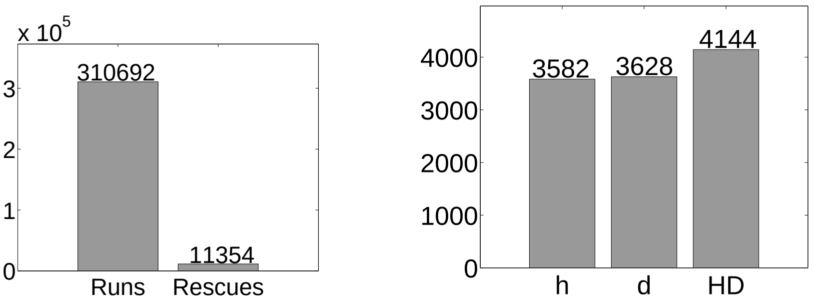


Figure III3.4: Runs and rescues. (*A*) Total runs and rescues. One third of the runs is for each genetic system. (*B*) Rescues per genetic system. h: haploid rescues; d: diploid rescues; HD: haplodiploid rescues. No error bars are included because this is a deterministic system.

respectively reduce to

$$c_r < c_{ai}\frac{(1-q_i)(v_i-r_i)}{r_i+(1-q_i)(v_i-r_i)} \tag{III.25}$$

$$c_r < c_{\neg hi} \tag{III.26}$$

$$c_r < c_{ai} - \frac{r_i}{v_i}\left(c_{ai} - c_{\to\delta i} + c_{ai} - c_{\neg hi}\right). \tag{III.27}$$

III.5.7 Maternally induced benefits as reduced maternal investment or extra maternal fertility

Let the maternally induced benefit to a second-brood individual j be $e_j = e_0(1-y_j)$, where y_j is the condition in which the mother leaves offspring j ($0 \leq y_j \leq 1$) and e_0 is the benefit that a minimal-condition individual receives when helped. In turn, let the condition of j be $y_j = 1$ for $j < j_0$ and $y_j = 0$ for $j \geq j_0$, where j_0 is the second-brood offspring at which the mother stops providing care. The maternally induced benefit is $e = \int_0^n e_j dj$, where n is the number of second-brood offspring. Then, $e = e_0(n - j_0)$.

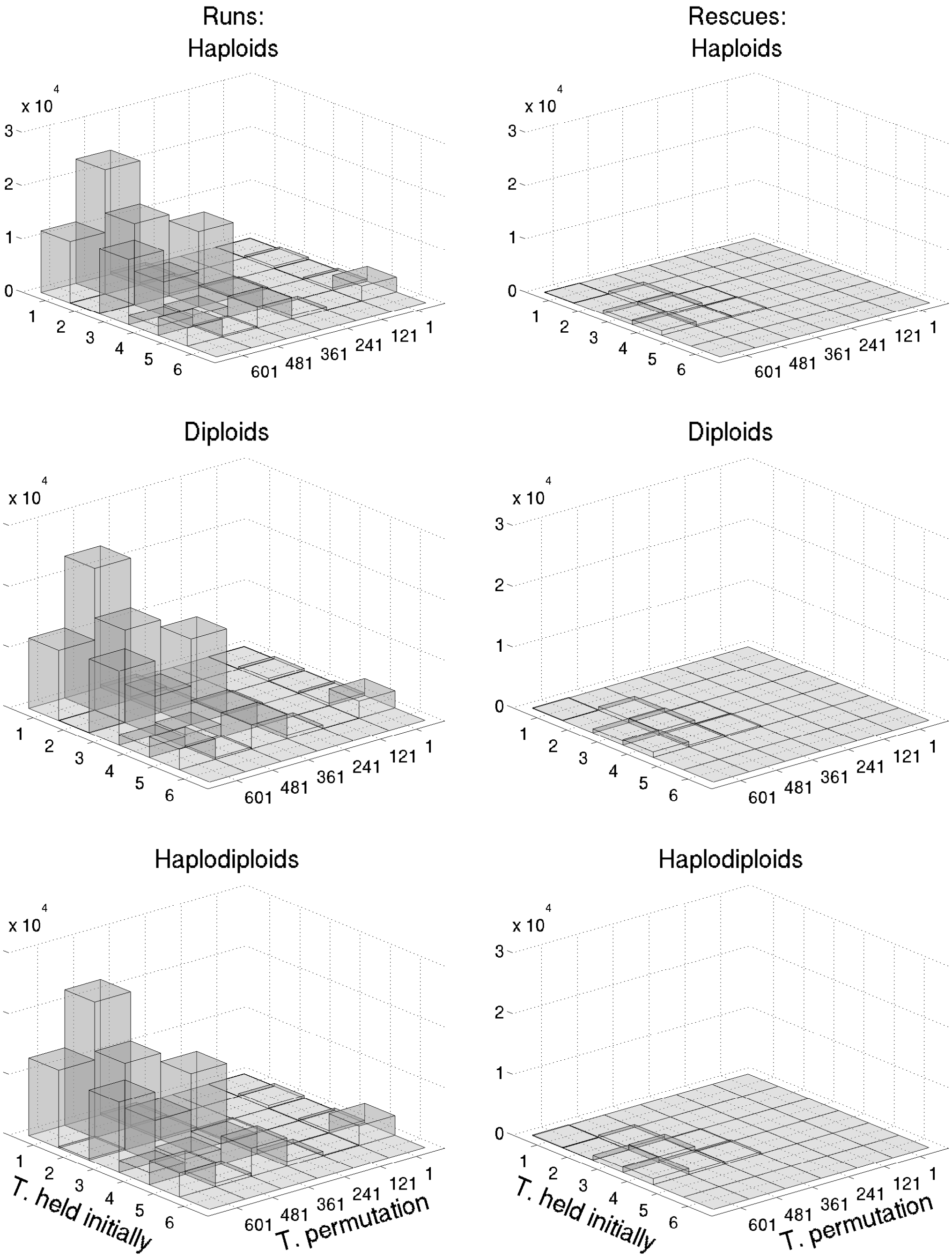


Figure III3.5: Number of runs and rescues against the initial arrangement of thresholds and how many of them were initially met. The right-hand horizontal axis gives the initial arrangement of thresholds, obtained by numbering the permutations of the 6 thresholds (i.e., permutations of $T_{i_1} \leq T_{i_2} \leq T_{i_3} \leq T_{i_4} \leq T_{i_5} \leq T_{i_6}$ produces 720 of them). The left-hand horizontal axis gives the number of thresholds that are initially met for a given permutation. Left-column panels give the number of runs and right-column panels give the number of rescues.

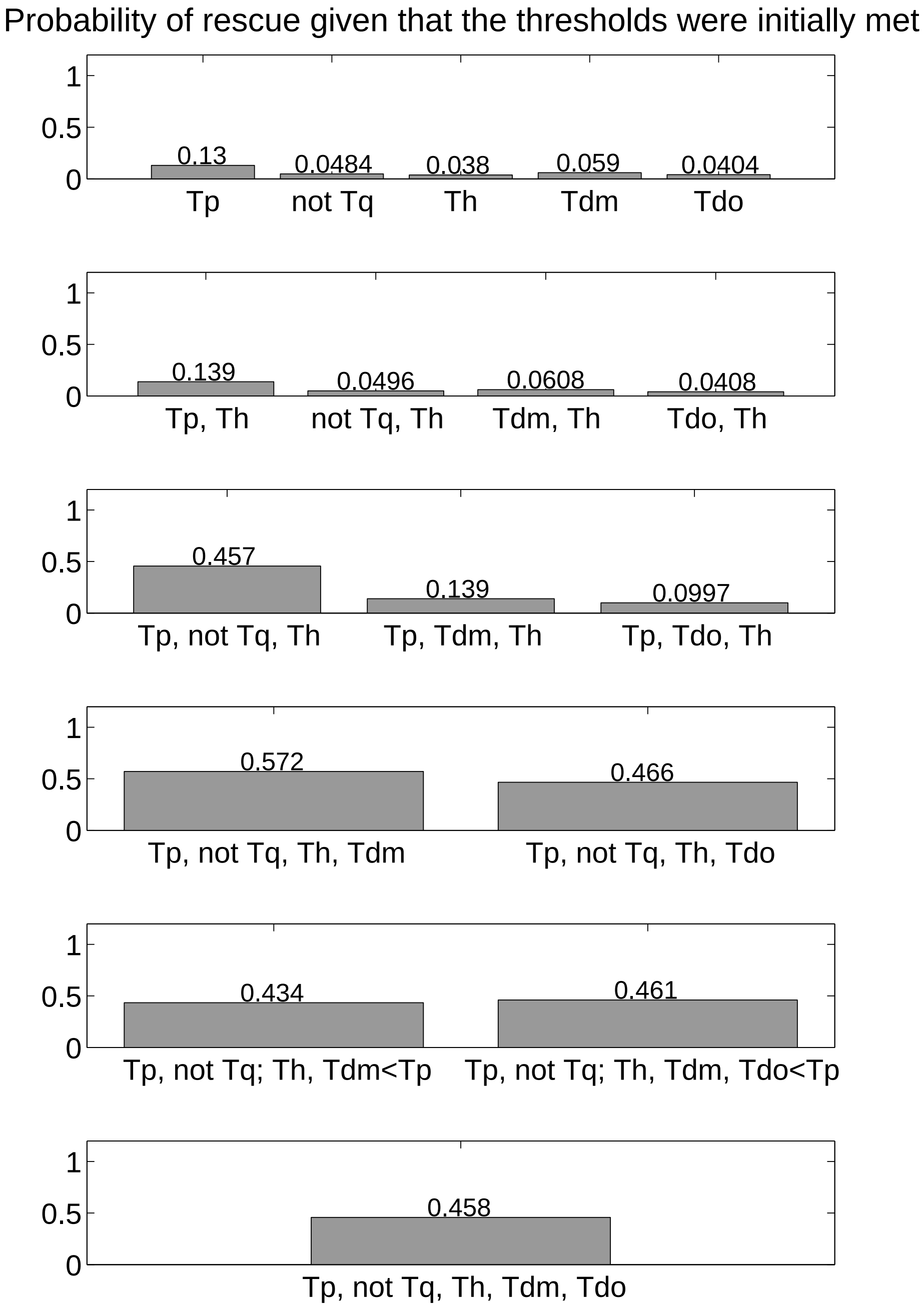


Figure III3.6: Tests for sufficient conditions. The bars give the probability of rescue given that the indicated thresholds were initially met. The probability is calculated as $P(x|y)$ = # rescues with thresholds met/# runs with thresholds met. T_e was never met initially, therefore the probabilities involving it are undefined. A probability of 1 indicates that the condition is sufficient for rescue. For the fifth panel, the conditions after the semicolon are that the indicated thresholds are smaller than T_p. None of the evaluated conditions was entirely sufficient to produce a rescue.

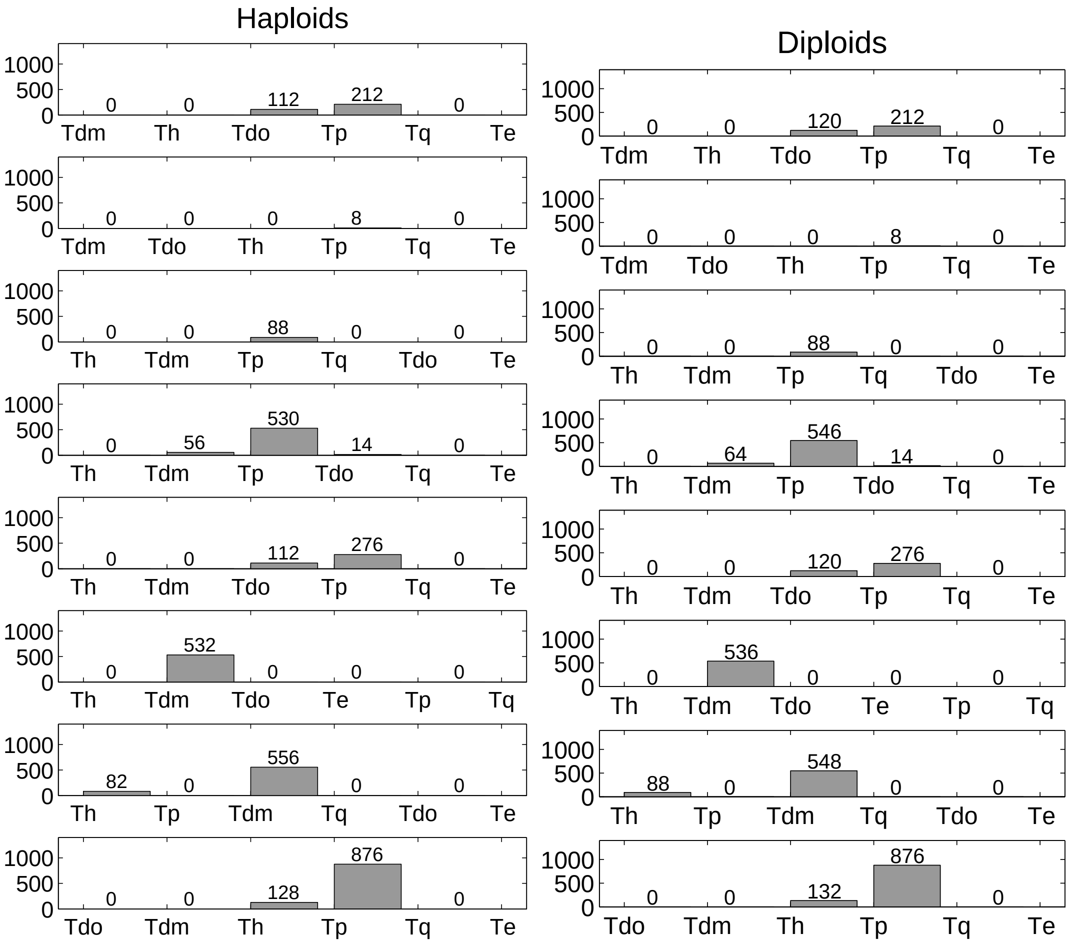


Figure III3.7: Threshold arrangements that produced rescues in haploids and diploids. The horizontal axis is $a_0 + e$ and the relative position of the thresholds at the start of numerical solutions is shown (i.e., $T_{i_1} \le T_{i_2} \le T_{i_3} \le T_{i_4} \le T_{i_5} \le T_{i_6}$ even though they are shown as necessarily unequal for computational ease). The bars give the number of rescues in which initially $T_i \le a_0 + e < T_{i-1}$. For example, for the upper left panel, 112 rescues occurred in which initially only $T_{\delta m}$, T_h and $T_{\delta o}$ were satisfied. The fact that p increases in cases in which T_p is not satisfied is because the numerical solver (the standard Runge-Kutta (4,5) method (Dormand and Prince, 1980)) uses midpoints between integration limits to calculate the value at the next time step. Thus, the thresholds may change in the midpoints so that a variable may increase at the next integration time step even though the threshold was initially not satisfied. Notice that initially T_h must be satisfied and that $T_p, T_h, T_{\delta m} < T_q$ for rescues to occur.

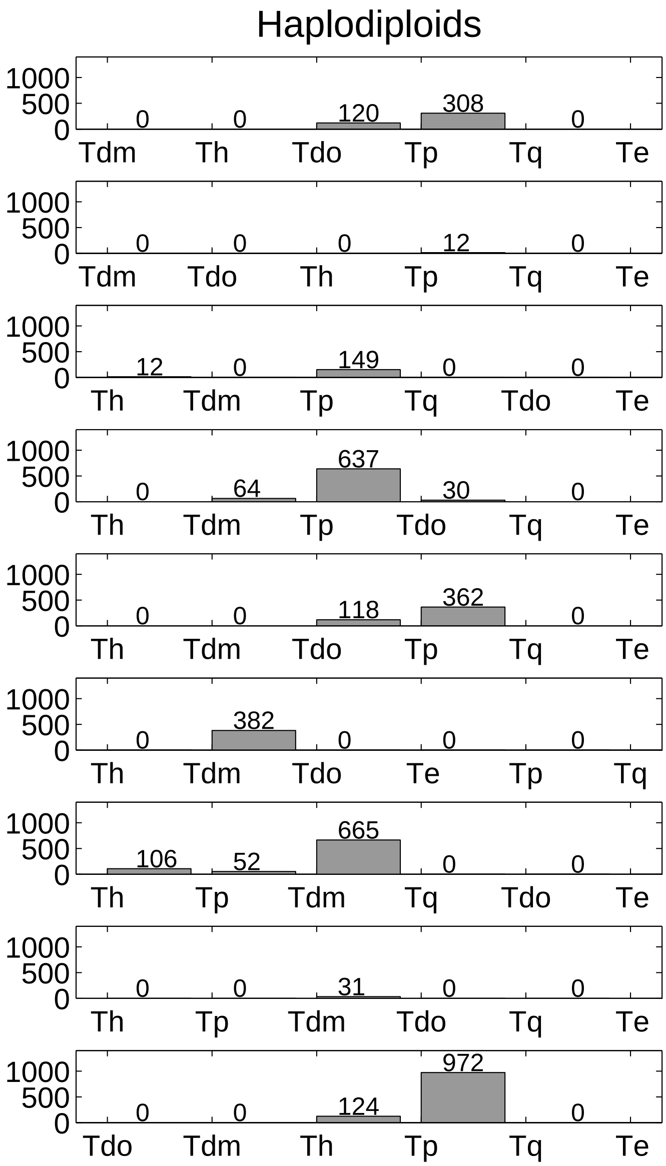


Figure III3.8: Threshold arrangements that produced rescues in haplodiploids. The legend of Fig. III3.7 applies. The only unique threshold arrangement relative to haploids and diploids is the eighth panel.

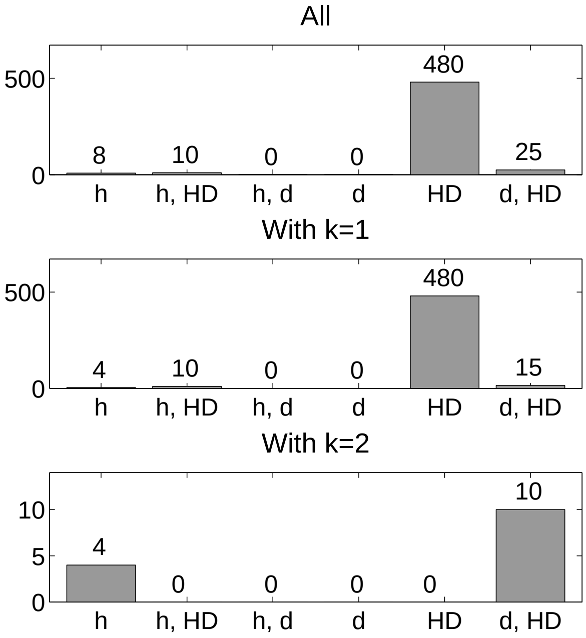


Figure III3.9: Unique advanced eusocial outcomes. Unique advanced eusocial outcomes were defined as occurring when, for a given parameter combination, advanced eusociality was obtained in some but not all three genetic systems (advanced eusociality defined as when $e(\text{end}) > 0.1$). The bars give the number of unique advanced eusocial outcomes for the genetic systems indicated (h: haploid, d: diploid, HD: haplodiploid). Although a larger number of unique advanced eusociality occurs in haplodiploids (top panel), this is due to the absence of dosage compensation ($d = 1$) and thus the half ability to resist among males (middle panel). With dosage compensation ($d = 2$), advanced eusociality that occurs only in diploids and haplodiploids was most common (bottom panel).

III.5.8 Artificialities

In the numerical solutions, sex ratio is assumed to be constant and the time scale may at times be unrealistically large. Also, it is assumed that offspring helping efficiency keeps up with maternally induced benefits (i.e., $b_{\max}$ is assumed to be $a_0 + e_{\max}$).

Vita

Mauricio González-Forero was born in Medellín, Colombia on October 14th, 1981. He attended el Colegio San José in Medellín from 1986-1998. He majored in Biology at the Universidad de Antioquia from 1999-2006. In 2007 he started graduate studies in the Department of Ecology and Evolutionary Biology at the University of Tennessee. He graduated from his PhD in the Summer of 2013. He then moved to Switzerland for postdoctoral research.