Suppression of Social Conflict and Evolutionary Transitions to Cooperation

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abstract: Evolutionary conflict arises at all levels of biological organization and presents a barrier to the evolution of cooperation. This barrier can be overcome by mechanisms that reduce the disparity between the fitness optima of subunits, sometimes called the "battleground" of conflict. An alternative, unstudied possibility is that effort invested in conflict is unprofitable. This possibility has received little attention because most existing models of social conflict assume that fitness depends on the ratio of players' conflict efforts, so that "peaceful" outcomes featuring zero conflict effort are evolutionarily unstable. Here I show that peaceful outcomes are stable where success depends on the difference rather than the ratio of efforts invested in conflict. These difference form models are particularly appropriate to model strategies of suppression or policing. The model suggests that incomplete information and asymmetries in strength can act to eliminate costly conflict within groups, even among unrelated individuals, and thereby facilitate the evolution of cooperation.

Keywords: conflict resolution, eusociality, genomic imprinting, intragenomic conflict.

Introduction

Evolutionary conflict arises in social interactions when the individual optima of interactants cannot be satisfied simultaneously (Parker 2006). This disparity between optima has been labeled the "battleground" of evolutionary conflict (Godfray 1995; Cant 2006). Conflict arises at all levels of biological organization (i.e., between genes, cells, individuals, and groups; Alexander 1987; Frank 2003; Lachmann et al. 2003; Queller and Strassman 2009) and presents a barrier to cooperation because it generates selection for costly or disruptive acts aimed at securing a larger share of the fitness profits of cooperation (Reeve 2000; Queller and Strassman 2009; Cant 2011). Most models of cooperation assume that evolutionary conflict is overcome through mechanisms that draw together the fitness optima of individual subunits—for example, via genetic relatedness, intergroup competition, repeated inter-

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actions, or reproductive leveling (Hamilton 1964; Alexander 1987; Frank 2003; Roberts 2005; Bowles 2006; Lehmann and Keller 2006; Nowak 2006; Gardner et al. 2011). A second possibility is that individual optima remain divergent but that effort invested in conflict is unprofitable—in other words, a battleground exists but does not result in selection for costly or disruptive competitive acts.

This second possibility has received little attention to date because it is ruled out by most existing models of social conflict, which assume a particular relationship between effort invested in competition and relative success (table 1). Specifically, in these models the contest success function (CSF; Hirshleifer 1989), which relates an individual's competitive effort to its success, takes the form of a ratio, with individual effort as the numerator and either mean or summed effort of all contestants as the denominator. In ratio form models, zero investment in conflict necessarily brings zero success. As a consequence, "peaceful" outcomes, defined as outcomes in which no players invest in conflict, are always evolutionarily unstable in these models. Outcomes involving "one-sided peace," in which some players invest effort in the conflict while others do not, are also evolutionarily unstable in ratio form models (Hirshleifer 1989). Thus, according to existing theory the presence of a battleground of conflict always selects for costly and disruptive acts of selfishness by all parties. In many cases, however, this appears not to be the case. In many cooperative societies, there is much potential for conflict, but this is not manifested in costly or overt acts (Packer and Pusey 1982; Jamieson et al. 1994; Kardile and Gadagkar 2002; Endler et al. 2007). In other societies, one party (e.g., a dominant individual) engages in competitive acts or attempts at suppression while others do not (Grantner and Taborsky 1998; Ratnieks and Wenseleers 2005; Saltzman et al. 2008; Clutton-Brock et al. 2010). During sexual reproduction, unrelated haploid genomes, which have great potential for evolutionary conflict, fuse with little actual conflict (Queller and Strassman 2009).

This discrepancy between theory and data can be addressed using insights from economic rent-seeking models,

Table 1: Ratio form models of social conflict at different levels of biological organization

Level of organization, contested resource	No. players	CSF	Reference
Gene:			
Maternal investment	2	$x_1/(1 + x_2)$	Kondoh and Higashi 2000
Maternal investment	N	$x_i/\sum x$	Haig and Wilkins 2000
Individual:			
Reproduction	2	$x_i/\sum x$	Cant 1998
Reproduction	2	$x_i/\sum x$	Cant and Shen 2006
Reproduction	2	$x_i/\sum x$	Johnstone 2000
Reproduction	2	$x_i/\sum x$	Reeve et al. 1998
Parental care	2	$x_i/\sum x$	Parker 1985
Food/territory	2	$x_i/\sum x$	Parker 1974
Territory	2	$x_i/\sum x$	Parker and Knowlton 1980
Food	N	$x_i/\sum x$	Shaw et al. 1995
Food/resources	N	$x_i/\sum x$	Parker 2000
Public goods	N	$x_i/\bar{x}$	Frank 1995
Public goods	N	$x_i/\bar{x}$	Frank 2003
Group:			
Ecological resources	N	$x_i/\sum x$	Reeve and Hölldobler 2007

Note: The contest success function (CSF) in these models is a ratio of a focal player's effort (χ_i) to either the mean or the summed efforts of all competitors ($\bar{x}$ or $\sum x$, respectively).

which have been used to study conflict resolution in a range of economic, military, and legal contexts (Lockard and Tullock 2001). Typically, the CSF in these models takes the form of a ratio, and as a result peaceful outcomes are unstable. However, peaceful and one-sided peace outcomes are all possible in rent-seeking models, which assume that the probability of success depends on the difference between each player's conflict effort (Hirshleifer 1989). The ratio and difference forms of the CSF represent two canonical forms that have distinct properties and are appropriate to different types of conflict (Hirshleifer 1989, 2001; Garfinkel and Skapaderas 2007). Unlike in ratio form models, in difference form models a player who invests nothing in the conflict need not lose everything at stake. In economics, the difference form of the CSF is appropriate to nonideal conflict scenarios—for example, where information is imperfect, players suffer from fatigue or one party is unable to fully suppress or exploit the other (Hirshleifer 2000). Similarly, in evolutionary conflicts physical or informational constraints may prevent one party from fully suppressing another, so their opponent may still gain a positive fitness payoff or a share of a contested resource even if they invest nothing in conflict. In cooperative breeders, for example, adults may refrain from policing if they cannot discriminate the parentage of offspring (Hodge et al. 2011) or, in hymenopterans, if they are unable to distinguish haploid male eggs from diploid female ones (Beekman et al. 2003). Within genomes, alleles can be selected to suppress each other's expression or phe-

notypic effects, but suppression can be incomplete or cost-ineffective (Burt and Trivers 2006; Haig 2006).

To crystallize the biological distinction between ratio and difference form models of social conflict, consider the case of reproductive conflict between two females laying eggs in a shared nest. Where competition takes the form of a scramble between offspring, success will depend on proportional representation in the number of eggs laid, and hence a ratio form CSF would apply well. If, however, competition takes the form of infanticide after eggs are laid, females who invest nothing in infanticide may still achieve some reproductive success (since discrimination may not be perfect), and hence the difference form CSF more accurately captures the expected gains of effort invested in conflict. In the former case, success depends on maximizing the production of competitive units (in this case, offspring) or competitive acts. For convenience, I label this "production competition." In the latter case, success depends on suppressing or eliminating the competitive units produced by others or nullifying their competitive acts. I term this "suppression competition." In reality, some biological conflicts may involve elements of production and suppression. Note also that there is some resemblance here to the distinction in ecology between exploitation versus interference competition, although these categories are usually defined according to whether individuals interact indirectly (via effects on a shared resource) or directly (Begon et al. 1996)—not by the form

of the CSF. Some candidate biological examples of these two types of competition are shown in table 2.

Here I show why solutions involving zero conflict investment by one or more parties are evolutionarily unstable when the CSF takes the form of a ratio, and I analyze a difference form (or suppression) model in which mutual peace, one-sided peace, and mutual conflict are all demonstrably evolutionarily stable outcomes. The results highlight the factors that can eliminate costly conflict among potential cooperators despite large disparities in fitness optima and thereby facilitate cooperative transitions.

The Model

Consider two players that invest efforts x and y to win a contest over a resource of value V. The CSF (denoted F) specifies how the efforts of players 1 and 2 convert into their relative success in the contest, which will be denoted F_1 and F_2, respectively ($F_1 + F_2 = 1$). Where the resource is indivisible (as is typically assumed in contest competition), F_i can be interpreted as the probability that player i wins sole control of it. Alternatively, where the resource is divisible (as in biological scrambles; Parker 2000), F_i gives the fraction of resource obtained by player i.

Because I focus on social conflict, I assume that effort invested in conflict impacts group productivity or performance, so that group productivity V is a declining function of effort x and y. This is a common assumption in models of social conflict; for example, both the policing models of Frank (1995, 2003) and the tug-of-war reproductive skew model of Reeve et al. (1998) assume that effort reduces the value of a communal resource. Specifically, in Frank's (1995, 2003) models the productivity of the group declines with the mean effort level $\bar{x}$ of group members, such that the fitness of player i is proportional to $(x_i/\bar{x})(1 - \bar{x})$. In Reeve et al.'s (1998) two-player model, productivity declines with the sum of player efforts, such that the fitness of player 1 is proportional to $[x/(x + y)](1 - x - y)$. Here I allow for both social and personal costs of conflict and also incorporate a strength parameter b ($1 \leq b < 0$), which scales the effectiveness of player 2's effort relative to that of player 1 (as in Reeve et al.'s model). Player 2 is as strong or weaker than player 1.

The fitness function for player 1 is

$$W_1(x, y) = F_1(x, y)V(x, y) - C_1(x), \qquad (1)$$

where $C_1(x)$ describes the personal costs to player 1 of effort level x. I assume that the personal fitness costs are monotonically increasing in x and that the costs of a given level of effort for player 2 are equal to or greater than those for player 1 (i.e., $C_1(z) \leq C_2(z)$ and $C_1'(z) \leq C_2'(z)$, where $C_1'(z) = \partial C_1(z)/\partial z$). I also assume initially that social

Table 2: Candidate biological examples of production and suppression competition in biological systems

Production (success ∝ ratio of efforts)	Suppression (success ∝ difference in efforts)
Scramble competition	Infanticide
Communal breeding	Policing
Sibling rivalry	Interlocus suppression
Maternal-fetal conflict	Mate guarding
Sperm competition	Sexual coercion
Superparasitism	Host-pathogen conflict

Note: Production competition involves maximizing the proportion of competitive efforts or units produced (e.g., offspring). Suppression competition involves suppressing, nullifying, or eliminating the competitive effort or units produced by others. In suppression competition, individuals can gain a positive fitness payoff even if they invest zero effort in conflict.

partners are unrelated, but I consider the role of relatedness later.

Consider the following two forms of the CSF $F_1(x, y)$:

$$\text{ratio form: } F_1(x, y) = \frac{x^d}{x^d + by^d} \qquad (2)$$

and

$$\text{difference form: } F_1(x, y) = \frac{1}{1 + e^{d(by - x)}}. \qquad (3)$$

The ratio CSF given by function (2) is a more general form of that used in the tug-of-war model of Reeve et al. (1998). This additional generality arises because I incorporate a decisiveness parameter d ($0 \leq d \leq \infty$), which scales the marginal returns of superior conflict effort, as is standard in economic rent-seeking models (Hirshleifer 1989; Nitzan 1994). Function (3) is adapted from the difference form economic conflict model of Hirshleifer (1989, 2001). The CSF for player 2 in both cases is $1 - F_1(x, y)$. The models could in principle be extended to N players—for example, the N-player version of the ratio form CSF is

$$F_i = \frac{x_i^d}{x_i^d + \sum_j x_j^d}$$

where $j = 1$ to N and $i \neq j$ (Nitzan 1994). For simplicity (and because it is adequate to illustrate the properties of difference versus ratio form models), I consider only the two-player case here.

The properties of functions (2) and (3) are illustrated in figure 1. In ratio form models, the CSF is rooted at the origin for all values of decisiveness d greater than 0, so zero effort always brings zero relative success in these cases. In the difference form model, by contrast, low decisiveness increases the reward of zero conflict effort. In both the ratio and the difference form models there are two limiting
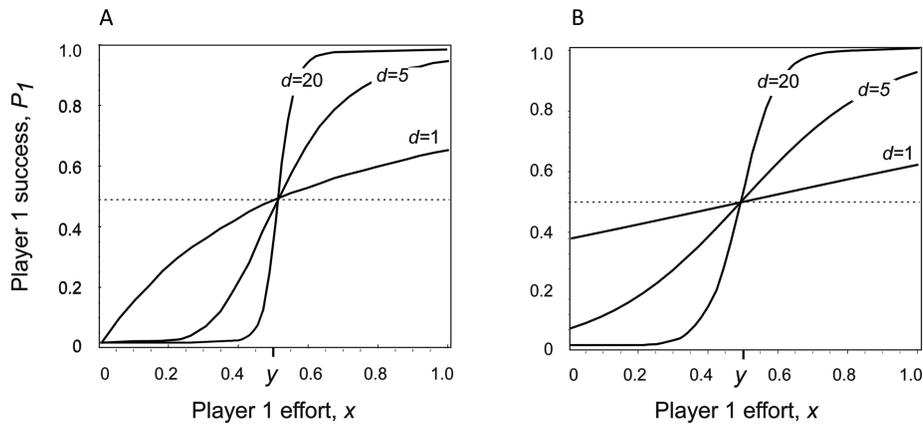
Figure 1: Ratio form versus difference form contest success functions (CSFs). *A,* Relative success of player 1 (F_1) as a function of its conflict effort *x,* assuming that player 2 invests $y = 0.5$. The CSF is $F_1 = x^d/(x^d + by^d)$, where *d* ($0 \le d \le \infty$) is decisiveness and *b* is the relative strength of player 2 (in the example shown, $b = 1$ for simplicity). Curves show the effect of the decisiveness parameter *d;* the horizontal dotted line shows the case where $d = 0$. *B,* Equivalent contest success of player 1 for the difference form CSF given by $F_1 = 1/(1 + e^{d(by-x)})$. Again, $b = 1$ in this example. In the difference form CSF, player 1 can gain some success even if it does not invest in conflict.

cases: where $d = 0$, relative success is independent of effort, and the relative success of both players is 0.5 (the dotted horizontal line); where $d = \infty$, the player who invests the least has zero payoff (in figure 1*A* and 1*B,* this would be a vertical step function at $x = y = 0.5$).

The evolutionarily stable solution (ESS) effort levels for the models based on contest success functions (2) and (3) are those that satisfy the simultaneous equations $\partial W_1/\partial x = 0$ and $\partial W_2/\partial y = 0$, subject to the second-order conditions $\partial^2 W_1/\partial x^2 < 0$ at $x = x^*$ and $\partial^2 W_2/\partial y^2 < 0$ at $y = y^*$.

Ratio Form Model: Analysis

An important property of the ratio form model is that no stable equilibrium exists where both players invest zero effort. Suppose that both players invest zero effort. At this point, $F_1 = F_2 = 0.5$ by assumption, and thus both players stand to gain by unilaterally increasing their level of selfish effort (by an infinitesimal amount) because by doing so they increase their relative success from 0.5 to 1. The marginal gains of investment at $x = y = 0$ are infinite, and hence a situation of mutual peace is unstable. The same argument applies if we assume any other value of F_1 (<1) and F_2 at $x = y = 0$.

An outcome of one-sided peace, which is defined here as a situation where one party invests in selfish effort but not the other (e.g., $x > 0$, $y = 0$), is also not an ESS in this model. Substituting $y = 0$ in functions (2) and (1) and differentiating with respect to *x,* we have

$$\partial W_1/\partial x|_{y=0} = -\partial C_1/\partial x + \partial V/\partial x.$$

Since the right-hand side is negative, player 1 cannot gain from positive selfish effort given that player 2 invests zero effort. The same argument holds for player 2 in the case where $x = 0$. In this model, therefore, neither mutual peace nor one-sided peace are evolutionarily stable outcomes. This is a general feature of models in which the CSF takes the form of a ratio (Hirshleifer 1989, 2000; Garfinkel and Skapaderas 2007).

It should be noted that some ratio form models of policing in social insects (Wenseleers et al. 2004*a,* 2004*b*) do predict one-sided peace in the form of acquiescence by workers to the policing effort of queens and nestmates. This is because these models assume that policing effort (or efficiency) is a fixed parameter and does not coevolve with the level of worker reproduction. Zero investment by one party can be an ESS in ratio form models of evolutionary conflict when the investment of other parties is fixed. For example, in model (2) above we could fix *x* at some level and solve for the conditions for which $y = 0$ is a best reply. However, this raises the problem of how selection for policing effort is maintained when there is nothing to police (Cant and Johnstone 2006). Where effort levels of both parties are allowed to coevolve (e.g., Frank 1995), peaceful outcomes are unstable in ratio form models (Hirshleifer 1989).

Difference Form Model: Analysis

In the difference form model, I again assume that if neither player invests any effort they share the resource in the ratio evenly (relaxing this assumption does not affect the

qualitative predictions of the model). Following Reeve et al. (1998), I assume that the social costs of conflict are described by the function

$$V(x, y) = V(1 - x - y),$$

so that group productivity declines with the sum of effort invested in conflict.

We can first ask whether mutual peace is possible in this model—that is, whether $x^* = 0$ and $y^* = 0$ is a possible ESS. Substituting $y = 0$ in function (3) and then substituting function (3) into function (1) and solving for a fitness maximum at $x = x^* = 0$ yields the following condition for which the stable outcome is mutual peace:

$$d < d_{\text{crit}} = \frac{2(V + 2C_1')}{V}, \tag{4}$$

where $C_1' = \partial C_1'/\partial x$ and is evaluated at $x = 0$. In a model in which the two players are related by coefficient r, the condition for mutual peace is $d < 2[V(1 + r) + 2C']/[V(1 - r)]$ (see the appendix, available online as a zip file).

What about one-sided peace or submission—that is, stable outcomes where only one player invests selfish effort? To investigate this question, I examined the behavior of the model in the region $d_{\text{crit}} + u$, where u is an arbitrarily small positive constant. If solutions of the form $x^* > 0$ and $y^* = 0$ exist, then for arbitrarily small u the derivative of player 1's fitness with respect to its effort x at $x = 0$ and $y = 0$ should be positive (indicating that the value of x that maximizes player 1's fitness in this region is >0), and the derivative of player 2's fitness with respect to its effort y at $x = 0$ and $y = 0$ should be negative (indicating that player 2's fitness is maximized at $y < 0$ in this region). Conversely, if solutions of the form $x^* = 0$ and $y^* > 0$ exist in the region $d_{\text{crit}} + u$, then we expect $\partial W_1/\partial x < 0$ and $\partial W_2/\partial y > 0$ at $x = 0$ and $y = 0$. Finally, if no solutions featuring one-sided peace exist, then the derivative of both players' fitness with respect to their effort (evaluated at $x = 0$ and $y = 0$) should always have the same sign in the region $d_{\text{crit}} + u$.

Substituting $d = [2(V + 2C_1')/V] + u$ into functions (3) and (1); differentiating with respect to x and y, respectively; and evaluating these derivatives at $x = 0$ and $y = 0$ yields

$$\partial W_1/\partial x = uV(1 - r)/4 \tag{5}$$

and

$$\partial W_2/\partial y = \frac{1}{4}\Big[(2V + 2rV)(b - 1) + Vb(u - ru) + 4bC_1' - 4C_2'\Big], \tag{6}$$

where $C_2' = \partial C_2'/\partial y$ and is evaluated at $y = 0$. For arbi-

trarily small positive u (and given our assumption that $C_1' \leq C_2'$), expression (5) is positive, while expression (6) is negative. Hence, solutions of the form $x^* > 0$ and $y^* = 0$ exist. This conclusion holds for a model in which players are related by coefficient r (see the appendix). The model therefore predicts a zone of parameter space where the equilibrium solution is for the stronger player to invest positive effort and the weaker player to invest zero effort.

Results

I plot the results of the model assuming no personal costs of conflict, since inclusion of these costs does not alter the qualitative predictions, and setting the value of the contested resource $V = 1$ for simplicity (V does not in any case affect the results when there are no personal costs). The zones of parameter space for which the stable outcome is mutual peace ($x^*, y^* = (0, 0)$), one-sided peace $(+, 0)$, and mutual conflict $(+, +)$ are shown in figure 2*A* as a function of the two parameters of the model, b and d. Below a threshold level of decisiveness, the evolutionarily stable outcome is zero actual conflict. Where players are related by coefficient r, the region of mutual peace is expanded to $d < 2(1 + r)/(1 - r)$ rather than $d < 2$ (fig. 2*B*). Evolutionarily stable (ESS) efforts decline with increasing asymmetry in strength (fig. 2*C*). Effort levels decline—and hence conflict is resolved at lower cost to team productivity—as decisiveness decreases (fig. 2*D*). In outcomes of one-sided peace $(+, 0)$, it is always the stronger player that invests positive effort and the weaker that invests zero effort (as per the proof in the preceding section).

Discussion

The analysis shows that a seemingly innocuous change in the assumed form of the CSF can dramatically alter the predicted outcome of evolutionary conflict. This is important because ratio form models are commonly employed for reasons of tractability and may not be best suited to all biological conflicts. Difference form models have been used to investigate evolutionary conflict in non-social contexts—for example, sexual conflict (Gavrilets et al. 2001; Rowe et al. 2005) and host-pathogen conflict (van Baalen 1998). In the context of social evolution, however, previous theory has been limited to ratio form approaches (table 1). As a consequence, little attention has been paid to factors that can eliminate costly conflict between social partners and thereby increase the fitness incentive to cooperate. The current model shows that the ability to suppress directly the fitness of social partners (suppression competition) rather than simply to outproduce them (production competition) is favorable to the evolution of cooperation.
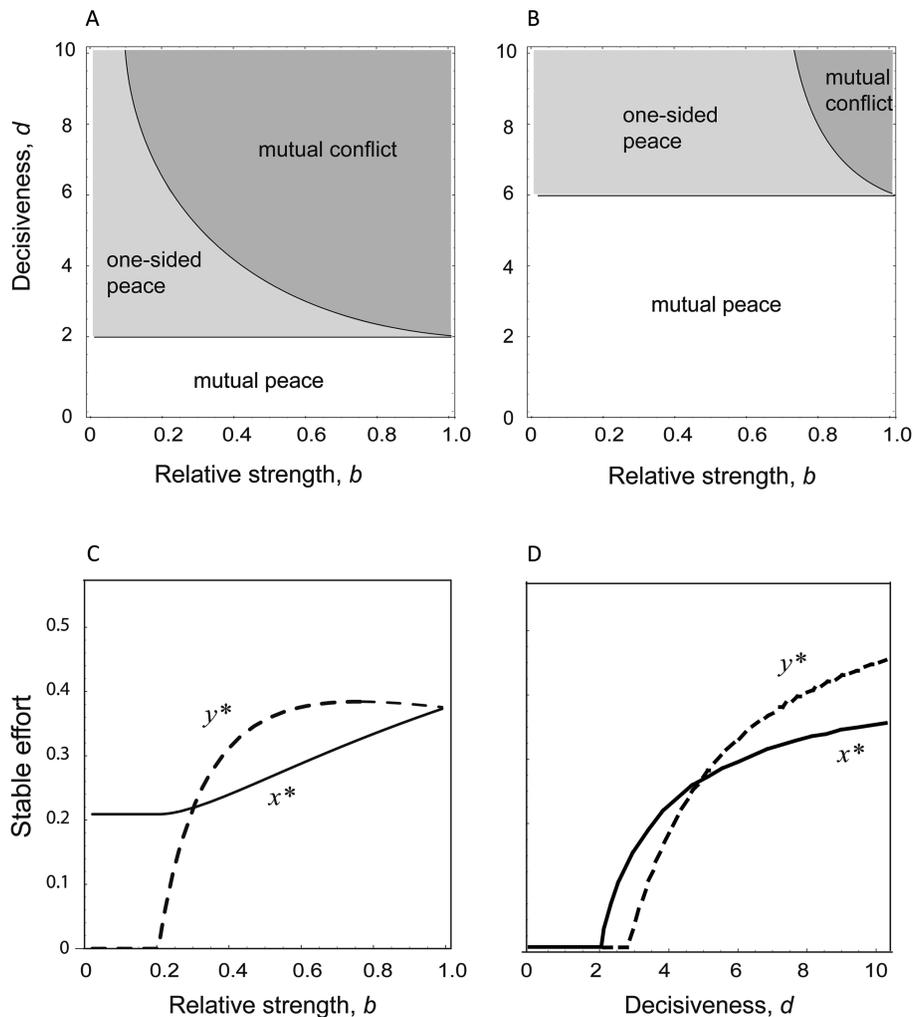
Figure 2: Results of the difference form model. *A* and *B* show zones for which mutual peace, one-sided peace, and mutual conflict are evolutionarily stable outcomes as a function of relative strength and decisiveness. *A* shows results for nonrelatives (i.e., relatedness; $r = 0$); *B* shows results for $r = 0.5$ (see the appendix, available online as a zip file). *C* and *D* show evolutionarily stable levels of effort in conflict invested by player 1 (x^*) and player 2 (y^*) as a function of relative strength and decisiveness, respectively (other parameters are as follows: in *C*, $r = 0$, $d = 6$, $V = 1$; in *D*, $r = 0$, $b = 0.7$, $V = 1$). Evolutionarily stable solution (ESS) effort levels were found using numerical methods in Mathematica 8 (see the appendix). Low decisiveness leads to zero actual conflict despite high potential conflict. In the case of nonrelatives, the ESS conflict effort of both parties is 0 below a threshold level of decisiveness equal to 2 (*A* and *D*).

The suppression model presented here suggests that three main factors promote peaceful and profitable outcomes of social conflict: high relatedness, asymmetry in strength, and low decisiveness. Relatedness has a dual effect: it reduces the disparity in optima between interactants (or the width of the battleground) and moreover reduces the inclusive fitness payoff of investing in acts of suppression. Asymmetry in strength reduces the cost of conflict resolution because it requires little effort to suppress and subjugate a weak social partner. The model predicts,

therefore, that (i) cooperative associations consisting of strong and weak individuals are less likely to be disrupted by costly acts of conflict than are associations among equals and (ii) both strong and weak individuals can gain from seeking each other out as social partners. Evidence in support of prediction (i) comes from the paper wasps, cleaner fish, cooperative cichlids, and coral-dwelling fish size hierarchies, where conflicts are more intense among social partners of similar size and there are measurable costs of aggression (Nonacs and Reeve 1995; Heg et al.

2004; Raihani et al. 2011; Ang and Manica 2010). In the context of intragenomic conflict, predictions (i) and (ii) derive from the same logic as Cosmides and Tooby's (1981) cytoplasmic conflict model for the evolution of anisogamy—namely, that power asymmetry among social partners can reduce costly conflict and facilitate cooperation.

The third parameter of the model, decisiveness, measures the efficiency with which an advantage in conflict effort converts to an advantage in success and can be interpreted biologically in a number of ways. Decisiveness will be high in trials of strength or endurance where success depends on outlasting one's opponent in the manner of a war of attrition. Indeed, in both the war-of-attrition model (Maynard Smith 1974) and the Lanchester models of conflict (Maynard Smith 1974; Adams and Mesterton-Gibbons 2003) decisiveness is effectively infinite because an individual that invests fractionally more than their opponent wins the resource with probability one. At the other end of the scale, decisiveness will be low where conflict is risky or success is to some extent arbitrary. In line with intuition, therefore, the model predicts a high probability of peace and one-sided peace where fighting is stochastic or contestants possess potentially lethal weaponry (as in lions [Packer et al. 2001], banded mongooses [Hodge et al. 2011], and hymenopterans [Reeve 1991; Cant et al. 2006; Ratnieks et al. 2006]). Decisiveness will also be low in social queues where subordinates can inherit a contested resource by outliving their immediate dominant (Kokko and Johnstone 1999; Field and Cant 2009; Leadbeater et al. 2011). In biological systems, it may be possible to manipulate decisiveness experimentally by varying the stochastic component of contest success, at least in systems where contestants can learn contest characteristics on the basis of previous experience (Oliveira et al. 2009).

A particularly interesting influence on decisiveness is the level of uncertainty in the contest. Where players have incomplete information about relative strength, there will be some uncertainty about the opponent's effort, with the effect that the effective or "realized" decisiveness of the contest may be lower than is the case under conditions of perfect information. Increased uncertainty on both sides about the opponent's strength is therefore expected to lead to an increased frequency of one-sided peace or mutual peace outcomes and lower total effort invested in conflict at equilibrium (see Fey 2008). In line with previous suggestions, the machinery of meiosis can be interpreted in this light as a mechanism to scramble information about the benefits of conflict investment and thereby promote intragenomic peace (Alexander 1987; Buss 1988; Haig and Grafen 1991).

Finally, in the region for which one-sided peace is the stable outcome a stronger individual benefits from a marginal increase in decisiveness, whereas a weaker individual gains from a marginal decrease in decisiveness (see the appendix). Consequently, where there is some uncertainty about relative strength an individual that knows itself to be stronger than its opponent may gain from reducing uncertainty about relative strength, whereas an individual that knows itself to be weaker than its opponent can gain from increasing this uncertainty. This raises the intriguing possibility that dominant-submissive behaviors in animals and humans reflect selection for dominants to advertise their strength and for subordinates to conceal it (mirroring a recent result in economic conflict theory; Katsenos 2010). An important future step is to investigate how decisiveness itself may evolve—for example, through information transfer or via the mechanistic sequence of competitive acts—rather than assuming it to be an external parameter of the conflict, as I do here. Such models could help to understand how low decisiveness can emerge endogenously from selection acting on individual mechanisms and tactics, with potentially broad implications for the evolution of cooperation among genes, cells, and individuals.

Acknowledgments

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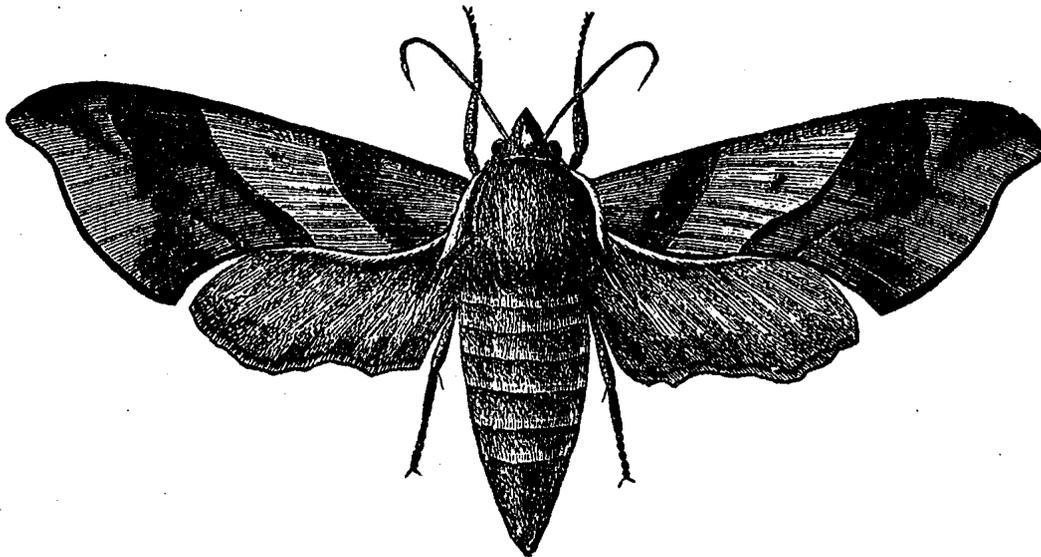
Vine dresser moth *Choerocampa pampinatrix*, "a single caterpillar of which will sometimes 'strip a small vine of its leaves in a few nights' and sometimes nips off bunches of half-grown grapes." From "Review: *Economical Entomology in Missouri*" (*American Naturalist*, 1870, 10: 610–615).