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Evolution of Manipulated Behavior

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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.

Keywords: manipulation, resistance, evolutionary conflict, coevolution, altruism, indirect genetic effects.

Behaviors that affect the reproductive success of other individuals are often referred to as social (Hamilton 1964). 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; Adamo 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, 2010b; 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

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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, and so forth. 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 at 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 nonanimals (Maestri-pieri 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 evo-

lution 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; Gavrillets et al. 2001; Wenseleers et al. 2004; 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., nonmanipulated) 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.

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 prob-

ability 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

$$w_m = p(1 - c_m) + (1 - p) \tag{1}$$

$$= 1 - c_m p.$$

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

$$w_s = P(1 - q)(1 - c_a) + Pq(1 - c_r) + (1 - P) \tag{2}$$

$$= 1 - c_a P(1 - q) - c_r Pq.$$

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

$$w_t = \Pi(1 - Q)(1 + b) + \Pi Q + (1 - \Pi) \tag{3}$$

$$= 1 + b\Pi(1 - Q).$$

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 heritable component of the trait of the actor (i.e., the individual expressing the trait) with the heritable component 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 1975; Grafen 1984; Frank 2012), and manipulation, punishment or partner choice (Queller 2011). In addition, heritability is here defined in a broad sense in that it need not be genetic, for example, as transmission of information from "parent" to "offspring" via social learning (Frank

1998). 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 nongenetic 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

$$w = 1 - k_m c_m p - k_s [c_a P(1 - q) + c_r Pq] \tag{4}$$

$$+ k_t b \Pi(1 - Q).$$

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

$$\frac{dp}{d\theta} = v_p k_m h_p, \tag{5a}$$

$$\frac{dq}{d\theta} = v_q k_s h_q, \tag{5b}$$

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

$$h_p = br_{tm}(1 - q) - r_{sm}[c_a(1 - q) + c_r q] - c_m, \tag{6a}$$

$$h_q = -p[br_{ts} - (c_a - c_r)]. \tag{6b}$$

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. [6a]) the actors are manipulators ($i = m$), while for resistance (eq. [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. 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

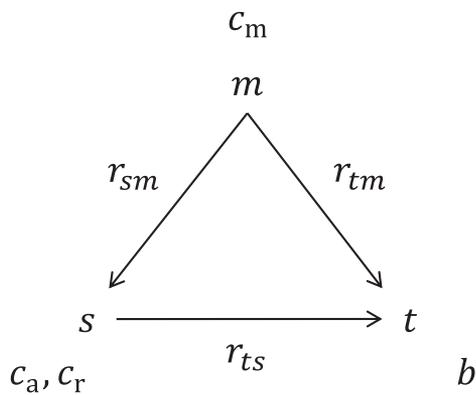


Figure 1: Relatednesses among social partners and their corresponding payoffs. At a given time, individuals are either manipulators (m), subjects of manipulation (s), or targets of manipulated behavior (t). Arrows correspond to the life-for-life relatedness r_{ij} of actor i to recipient j . A manipulator 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.

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. [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. [6a]) 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 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 (eq. [6]) as

$$h_p = M_0 - qM, \tag{7a}$$

$$h_q = pR. \tag{7b}$$

where

$$M_0 = br_{tm} - r_{sm}c_a - c_m, \tag{8a}$$

$$M = br_{tm} - r_{sm}(c_a - c_r), \tag{8b}$$

$$R = -[br_{ts} - (c_a - c_r)]. \tag{8c}$$

Term 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 the critical resistance probability

$$q^* = \frac{M_0}{M}. \tag{9}$$

The model dynamics are analyzed in appendix B.

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

$$br_{ts} + c_r > c_a; \tag{10a}$$

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

$$br_{tm} > c_a r_{sm} + c_m. \tag{10b}$$

That is, the direct or indirect fitness effect to manipulators (br_{sm}) 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 (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 (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

$$q_0 < q^* + p_0u, \tag{11}$$

where $u = [-v_qk_sR/(v_pk_mM)]^{1/2}$, which measures the rate of change in acquiescence relative to the rate of change in selection for manipulation. The quantities p_0 and q_0 denote the initial manipulation and resistance probabilities. Condition (11) states that for manipulated behavior to be obtained when $r_{sm} > -c_m/c_r$, resistance must be initially sufficiently small.

Figure 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 resistance is initially small (gray area); if it is large, manipulation disappears. Figure 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 [10a] is not satisfied) and

$$r_{sm} < -c_m/c_r. \tag{12}$$

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 pos-

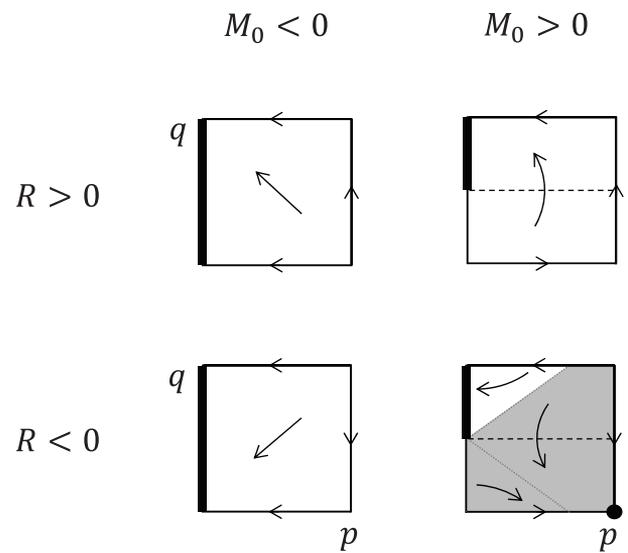


Figure 2: Coevolutionary dynamics of manipulation and resistance when $r_{sm} > -c_m/c_r$ (hence, $M_0 < M$). Columns correspond to the sign of the selection gradient for manipulation without resistance (M_0). Rows correspond to the sign of the selection gradient for resistance (R). The direction of selection for manipulation changes at the horizontal dashed line (q^*). The arrows indicate the direction of evolutionary change for manipulation (p) and resistance (q) (the arrows at the boundaries indicate the partial change with respect to the direction of the boundary). Stable equilibrium points and lines are in thick strokes.

sible 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 [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 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).

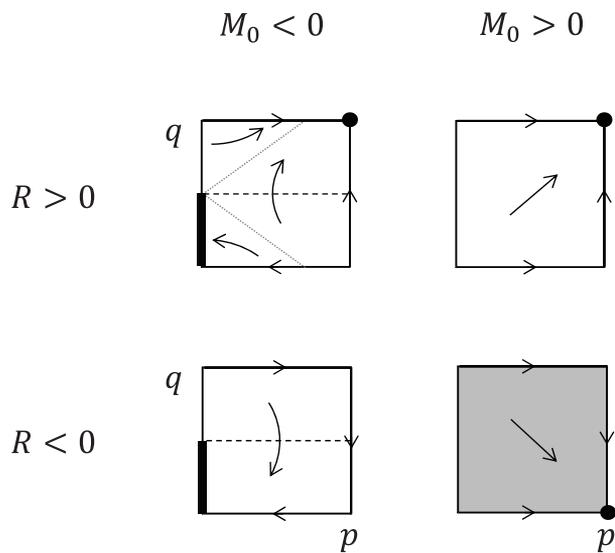


Figure 3: Coevolutionary dynamics of manipulation and resistance when $r_{sm} < -c_m/c_r$ (hence, $M_0 > M$). See the legend in figure 2 for explanation.

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 nonmanipulated behavior; that is, behavior that is fully under control of the individuals expressing it. As stated above, we refer to nonmanipulated behavior as spontaneous behavior.

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_{is} ; i.e., $r \approx r_{is}$). Manipulated behavior can be established under less stringent conditions than spontaneous behavior when inequalities (10) hold and $br_{is} < c_a$. This happens when

manipulation is favored in the absence of resistance (inequality [10b] holds) and the following condition holds:

$$0 < c_a - br_{is} < c_r. \quad (13)$$

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 (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; Michener and Brothers 1974; Trivers 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. 2004; 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 (Metcalf 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 (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 (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 (11), if the initial resistance probability q_0 is smaller than $T_p^* = q^* + p_0 u$, then manipulated behavior is obtained when both acquiescence and manipulation in the absence of resistance are favored. Assume that manipulation is of little cost to the mother; 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 4A 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 4B. 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.

Discussion

Many social behaviors are triggered by social partners. The social trigger may sometimes be the result of manipulation,

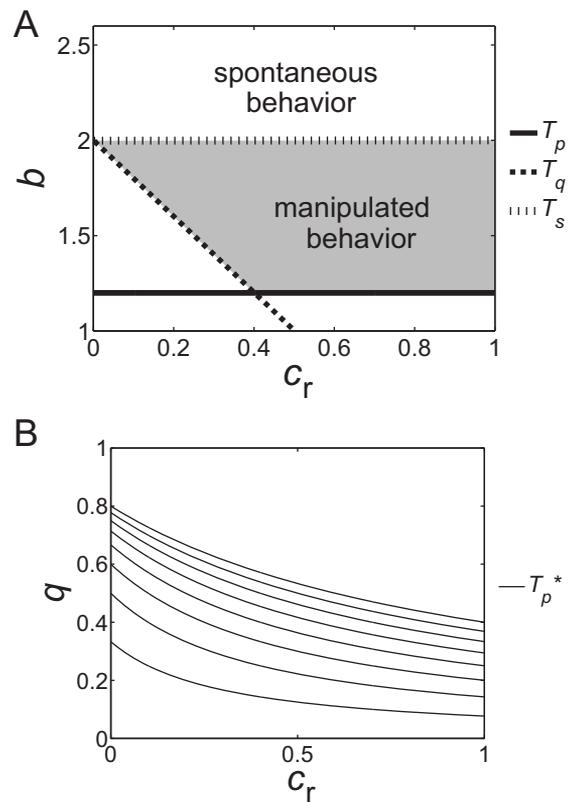


Figure 4: Illustration for maternally manipulated behavior. A, When the benefit b is greater than T_p , manipulation in the absence of resistance is favored; when b is greater than T_q , acquiescence is favored; and when b is greater than T_s , spontaneous behavior is favored. B, When the initial resistance probability q_0 is below T_p^* , manipulated behavior is obtained if both acquiescence and manipulation in the absence of resistance are favored. Parameter values are $c_a = 1$, $c_m = 0.1$, and $r_{ts} = r_{tm} = r_{sm} = 1/2$. For T_p^* , we let $p = 0$ and lines from bottom to top are for b from 1.3 to 2.

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 (Parker and Macnair 1979; Pagel et al. 1998; Robert et al. 1999; Reuter 2004; Wenseleers et al. 2004; 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 [10a] is violated), then manipulated behavior is eliminated. When acquiescence is favored, manipulated behavior can be es-

tablished. 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 [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 [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., Gavrillets 2000; Gavrillets et al. 2001; Reuter 2004; 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 [11]) if manipulators' relatedness to sub-

jects 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 (Reuter 2004); 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 (Gavrillets 2000; Gavrillets 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 nonzero genetic variances can only change the basin of attraction towards either outcome.

The inclusive fitness effect of manipulation (eq. [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. [B1]). On the other hand, the inclusive fitness effect of acquiescence (eq. [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 nonkin (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 that 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 [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 (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 (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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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 noncontributing 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 $dj/d\theta = v_j \partial w / \partial g_j$ 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. [5a]) the actors are manipulators (m) while for resistance (eq. [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, $r_{ji} = \rho_{ji} k_j / k_i$.

APPENDIX B

Analysis

Assume first that $p \neq 0$, so that some manipulation is present. Then equation (6b) tells us that if $R < 0$, then resistance disappears ($q \rightarrow 0$). 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 ($q \rightarrow 1$). 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 $q \rightarrow 0$ and $R < 0$, $M_0 > 0$, then the system evolves to $p = 1$, $q = 0$.

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

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

- If $q \rightarrow 1$ 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 toward 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 (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 $u = [-v_q k_s R / (v_p k_m M)]^{1/2}$ (gray region in fig. 2). The inequality $q < q^* + pu$ can be rearranged into

$$h_p + Mpu > 0, \quad (\text{B1})$$

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.

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