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PERSPECTIVE:
REPRESSION OF COMPETITION AND THE EVOLUTION OF COOPERATION

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Abstract.—Repression of competition within groups joins kin selection as the second major force in the history of life shaping the evolution of cooperation. When opportunities for competition against neighbors are limited within groups, individuals can increase their own success only by enhancing the efficiency and productivity of their group. Thus, characters that repress competition within groups promote cooperation and enhance group success. Leigh first expressed this idea in the context of fair meiosis, in which each chromosome has an equal chance of transmission via gametes. Randomized success means that each part of the genome can increase its own success only by enhancing the total number of progeny and thus increasing the success of the group. Alexander used this insight about repression of competition in fair meiosis to develop his theories for the evolution of human sociality. Alexander argued that human social structures spread when they repress competition within groups and promote successful group-against-group competition. Buss introduced a new example with his suggestion that metazoan success depended on repression of competition between cellular lineages. Maynard Smith synthesized different lines of thought on repression of competition. In this paper, I develop simple mathematical models to illustrate the main processes by which repression of competition evolves. With the concepts made clear, I then explain the history of the idea. I finish by summarizing many new developments in this subject and the most promising lines for future study.

Key words.—Altruism, kin selection, levels of selection, social evolution, symbiosis.

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> *The function of laws is to regulate . . . the reproductive strivings of individuals and subgroups within societies, in the interest of preserving unity in the larger group. . . . Presumably, unity in the larger group feeds back beneficial effects to those . . . that propose, maintain, adjust, and enforce the laws.* (Alexander 1979, p. 240)
>
> *A corollary to reproductive opportunity leveling in humans may occur through mitosis and meiosis in sexual organisms. . . . The leveling of reproductive opportunity for intragenomic components . . . is a prerequisite for the remarkable unity of genomes.* (Alexander 1987, p. 69)
>
> *One can recognize in the evolution of life several revolutions in the way in which genetic information is organized. In each of these revolutions, there has been a conflict between selection at several levels. The achievement of individuality at the higher level has required that the disruptive effects of selection at the lower level be suppressed.* (Maynard Smith 1988, pp. 229–230)

Individuals often live in groups. Genes live in genomes; symbionts live in hosts; siblings live in families; honeybees live in hives. Proximity brings neighbors and kin into intense competition. Genes compete for transmission through gametes; siblings fight for a larger share of family resources.

Proximity also binds the success of each individual to the efficiency of the group. Genes do well in harmonious genomes; honeybees do best with coordinated division of labor. The universal tension of sociality arises from the simultaneous competition between neighbors and the binding of neighbors' interests with those of the group.

If neighbors could not compete, each individual could increase its own success only by increasing the efficiency and productivity of the whole group (Leigh 1977). Repression of competition unites the interests of neighbors and makes the group a cohesive, functional unit.

Fair meiosis was perhaps the first biological problem to be understood in terms of repression of competition (Leigh 1971). In fair meiosis, each paired chromosome has an equal chance of being transmitted in a gamete. Meiotic randomization guarantees the same average success to all chromosomes, preventing any particular chromosome from beating its homolog in the competition to be transmitted. With no

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[1] This paper is dedicated to Richard Alexander on his retirement from the University of Michigan.

opportunity for local competition, all chromosomes gain only with enhanced success of the whole genome. The unity is so nearly complete that one often thinks of a genome in a unitary way rather than as a collection of cooperating genes.

Meiotic drive occurs when one chromosome can outcompete its paired homolog for transmission through gametes (Zimmering et al. 1970). Meiotic drive reminds one that reproductive fairness and the near unity in the genome evolved in the face of competitive pressure between neighbors. The puzzle concerns the selective forces and the biochemical mechanisms that repress internal competition.

Meiotic fairness and its exceptions in meiotic drive became an important topic in the 1960s and 1970s (Zimmering et al. 1970; Crow 1979). As interest increased in the general problems of group selection and the evolution of cooperation, the tension between internal competition and group unity attracted attention in other systems (Alexander and Borgia 1978). Studies ranged from the evolution of the earliest genetic systems and the origin of cells to competition in social insect colonies (Maynard Smith 1979; Ratnieks and Visscher 1989). Suppression of reproductive competition in humans was also proposed as the key process in the evolution of larger group sizes and more complex societies (Alexander 1979, 1987).

In each case, reduced internal competition produces more efficient groups that increase the average success of members within the group. However, natural selection does not always favor greater efficiency and higher average success in social competition. There is a continual pressure for individuals to compete against neighbors and grab a larger share of the local resources, causing lower group efficiency and lower average success of group members. The puzzle is how mechanisms that repress internal competition evolve in the face of the ubiquitous drive toward individual selfishness (Maynard Smith 1988; Frank 1995; Maynard Smith and Szathmáry 1995).

For each topic, particular theories and specialized models explain the evolution of mechanisms that control internal competition. Naturally, the models that apply to competition between cellular lineages differ somewhat from models about repression of competition between bacterial symbionts within hosts or between worker insects within social colonies. Each special topic has been developed to the point where it is now difficult to distinguish between common themes and the truly particular attributes of each case.

I begin with simple, abstract models that make clear the few general processes that underlie most examples. With the essential ideas made clear, I use hindsight to make sense of the history of this subject. Finally, I discuss several active topics of study.

SIMPLE MODELS THAT ILLUSTRATE FUNDAMENTAL CONCEPTS

Repression of competition occurs in several different ways within social groups. In the following subsections, I organize the topic into a coherent framework through a series of models. Here, I provide a brief summary of the conclusions from those models. Readers who prefer to skip the technical details may wish to read this summary and then jump ahead to the later sections, in which I discuss the conceptual history of the topics, current research, and future directions.

The first subsection provides an overview of the models. Each model studies the joint evolution of two characters, the repression of competition and the selfish or competitive behavior that is the target of repression.

The second subsection analyzes repression that shifts reproduction from one class to another (Starr 1984; Woyciechowski and Łomnicki 1987; Ratnieks 1988). Such repression by itself does not necessarily enhance cooperation and group efficiency. Repression of reproduction may favor the repressed individuals to allocate more energy to helping related neighbors and less to direct reproduction. Such reallocation could improve group efficiency.

The third subsection studies competitive characters that directly disrupt group efficiency (Frank 1995, 1996a). Repression of competition therefore contributes an immediate benefit to the group, enhancing the reproductive success of those that invest in policing selfish neighbors. Repressing selfish neighbors imposes a direct cost on those that police, thus policing spreads only when the beneficial effects of improved group success flow back to the policing individuals and their kin.

Policing increases from zero when $r < 1 - c$, where r is the relatedness of an individual to its group and c is the cost to an individual for investing its resources in policing. Note that low relatedness favors policing. When relatedness is high, selection favors self-restraint and cooperation without the need for policing by neighbors. As relatedness declines, selfishness tends to increase, causing a drop in group efficiency and the average success of each group member. Under conditions of poor group efficiency, policing increases because it enhances the quality of life and the success of those that police.

The fourth subsection considers cases in which repression of selfish neighbors provides no immediate benefit to the policing individual or the group. Such behavior is sometimes called ‘‘punishment’’ because of the lack of direct benefit to the punisher (Boyd and Richerson 1992; Clutton-Brock and Parker 1995). Clearly, punishment can evolve only when there is some type of future feedback to the punisher or its relatives. This problem has led to a rather complex literature, mostly emphasizing when punishment can induce selfish individuals to alter their future behavior toward more cooperative expression. I present a new model of ostracism that captures the key issues in a very simple way.

In this ostracism model, individuals behave cooperatively or selfishly in the first time period. The cooperative individuals can, at a cost to themselves, ostracize (or kill) selfish individuals. Those individuals that invest in policing their selfish neighbors gain by living in a more cooperative group in the second time period of interaction within groups. Competition between groups limits second-order defection, in which cooperative individuals do not invest in policing neighbors and gain the benefits from cooperative neighbors that do pay the costs of imposing ostracism on selfish group members.

The fifth subsection explains why dominant or resource-rich individuals take on most of the policing (Clutton-Brock and Parker 1995; Frank 1996a). This occurs because greater strength or resources reduce the relative cost of policing, causing the well endowed to take over social control. Small variations in resource level lead to large differences in allocation to policing behaviors.

The final subsection turns to domestication, in which a powerful partner dominates subordinates (Frank 1997). For example, a host may dominate and domesticate its symbionts. Reproductive conflict between symbionts can favor the symbionts to invest some of their resources in competition against their neighbors. The symbionts' competitive behavior can reduce the resources that flow to the host.

Host repression of symbiotic competition may increase cooperative behavior between symbionts in two different ways. First, the host may directly block competitive symbiont behaviors that disrupt the host. Second, hosts may interfere with symbiont competition by blocking opportunities for the symbionts to outcompete their neighbors. With opportunities for competition blocked, symbionts can raise their own success only by enhancing the success of the host-symbiont group. If no direct benefit accrues to hosts that block symbiont (or subordinate) competition, then repression of competition may not increase without an additional process (Hoekstra 1987). For example, related hosts may share symbionts over a period of time and those related hosts may compete against other groups of hosts.

Overview of the Models

A model for repression of competition must consider the joint evolution of two characters (Frank 1995). First, some individuals in the group invest in a trait that represses the selfish or competitive behaviors of other group members. Repression is sometimes called ''policing'' or ''punishment,'' depending on the context. I use the variable a to describe the repression character. The second character is the selfish or competitive behavior that is the target of repression. I use the variable z for the competitive character.

Studying the joint evolution of two characters can be complicated (Lande and Arnold 1983; Frank 1998). One must account for both the direct selection on each character and the indirect selection that arises through the correlation between the characters. To keep the analysis simple, I assume that the characters are uncorrelated. This assumption provides a good approximation if mutations do not have pleiotropic effects and if linkage disequilibrium remains small. Low linkage disequilibrium often results when mutations typically change the character values by small amounts and genetic variances remain small. Under these assumptions, the analyses here provide a good approximation. If mutations are usually of large effect or character variances tend to be large, then the analyses here still highlight fundamental processes but do not necessarily provide a full description of evolutionary dynamics.

Shift Reproduction from One Class to Another

In some social Hymenoptera, workers can produce sons by laying unfertilized eggs. Other workers sometimes eat those worker-derived eggs, effectively policing against reproduction by females other than the queen (Ratnieks and Visscher 1989). Roughly speaking, policing is favored when the value of worker-derived eggs multiplied by the policing individuals' relatedness to those eggs is less than the value of the queen-derived eggs in direct competition with worker-derived eggs multiplied by the policing individuals' relatedness to queen-derived eggs (Starr 1984; Woyciechowski and Łomnicki 1987; Ratnieks 1988).

The general problem concerns a behavior that represses reproduction by one class and thereby shifts reproduction to another class. To show a simple example, I assume that worker and queen Hymenoptera compete only over the production of males. This allows me to ignore the complexities that arise when the interactions between worker and queen reproduction affect the sex ratio and therefore the relative reproductive values of male and female offspring (Bourke and Franks 1995; Crozier and Pamilo 1996).

Let the number of sons produced by the single queen in a colony be

$$W_q = K - \alpha n\bar{z}(1 - \bar{a}), \qquad (1)$$

where K is the number of sons in the absence of competition with egg-laying workers, α is the substitution rate at which a worker-derived male replaces a queen-derived male, n is the number of workers, $\bar{z}$ is the average number of sons per worker, and $\bar{a}$ is the average suppressive effect of worker policing on the reproduction of workers. Note that $n\bar{z}(1 - \bar{a})$ is the total number of worker-produced males that survive policing.

The number of sons produced by a randomly chosen worker is

$$W_p = z(1 - \bar{a}), \qquad (2)$$

where z is the number of eggs produced and $\bar{a}$ is the fraction of those eggs eaten by policing workers.

I use the methods in Frank (1998) to obtain the conditions for the increase in worker laying, z, and in policing, a. The total fitness of sons in the colony is

$$W = W_q + nW_p. \qquad (3)$$

In this notation, z and a are phenotypes of the worker class. Here, the workers are the actors with behaviors that affect fitness. The recipients are those individuals that have fitnesses affected by the actor phenotypes. In this case, both queen-derived males and worker-derived males are recipients.

We need symbols for the breeding values of the recipient classes—the genetic contributions of the recipient classes to the characters z and a. Let Z_q be the breeding value in queen-derived males for the trait z; let Z_p be the breeding value in worker-derived males for the trait z; let A_q be the breeding value in queen-derived males for the trait a; and let A_p be the breeding value in worker-derived males for the trait a.

Natural selection increases the value of characters when there is a positive slope of fitness on the breeding values transmitted through recipient (reproducing) classes. For the character z, worker-laying, this slope is positive when

$$\frac{dW}{dZ} = \frac{dW_q}{dZ_q} + n\frac{dW_p}{dZ_p} > 0. \qquad (4)$$

The individual terms, evaluated at the population averages $a = \bar{a} = a^*$ and $z = \bar{z} = z^*$, are expanded as

$$\frac{\mathrm{d}W_q}{\mathrm{d}Z_q} = \frac{\partial W_q}{\partial z}\frac{\mathrm{d}z}{\mathrm{d}Z_q} + \frac{\partial W_q}{\partial \bar{z}}\frac{\mathrm{d}\bar{z}}{\mathrm{d}Z_q}$$

$$= -\alpha n(1 - a^*)r_{pq} \qquad (5)$$

where $r_{pq} = \mathrm{d}\bar{z}/\mathrm{d}Z_q$ is the direct fitness coefficient of relatedness between workers and the sons of the queen. For the workers,

$$\frac{\mathrm{d}W_p}{\mathrm{d}Z_p} = \frac{\partial W_p}{\partial z}\frac{\mathrm{d}z}{\mathrm{d}Z_p} + \frac{\partial W_p}{\partial \bar{z}}\frac{\mathrm{d}\bar{z}}{\mathrm{d}Z_p}$$

$$= 1 - a^* \qquad (6)$$

where $\mathrm{d}z/\mathrm{d}Z_p = 1$ because the slope of a worker's phenotype, z, on the breeding value of its son, Z_p, is one since haploid workers produce males by unfertilized haploid eggs.

Combining terms, the condition for $\mathrm{d}W/\mathrm{d}Z > 0$ is $1 > \alpha r_{pq}$. The relatedness term, r_{pq} is less than one, and typically α would also be less than one. In this case, worker-laying is always favored because the only cost is a reduction in queen-laid sons, and workers are more closely related to their own sons than they are to the queen's sons. More complex models could account for other costs of worker laying, such as reduced energy available for colony maintenance or disruption caused by overt conflicts between laying workers and policing workers.

The same approach can be applied for the policing character, a, yielding the condition for $\mathrm{d}W/\mathrm{d}A > 0$ as $\alpha r_{pq} > r_{pp}$. If we take the substitution rate, α, as one, then policing increases when workers are more closely related to the queen's sons, r_{pq}, than are workers related to the sons laid by neighboring workers, r_{pp}. Using direct fitness relatedness coefficients (Frank 1998) with random mating, $r_{pq} = 1/2$ and $r_{pp} = 1/4 + 1/2n$, where n is the effective number of mates for the queen. The effective number of mates means that $1/n$ is the probability that two daughters have sperm from the same father. Thus, policing is favored for $\alpha = 1$ and $n > 2$ (Starr 1984; Woyciechowski and Łomnicki 1987; Ratnieks 1988).

The same result could have been written directly by application of simple inclusive-fitness methods. But the class-based method here has the advantage that it extends readily to more realistic assumptions about demography and fitness interactions, whereas inclusive fitness can be difficult to apply in many realistic cases (Frank 1998).

More complex models could account for other costs of worker policing, leading to feedbacks between the levels of worker policing and worker laying on the costs and benefits of the two characters. With such feedbacks, policing could increase colony efficiency by favoring workers to reduce investment in direct reproduction and increase investment in colony success (Ratnieks and Reeve 1992; Bourke 1999). However, the main point of this model is that worker policing arises by a shift in reproduction from one class to another rather than by an increase in group efficiency.

Directly Repress Disruptive Behavior

I assume in this subsection that the repression trait, a, has a cost, c. Thus, a increases only when there is some associated benefit to individuals for increasing their investment in repressing neighbors.

One type of benefit arises when the competitive behavior of neighbors disrupts group productivity. This may occur because overly competitive behavior leads to imprudent use of local resources (Hardin 1993). For example, overgrazing may increase the relative success of an individual compared with its neighbors, but may also lead to lower total yield available to the group. Repression of overgrazing increases the amount of resources available to the group and thus may directly increase the fitness of the individuals that invest in repressing rapacious neighbors. Here I focus on a simple model that illustrates the joint dynamics of repression, a, and competition, z (Frank 1995, 1996a).

In this model, the fitness of an individual is

$$w = (1 - ca - dz)[\bar{a} + (1 - \bar{a})z/\bar{z}][1 - (1 - \bar{a})\bar{z}], \qquad (7)$$

where overbars denote averages in the local group. The parameter c is the cost to an individual for investing in a, the repression or policing of neighbors' competitive traits, and d is the cost to an individual for investing in z, the competitive tendency to take additional local resources. Here ''policing'' means that some individuals actively repress the competitive behaviors of their neighbors.

The first fitness term of equation (7) is $1 - ca - dz$, the vigor of an individual after paying the costs of policing and competitiveness. The second term, $\bar{a} + (1 - \bar{a})z/\bar{z}$, describes the division of local resources among group members. A proportion $\bar{a}$ of the resources is divided fairly because $\bar{a}$ is the degree to which competition is repressed. A proportion $1 - \bar{a}$ of resources is open to competition, of which an individual with trait z obtains a share in proportion to $z/\bar{z}$. The third term, $1 - (1 - \bar{a})\bar{z}$, is group success, which is disrupted by the degree to which competitiveness, $\bar{z}$, is not repressed, $1 - \bar{a}$.

I limit my discussion of this model to brief summaries of two issues (for analysis, see Frank 1995, 1996a). Under what conditions can the policing trait, a, increase from zero? How do the values of policing, a, and competitiveness, z, jointly adjust to each other at equilibrium?

For $d = 0$, Figure 1A shows that policing increases when $r < 1 - c$, where r is the relatedness of an individual to its group (including itself). Low relatedness is more conducive to the spread of a policing trait than is high relatedness. Figure 1B shows the reason. When policing is absent, $a = 0$, then the equilibrium level of competitiveness is governed by the degree of self-restraint favored by kin selection, $z^* = 1 - r$ (Frank 1994). Thus, at equilibrium, $w = 1 - z^* = r$, illustrated by the solid line in Figure 1B.

A rare individual that polices in a group with no policing has fitness shown by the dashed lines. For low relatedness, r, the policing strategy typically has higher individual fitness than nonpolicing. The policing curve crosses below the nonpolicing line such that, for high relatedness, nonpolicing is favored. As expected, the lower the cost, c, the higher is fitness and the higher the value of r at which the curves cross. Thus, high-cost policing can only be favored when r is low.

The reason that high-cost policing is favored only with low r is that the baseline fitness from which a nonpolicing population starts is r. When r is low, group competition is severe

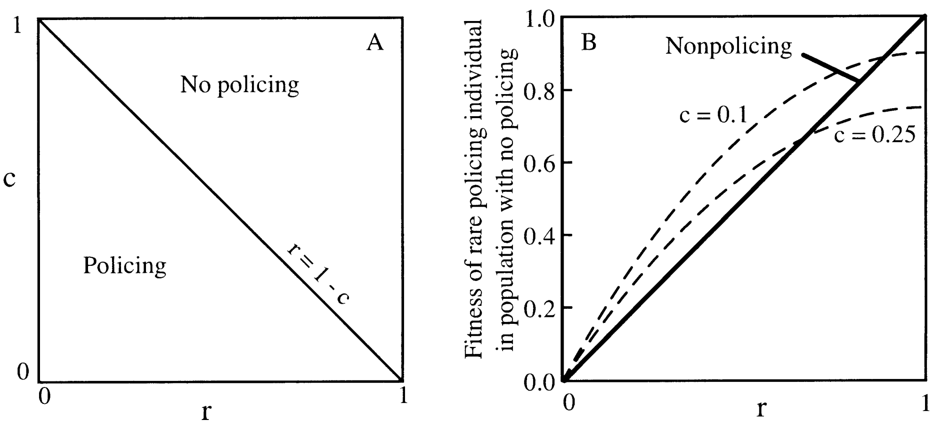

FIG. 1. Invasion of policing trait into nonpolicing population. (A) Low relatedness is more conducive to the increase of policing traits. The condition for the increase of policing is $r < 1 - c$ when mutations have small effect. (B) Fitness of nonpolicing (solid line) and policing (dashed lines) individuals in a nonpolicing population.

and group fitness is low. Any small boost in individual fitness caused by policing is sufficient to provide an advantage. When r is high, individual fitness is already high because self-restraint reduces group competition. In this case costly policing is likely to lower individual fitness. Note that, for the definition of fitness used here, an individual is part of its group. Thus, when relatedness between pairs of different group members is zero, then $r = 1/n$, where n is the size of the group, because there is a $1/n$ chance that two randomly chosen individuals from the group would be the same individual (see Frank 1996a).

Next, I consider how a rise in policing, a, affects individuals' investment in competitiveness, z. Two forces oppose each other. On the one hand, as policing rises, an increasing proportion of an individual's competitiveness is repressed. One can think of a proportion a of investment in competitiveness that must go to avoiding the police. If the cost of competitive traits, d, is zero, then repression of competition causes an increasing allocation by individuals to competitive traits.

The competitiveness trait, z, will often increase above one as a increases. The high level of allocation to competitiveness in a policing population, if introduced into a nonpolicing population, would cause the fitness contribution of these traits to be negative (with $a = 0$, average fitness is $1 - \bar{z}$, which is negative when $\bar{z} > 1$). The high competitiveness in a policing situation is no different from high internal pressure in a fish that lives at great depth. The fish brought to the surface explodes; intense competition and avoidance of repressive policing causes chaos when the same amount of energy is devoted to competition in the absence of repressive policing.

On the other hand, an increase in z reduces fitness if the cost of competitiveness, d, is greater than zero. As a rises, more of an investment in competitiveness is rendered without value, but all of the investment carries the cost, d. Thus, high values of a may favor a decline in z. The net consequence of joint evolution depends on such feedbacks. Figure 2 shows equilibrium values for various parameter combinations.

Punish Selfish Behavior in Repeated Interaction

In the first model above, policing shifts reproduction from one class of individuals to another class. Policing is favored when the reproductive costs and benefits, weighted by relatedness coefficients, combine to provide a net gain in the transmission of the policing character. In the second model of direct repression, an individual that polices gains by immediately improving group efficiency. Improvement follows because policing represses the expression of selfish, disruptive behavior.

A common problem of social cooperation arises when punishing the selfish behavior of a social partner provides no immediate benefit to the actor that punishes (Boyd and Richerson 1992; Clutton-Brock and Parker 1995). In reciprocal altruism, the punishment may induce the selfish partner to become more cooperative in future interactions with the punishing actor (Trivers 1971). However, if the actor has only a low chance of interacting again with the selfish individual, then any changed behavior by the selfish individual must flow back to the actor via some indirect route (Alexander 1987).

Individuals may use complex behavioral rules or learning to adjust their strategies in response to the payoffs of selfishness versus cooperation and the costs and benefits of punishing selfish individuals. A very simple model of innate tendencies for selfishness, z, and policing, a, provides a useful first step into this complex subject. In this model, policing individuals punish selfish behavior by ostracism from the group. Policing individuals lose an immediate cost for taking on the danger of imposing ostracism, but potentially gain in the future as the group becomes more cooperative by the purging of selfish individuals. Alexander (1987, p. 94) mentioned ostracism as one obvious form of punishment in social groups. S. Bowles and H. Gintis (unpubl. ms.) developed a model of ostracism that shows how punishing behavior can be maintained.

Here, I pare down the problem to bare essentials, to expose in a simple way the processes involved. This model divides behaviors into two periods. In the first period, individuals act selfishly with probability z and cooperatively with probability $1 - z$. The payoff to each individual in the first period is proportional to the average probability of cooperation, $1 - \bar{z}$. In addition, cooperators pay a cost d that reduces their fitness.

Among those individuals in the group acting cooperatively,

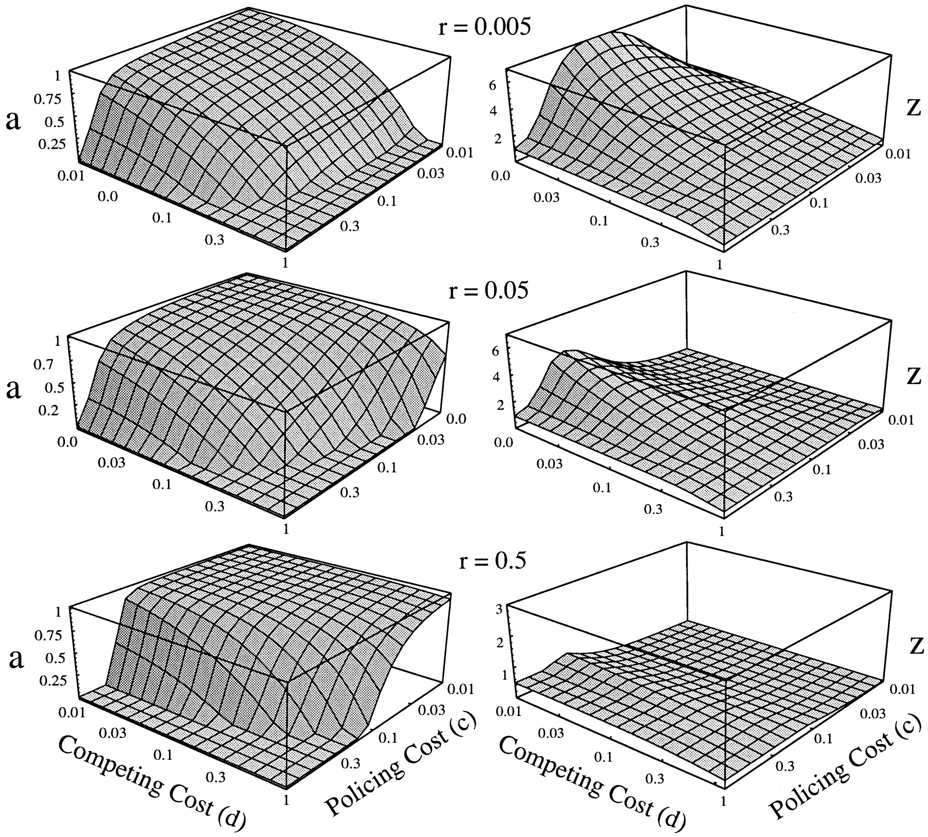

FIG. 2. Equilibrium values of policing, *a*, and competitiveness, *z*. When policing is high, there is little value to be gained by competitiveness. As the cost of competiveness, *d*, rises, competiveness declines and consequently investment in policing also declines. As the cost of policing, *c*, rises, policing declines. When policing is very high, competiveness is low because policing completely represses the value of competitiveness. As policing declines from high levels, competitiveness first increases as opportunities to compete rise. Then as policing falls to low levels, competitiveness declines because less investment in competitiveness is needed to overcome repression. Higher relatedness, *r*, favors less competitiveness (more self-restraint) and reduces investment in high-cost policing.

with probability $1 - \bar{z}$, each individual contributes a to policing selfish neighbors. Policing reduces the fitness of an individual in the first period by $ca\bar{z}$, where a is investment in policing, $\bar{z}$ is proportional to the number of selfish individuals that need to be repressed, and c is a cost parameter. The average contribution to policing among the group's cooperative individuals is $\bar{a}$. Repression of selfish individuals occurs by ostracism (or by killing). With probability $A = (1 - \bar{z})\bar{a}$, a selfishly acting individual is ostracized from the group after the first period of interaction.

In the second period, individuals repeat their selfish or cooperative behaviors as expressed in the first period. Selfish individuals get no payoff in the second period with probability $1 - A$, the probability of ostracism. Among the remaining individuals, the average level of selfishness is $(1 - A)\bar{z}$, so the payoff to each remaining individual is in proportion to $F = 1 - (1 - A)\bar{z}$. Putting the terms together gives the fitness of an individual with characters a and z in a group with average characters $\bar{a}$ and $\bar{z}$ as

$$w = z[(1 - \bar{z}) + K(1 - A)F] + (1 - z)(1 - d)[(1 - \bar{z})(1 - ca\bar{z}) + KF], \qquad (8)$$

where K is the weighting of second-period payoffs to first-period payoffs in calculating total fitness.

In the absence of policing, $a = \bar{a} = 0$, the equilibrium level of selfishness can be obtained by solving $dw/dz = 0$ at $z = \bar{z} = z^*$ (Frank 1998), yielding $z^* = 1 - r/[d(1 + r)]$ for $d(1 + r) > r$, otherwise $z^* = 0$. Here r is the coefficient of relatedness within the group. As in the model of direct repression above, $r = 1/n$ when average relatedness is zero between different group members.

In a population with no policing and at this z^* equilibrium, the condition for the increase of a is $dw/da > 0$ evaluated at $a = \bar{a} = 0$ and $z = \bar{z} = z^*$. Following this procedure, the condition for a rise in a from zero is

$$c < \frac{K(d - r)}{1 - d}. \qquad (9)$$

This condition shows that policing increases more readily as c, the cost of policing, declines; as K, the weighting of postostracism fitness, increases; as r, the relatedness within groups, declines; and as d, the cost of cooperation, rises. Low relatedness and high cost of cooperation raise the level of selfishness, z, and thus favor greater repression of selfishness.

As mentioned earlier, this model assumes that the a and z characters are uncorrelated when genetic variation is small. This gives a reasonable approximation of the equilibrium and invasion conditions for mutations of small effect. More detailed analysis should consider possible correlations between a and z created by selection and broken up by recombination.

This model assumes policing individuals gain by enhancing the future efficiency of their group. This indirect benefit through group productivity overcomes the commonly discussed problem of second-order defection in punishment models, in which an individual that cooperates but does not punish others has higher within-group fitness than individuals that both cooperate and pay the cost of policing (Oliver 1980; Axelrod 1986; Yamagishi 1986; Hirshleifer and Rasmusen 1989; Boyd and Richerson 1992). The problem is that, within groups, the cost of policing accrues to individuals, whereas the benefits of policing are shared equally by all cooperators in the group whether or not they contribute to policing. The indirect benefit of policing through future group efficiency partly overcomes the difficulty of second-order defection and allows at least some investment in punishment. This indirect benefit increases with relatedness in groups; thus, it can either be small and in proportion to $r = 1/n$ in random groups or large in groups of close relatives with high r.

Resource Variation Shifts Policing to Stronger Individuals

If individuals in a group vary in relative strength or resources, then the stronger individuals may be favored to take on most or all of the policing (Clutton-Brock and Parker 1995; Frank 1996a). This shift occurs because stronger individuals have more to gain if they control the majority of the group's reproduction; stronger individuals can more easily control the behavior of weaker individuals; and resource-rich individuals lose a smaller fraction of their total fitness for a particular investment in policing than do resource-poor individuals.

I extended the policing model in equation (7) to include resource variation among individuals (Frank 1996a). The only change to the model occurs in the first cost term, in which $k - ca - dz$ replaces $1 - ca - dz$, where the variable k measures the resource level of an individual. The cost of policing now scales with c/k, reducing the effective cost for resource-rich individuals.

Assume an average individual has $\bar{k} = 1$ resources, and express deviations from the average by α such that $k = 1 + \alpha$. I showed that small deviations cause the relatively strong to increase significantly their investment in policing, whereas the relatively weak quickly decrease their investment in policing to zero as their relative strength declines. Thus, the well endowed take over social control.

For the model of ostracism in equation (8), a similar extension would specify the resource level for each individual. Variation in resources would lower the effective cost of policing for stronger individuals, most likely shifting the burden for enforcing ostracism to those with relatively more resources.

Domestication

Many organisms harbor symbionts that provide advantages to the host. The symbionts retain their own genetic system and reproduction, sometimes greatly modified by the constraints imposed by the environment within the host. Such domestication probably played a significant role in the evolution of eukaryotic cells (Margulis 1981; Bell 1993). Domestication also occurs in a wide variety of other symbioses (Buchner 1965; Douglas 1994; Mueller et al. 2001).

Reproductive conflict between symbionts can favor the symbionts to invest some of their resources in competition against their neighbors. The symbionts' competitive behavior can reduce the resources that flow to the host.

Host repression of symbiotic competition may increase cooperative behavior between symbionts in two different ways (Frank 1997). First, the host may directly block competitive symbiont behaviors that disrupt the host. For example, symbiont movements to sites of transmission may disrupt host development (Buchner 1965; Frank 1996b). Control of symbiont movements prevents symbiont competition over transmission and reduces disruption to the host. In this case, the payback to the hosts for repressing symbiont competition is immediate. If host control is effective, over time symbionts may evolve to invest less in attempting to circumvent host control and invest more in improving the success of the host-symbiont group.

Second, hosts may interfere with symbiont competition by reducing the correlation between competitive characters of the symbiont and symbiont reproductive success. Hosts may, for example, randomize the chances for a symbiont to succeed in transmission to other hosts. The symbionts, with little opportunity to increase their success by investment in competition against neighbors, would eventually evolve to reduce competitive characters and perhaps to invest the savings in group-beneficial traits. In this case, the payback to hosts only occurs after a lag for evolutionary response. Thus, there is no direct benefit to a host to increase its control over its symbionts, even though such control would eventually provide benefits to the host population (Hoekstra 1987; Frank 1996b, 1996c). Host control would be favored only if there were sufficiently strong group-against-group competition between symbiont-bearing hosts on a time scale over which evolutionary response of symbionts would play a role.

A BRIEF HISTORY

The basic idea is that repression of competition within groups can enhance group success in competition against other groups. Some have argued that this is a fundamental process in the shaping of social behavior and the structuring of complex groups (Alexander 1979, 1987; Frank 1995; Maynard Smith and Szathmáry 1995).

Variations of this idea first appeared in analyses of economics and moral philosophy. The concept gathered momentum within evolutionary biology starting in the 1970s. Theories of economics and moral philosophy do not have any necessary relation to understanding evolutionary process. But theories of human behavior do sometimes provide the background from which evolutionary insight springs. Economic theory was certainly the midwife of great insight by both Darwin and Fisher. With these caveats, I begin with two precursors to evolutionary thought.

Economics and Moral Philosophy

Adam Smith (1996, pp. 127–132) was perhaps the first to outline the idea. In Leigh's (1991, p. 258) words, ''Adam

Smith argued that if individuals had sufficient common interest in their group's good, they would combine to suppress the activities of members acting contrary to the group's welfare.'' Smith relied on justice as the arbiter of social conduct and punishment. I am not certain of his exact conception of justice, but it seems to be captured by the notion that if a person ''would act so as that the impartial spectator may enter into the principles of his conduct . . . he must upon this . . . bring it down to something which other men can go along with'' (Smith 1996, p. 120).

Rawls's (1971) ''veil of ignorance'' developed a similar concept of justice. A just society establishes rules that individuals regard as fair from behind a veil of ignorance about their position within society. An individual may, in practice, end up on one end or the other of any particular social interaction. (Harsanyi [1953] developed a similar idea; see Skyrms [1996] for discussion of these ideas in an evolutionary context.)

It does not pay to argue the fine details of how precisely these humanistic thoughts presage current evolutionary understanding. These early thoughts do contain the following kernels: group cohesion returns benefits to individuals, and randomization of position levels expected opportunity and promotes fairness.

Meiosis and Human Sociality

Biologists took the next steps: fairness aligns individual interests with group interests; aligned interests enhance group efficiency; efficiency promotes group success in competition against other groups; thus, group-against-group competition favors fairness within groups. Mendelian segregation in meiosis was the first biological character to be understood in this light (Leigh 1971, 1977; Alexander and Borgia 1978; Crow 1979).

In standard diploid genetics, each genetic locus has one allele from the mother and one from the father. Each gamete made by an individual has either the maternal or paternal allele. Mendelian segregation, or fair meiosis, gives an equal chance to maternal and paternal alleles of being in a successful gamete. Meiotic drive subverts fairness by giving one allele a greater chance of transmission. The pieces of chromosomes that can drive against their partners gain a reproductive advantage by increasing their chance for transmission to offspring. As driving chromosomes spread because of their transmission advantage, they often carry along deleterious effects that are partly protected from selection by being associated with transmission advantage (Zimmering et al. 1970).

Other parts of the genome lose when a driving chromosome carries with it deleterious effects into the majority of gametes. Suppression of drive has the immediate effect of reducing association with the deleterious effects of driving chromosomes; it has the long-term consequence of taking away the transmission advantage that protects the deleterious effects. Drive suppression thus helps to purge the genome of the deleterious effects carried by driving chromosomes. The many genes of the genome repress the drive ''as if we had to do with a parliament of genes, which so regulated itself as to prevent 'cabals of a few' conspiring for their own 'selfish profit' at the expense of the 'commonwealth''' (Leigh 1977, p. 4543).

When meiosis is fair, randomization puts each allele behind a veil of ignorance with regard to its direct transmission (interests) in each progeny. Behind the veil, each part of the genome can increase its own success only by enhancing the total number of progeny and thus increasing the success of the group. However, discussing ''interests'' in arguments about how natural selection operates can be misleading. In this case, natural selection directly favors the immediate advantage of drive suppression, which reduces association with the deleterious effects that often hitchhike along with drive. The long-term advantage of purging the hitchhiked deleterious effects also contributes to favoring drive suppression when groups compete against groups, for example, species against species (Leigh 1977).

Leigh (1977) noted that alignment of individual and group interests shifts selection to the group level. However, meiosis was the only compelling case known at that time. Without further examples, there was no reason to emphasize repression of internal competition as an important force in social evolution and the formation of evolutionary units. From the conceptual point of view, it may have been clear that repression of internal competition could be important, but not clear how natural selection would favor such internal repression.

Alexander and Borgia (1978) joined Leigh in promoting the possible great potency of internal repression in shaping interests and conflicts in the hierarchy of life. From this, Alexander (1979, 1987) developed his theories of human social structure (see introductory quotes). In this theory, intense group-against-group competition dominated the success of humans and thus shaped societies according to their group efficiencies in conflicts. Efficiency, best achieved by aligning the interests of the individual with the group, favored in the most successful groups laws that partially restricted the opportunities for reproductive dominance. For example, Alexander (1987) argued that socially imposed monogamy levels reproductive opportunities, particularly among young men at the age of maximal sexual competition. These young men are the most competitive and divisive individuals within societies and are the pool of warriors on which the group depends for its protection and expansion.

Independent Lineages of Thought

In the late 1970s, the concept of internal repression remained limited to meiosis and perhaps some aspects of human social structure. The concept could not gain attention as a potentially important process in the history of life without further examples.

In the 1980s, three independent lineages of thought developed on social insects, cellular competition in metazoans, and domestication of symbionts. These different subjects would eventually contribute to a fuller understanding of the conceptual issues and biological significance of internal repression of competition. I introduce each of these topics in the next three subsections. I then turn in the following section to current research and future directions, in which I synthesize the different lineages of thought and update each topic with the latest work and promising directions for future study.

Social Insects

Female workers of hymenopteran societies have an interesting pattern of relatedness asymmetry to the reproductive males produced by the colony (Starr 1984; Woyciechowski and Łomnicki 1987; Ratnieks 1988). I introduced this topic in an earlier subsection, *Shift Reproduction from One Class to Another*. There I showed that a female worker is related to her mother's sons by 1/2 and to her sisters' sons by $1/4 + 1/2n$, where n is the number of effective mates for the queen. The effective number of mates means that $1/n$ is the probability that two daughters have sperm from the same father. If the queen mates once, $n = 1$, then workers are more closely related to their sisters' sons than to their mother's sons. If the effective number of mates is $n > 2$, then workers are more closely related to their mother's sons than to their sisters' sons.

Species with singly mated queens sometimes have many males produced by workers, whereas species with multiple-mated queens rarely have worker-produced males (Ratnieks 1988; Foster et al. 2001). Experiments show that honeybee workers can identify and remove worker-laid eggs (Ratnieks and Visscher 1989). Honeybee queens mate many times, so these experiments support the hypothesis that worker policing explains the rarity of worker-derived males in honeybees.

Worker policing arises in species with multiple mating because policing shifts reproduction to a more closely related class of reproductives. In this case, repressing competition has no direct effect on group efficiency. It is possible that workers, with opportunities for direct reproduction blocked, would respond either behaviorally or evolutionarily to reduce their effort toward direct reproduction and enhance their contribution to group success (Ratnieks and Reeve 1992; Bourke 1999). But such reallocation has not been shown empirically, and the conditions under which such changes could occur have not been studied theoretically.

Policing does not necessarily cause an evolutionary shift toward less worker investment in direct reproduction and more investment in colony efficiency. The evolutionary feedbacks between a selfish character, z, and a repression trait, a, can be complex. For example, it can happen that increased policing, a, leads to more investment in selfish behavior, z (see Fig. 1).

Cellular Competition in Metazoans

Many multicellular animals are differentiated into tissues that predominantly contribute to gametes and tissues that are primarily nonreproductive. This germ-soma distinction creates the potential for reproductive conflict when cells are not genetically identical. Genetically distinct cellular lineages can raise their fitness by gaining preferential access to the germline. This biasing can increase in frequency even if it partly reduces the overall success of the group.

One way to control renegade cell lineages is with policing traits that enforce a germ-soma split early in development (Buss 1987). This split prevents reproductive bias between lineages during subsequent development. Once the potential for bias has been restricted, a cell lineage can improve its own fitness only by increasing the fitness of the individual. This is another example of how reproductive fairness acts as an integrating force in the formation of units.

Maynard Smith (1988) agreed with Buss's logic about the potential for cell lineage competition, but he argued that metazoans solved their problems of cell lineage competition by passing through a single-celled stage in each generation. When an individual develops from a single cell, all variation among subsequent cell lineages must arise by de novo mutation. In Maynard Smith's view, such mutations must be sufficiently rare that the genetic relatedness among cells is essentially perfect. Thus, the somatic cells sacrifice reproduction as an altruistic act in favor of their genetically identical germline neighbors. Buss recognized the importance of de novo mutations within an individual but argued that these would be sufficiently common to favor significant cell lineage competition and policing.

The model in the subsection *Directly Repress Disruptive Behavior* showed the generality of this tension between self-restraint by kin selection and repression of competition by policing. In that model, lower relatedness reduces self-restraint and the efficiency of groups by favoring a rise in selfish behavior. Lower group efficiency enhances the value of policing to repress competitive and disruptive behavior. Buss argued that self-restraint would be sufficiently low among cellular lineages to favor repression of competition. Maynard Smith argued that by reducing the mixture of cellular lineages in seeding progeny, relatedness and self-restraint would rise to a sufficient level.

Domestication of Symbionts and the Mixing of Symbiotic Lineages

The degree to which lineages mix to form groups determines relatedness and self-restraint. Thus, hosts that harbor symbionts may gain by limiting opportunities for the mixture of symbiotic lineages. Reduced mixture increases relatedness among the symbionts, favoring reduced selfishness in the symbionts and a greater tendency for the symbionts to invest in traits that enhance the success of the host-symbiont group.

Control of symbiont mixing has been widely discussed in the context of genomic conflict and the evolution of uniparental inheritance of cytoplasmic elements (Eberhard 1980; Cosmides and Tooby 1981; Hurst 1994). When cytoplasmic lineages mix during syngamy, the relatedness among cytoplasmic elements is reduced. If the host can prevent mixing by imposing uniparental inheritance, then relatedness increases within hosts and greater self-restraint is favored. A similar problem arises in the early evolution of genomes. Mixture of replicating molecules keeps relatedness low and favors competition within groups (Maynard Smith 1979). Thus, the origin of cohesive genomes and early prokaryotes may have depended on physical controls that limited the mixing of lineages, such as membranes that separated replicating groups into compartments (Maynard Smith and Szathmáry 1995).

The hosts gain from low mixing and high relatedness of their symbionts. However, Hoekstra (1987) pointed out a complication with the evolution of host control over cytoplasmic mixing. Although reduced mixing would eventually cause symbionts to evolve lower selfishness in response to higher relatedness, that evolutionary response would occur over time and would not provide an immediate benefit to an individual host that restricted mixing of its cytoplasmic elements. This is the recurring problem of how group beneficial traits originate by natural selection.

Repression of mixing could have immediate, beneficial consequences. For example, restricted symbiotic mixing would gain an immediate advantage if it helped to avoid harmful parasites that invade during the mixing process (Hoekstra 1990; Hastings 1992). Restricted mixing is also advantageous when symbionts increase expression of their competitive and disruptive traits in direct response to local genetic diversity (Hurst 1990; Law and Hutson 1992).

Summary

Leigh (1971, 1977) may have been the first to emphasize how repression of internal competition aligns individual and group interests. However, meiosis provided the only good example at that time, so the idea did not lead immediately to new insight. Alexander (1979, 1987) used the idea and the example of meiosis as the foundation for his novel theories about human social evolution. I was aware of the discussion about meiosis in the 1970s, but I only realized the general implications for repression of competition as a powerful evolutionary force after reading Alexander (1987). With two examples—meiosis and the structuring of social groups—I could see how a simple idea could be applied to different contexts.

At the same time, Buss's (1987) argument appeared on the role of cellular competition and repression in the evolution of metazoans. Buss stimulated Maynard Smith (1988) to consider how social groups became integrated over evolutionary history. Maynard Smith disagreed with Buss's particular argument about the importance of the germ-soma separation in metazoans. But in considering the general issues, Maynard Smith had in hand several possible examples, including the origin and early evolution of prokaryotes, meiosis and genomic integration, limited genetic variability, and perhaps repression of cellular competition in metazoans and the social insects. From these examples, Maynard Smith restated the essential concept in a concise and very general way, as given in the introductory quote. I see these papers as together defining a fundamental evolutionary force with wide implications.

In summary, this historical section provides a rough sketch of some key ideas. Others no doubt followed a different path in the 1980s and see the history differently. Further study of the literature will likely turn up precedents that I have missed and further clarification of the development of ideas. The outline here provides a target for future research.

Current Research and Future Directions

I have argued that the works of Alexander (1979, 1987), Buss (1987), and Maynard Smith (1988) brought together different lines of thought and focused the essential concepts and problems of the subject. From that focal point, the expanding subject formed the basis for understanding new biological examples and refined theoretical analysis. In 1995, Maynard Smith and Szathmáry wrote a broad survey of the subject. Since that time, the field has developed significantly. I briefly discuss new issues in competition of cellular lineages, domestication, and social insects.

Competition of Cellular Lineages

The slime mold *Dictyostelium discoideum* provides an excellent model to study reproductive competition between cells within multicellular aggregations (Dao et al. 2000). After a single-celled feeding stage, the individual cells aggregate into a slug. The slug, which has on the order of 10^5 cells, migrates without feeding. Eventually the cells cooperate in a developmental process that produces a fruiting body borne on a stalk. The puzzle is why some cells differentiate into nonreproductive stalk cells to support the fruiting body, which contains reproductive spores.

Several studies have found cheating genotypes that disproportionately become spore cells rather than stalk cells (Filosa 1962; Buss 1982; Strassmann et al. 2000). Similar observations of cheating have been found in the aggregating social bacterium *Myxococcus xanthus* (Velicer et al. 2000). Selfish behavior occurs in aggregations, so what maintains the system of differentiation? Either self-restraint by strong relatedness within groups or repression of competition by policing may maintain group integrity (Wilson and Sober 1989; Frank 1995), as in the debate mentioned above between Buss (1987) and Maynard Smith (1988) on the origin of metazoans.

Slime molds and social bacteria are promising model systems because cells live both singly and in aggregations. This allows individual cellular biochemistry and behavior to be studied more easily than in typical metazoans. Several groups have started projects to analyze genetic relatedness and cellular competition (Dao et al. 2000; Strassmann et al. 2000; Velicer et al. 2000). It will be particularly interesting to learn if mechanisms exist to repress competition or randomize success within these aggregations.

Michod and Roze (2001) developed an extensive theoretical analysis of kin selection and repression of cellular competition in metazoans. The theory is made complicated by the need to follow different kinds of mutations in cells through complex life cycles. Mutations affect the dynamics of cellular lineage growth within aggregations and the probability of transmission to progeny.

Repression of competition may occur through different mechanisms (Michod and Roze 2001). Repression in the germline affects the way in which cells are chosen for transmission and possibly the number of cellular divisions and mutation rates for germ versus soma. Policing causes cells to invest in monitoring other cells and reduces the advantages of selfish behavior. Apoptosis causes mutant cells expressing selfish tendencies to self-destruct. Michod and Roze analyzed several models to determine the conditions under which such mechanisms can increase and contribute to the cohesion of metazoans.

Blackstone and Ellison (2000) compared metazoan developmental patterns in different groups in light of the evolutionary processes discussed by Michod and Roze (2001) and

Davidson et al.'s (1995) hypothesis about the evolutionary sequence of developmental plans in bilaterians. Blackstone and Ellison (2000, p. 101) concluded that in primitive patterns of bilaterian development most of the cell divisions ''occur during the cleavage of the zygote where maternal controls of cell division can override any advantage of a selfish variant (Buss 1987).'' In terms of the parameters from Michod and Roze's theories, primitive bilaterians limited the time available during development and the potential replicatory advantage of selfish cellular lineages. These limits to selfishness imposed by the developmental plan may have helped early bilaterians flourish.

Blackstone and Ellison (2000) noted that, according to Davidson et al. (1995, p. 1323), the most important evolutionary innovation that allowed larger and more complex body plans was the ''developmental use of yet undifferentiated set-aside cells, which retain indefinite division potential. . . . Among the genetic regulatory changes required to produce set-aside cells are the disconnection of the cell division controls that are a prominent feature of [evolutionarily primitive] embryos.'' Blackstone and Ellis argued that undifferentiated set-aside cells abrogated the features of primitive bilaterian development that limited cellular competition. They further argue that the sequestration of germ cells to create an early germ-soma distinction in development arose in evolutionary history in response to the release of constraints on cellular division. In support of this idea, Ransick et al.'s (1996) comparative analysis suggested that set-aside cells had arisen in evolutionary history at about the same time as the sequestration of the germline.

Needless to say, such comparative conclusions based on repression of cellular competition represent only one opinion on the forces that shaped metazoan developmental plans. The point here is that the theory has now matured to the stage where it is contributing to debates in a wide range of topics. To give one last example for this subsection, I conclude with Nunney's (1999) discussion of cancer.

Nunney began by noting that mice and humans have roughly the same incidence of cancer. This is a puzzle because greater size and longer life in humans require more cell divisions and opportunities for mutation and competition than in mice (Peto 1977). Nunney suggested that controls on cellular growth evolve to a higher level in larger, longer-lived, and more complex organisms and in tissues with relatively greater numbers of cellular divisions.

Cancer is interesting because there is no conflict in the long term between cellular and organismal interests—cancer cells usually do not infect other hosts. However, when groups last a long time relative to the life span of individual members, short-term selection can lead to harmful consequences for the group. In cancer, selection between cell lineages favors mutant lines that reproduce rapidly and spread within the host, even though the rapidly dividing cancer cells may cause early death. Put another way, within-group evolution happens so rapidly that traits can increase temporarily even though they have zero long-term success between groups.

The greater the potential rate of within-group evolution relative to between-group evolution, the greater the potential for competition within groups to reduce the efficiency of groups in competing against other groups. Thus, the relative scaling of within- and between-group competition may strongly influence mechanisms of social control. Alexander (1979, 1987) has followed similar logic in making comparative predictions about the legal and moral codes of different human societies.

Domestication

In insects, the most common pathway of transmission for beneficial symbionts is from mother to offspring via the eggs (Buchner 1965). This pathway of vertical transmission inevitably limits the number of symbionts that succeed in passage to the next generation. This limitation can potentially separate symbionts into those that are transmitted (germ cells) and those that are not (somatic cells). This germ-soma separation of symbionts is similar to the way in which metazoans separate cellular lineages into reproductive and nonreproductive tissues (Frank 1996b).

Hosts can control symbionts by imposing a germ-soma split among the population of symbionts that develop within the host (Frank 1996b). Somatic symbionts, denied access to the germline, can only increase their fitness by enhancing the success of the host and thereby increasing the reproductive rate of their kin in the germline. Reproductive fairness is imposed among symbionts if, early in host development, a random subset of symbionts is sequestered for the germline.

Buchner's (1965) review of transmission of insect symbionts provided considerable anecdotal evidence to evaluate this theory of germ-soma separation by symbionts. Buchner was not concerned with the theoretical ideas discussed here, yet he concluded his overview by noting a common progression within host lineages of limiting the transmissible symbionts to narrower subsets from spatially confined locations. Clear separation of germ and soma does not occur in all cases of symbiont transmission. Indeed, the subject is fascinating because of the great diversity of transmission patterns, which provides opportunity for comparative study.

Earlier, I discussed how the mixing of symbiotic lineages increases genetic diversity within hosts, favoring increased competition between symbionts. Symbiotic competition can disrupt the host. Thus, hosts gain from limiting the mixing of symbiotic lineages. Frank (1996c) extended the idea of host control over symbiotic mixing to a wide array of biological interactions.

Bot et al. (2001) applied this extended theory of host control over symbiont mixing to the domestication of fungi by ants. The fungi are typically transmitted vertically from ant colony to colony, with only a single fungal genotype in each colony. Bot et al. found genetic variation among fungal strains in different colonies of two sympatric ant species. The two ant species share all major strains of fungi, suggesting that horizontal transmission does occasionally occur. Mixtures of fungi may induce competition between the basidiomycete fungal strains, as happens in genetic mixtures of free-living basidiomycetes. Such competition could reduce fungal productivity, lowering the success of the ant colony. Thus, the ant hosts would be favored to police against invasion by foreign fungal strains.

Bot et al. (2001) tested the hypothesis that ants police against invasion by foreign fungi. They created experimental subcolonies by sampling ants from a single colony and fungi from the same colony or a different colony. They then measured fungal mass over time to determine if the ants were nuturing or destroying the fungi. The ants always nutured fungi from their own colony, but destroyed fungi from some of the other colonies. The ants destroyed the incompatible fungi by chewing with their mandibles. Such destructive behavior was never observed for ants tending their own fungi. Bot et al. concluded that ants actively police their colonies against invasion by fungi that differ genetically from their own crop.

These observations on insect symbiosis and ant-fungal interactions suggest that domestication may sometimes cause the dominant species to repress competition between genetic variants of the subordinates. Repression of competition between subordinates aligns the reproductive interests of the subordinates to the dominants. A great diversity of symbioses occur in nature, but only a few studies have considered how the repression of competition affects the evolution of cooperation.

Social Insects

Repression of worker reproduction does not necessarily enhance cooperation and efficiency in the colony. If, in response to destruction of worker-laid eggs, the workers reallocate their energy away from reproduction and toward colony productivity, then policing can ultimately improve group success (Ratnieks and Reeve 1992). This feedback process has not been formally modeled, and there is no direct evidence for it. However, Bourke (1999) suggested an evolutionary scenario in which colony size and policing of worker reproduction interact to change the morphology, behavior, and social structure of colonies.

Bourke (1999) began by noting that, across different taxa of social insects, small colonies tend to have relatively little morphological differentiation between reproductives and workers, and workers have a relatively high degree of reproductive potential. By contrast, large colonies tend to have strong morphological differentiation between workers and reproductives and reduced reproductive potential of workers.

Alexander et al. (1991) argued that in small colonies each worker has a significant probability of replacing the queen because there are relatively few competitors. By contrast, workers in large colonies have relatively little chance of succeeding to become queen. Thus, workers in large colonies are favored to reduce investment in reproductive potential and become more specialized for their worker roles. This leads to strong morphological differentiation between workers and queens and low reproductive potential of workers. Absence of potential reproduction by workers reduces conflict between workers and other colony members because the workers can enhance their fitness mostly by increasing the success of the colony.

Ratnieks and Reeve (1992) suggested that worker policing of reproduction by other workers may be ineffective in small colonies. If there are few other workers, then a single worker may be able to dominate her neighbors and succeed in producing sons. As the number of workers rises, policing becomes more effective because a single worker cannot dominate the collective.

Bourke (1999) combined these ideas to argue that positive feedbacks occur between colony size, policing, reproductive potential of workers, and morphological differentiation between workers and queens. As colony size rises, policing becomes more effective, which favors reduced allocation to reproduction by workers. As workers concentrate more on their colony-productive roles, conflict subsides and the colony becomes more efficient. Greater efficiency may drive colonies to larger size, further specializing workers for nonreproductive tasks and aligning the interests of the workers with the interests of the colony.

CONCLUSION

Repression of competition joins kin selection as the second major force in the evolution of cooperation. This idea developed from the recognition of meiosis as reproductive fairness (Leigh 1971, 1977; Alexander and Borgia 1978; Crow 1979), followed by extension of this insight and application to human sociality (Alexander 1979, 1987). Buss (1987) introduced a new example with his suggestion that metazoan success depended on repression of competition between cellular lineages. Maynard Smith (1988) synthesized different lines of thought on self-restraint by kin selection and repression of competition.

I have not discussed reciprocal altruism (Trivers 1971), another major force in the evolution of cooperation. Reciprocity is mostly limited to the small fraction of organisms with advanced cognitive abilities, and reciprocity often makes sense only for two-party interactions. For the vast majority of organisms, kin selection and repression of competition dominate the evolution of cooperation.

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