THE EVOLUTION OF SOCIAL BEHAVIOR

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INTRODUCTION

For several years the study of social behavior has been undergoing a revolution with far-reaching consequences for the social and biological sciences. Partly responsible are three recent changes in the attitudes of evolutionary biologists. First was growing acceptance of the evidence that the potency of natural selection is overwhelmingly concentrated at levels no higher than that of the individual. Second was revival of the comparative method, especially as applied to behavior and life histories. Third was spread of the realization that not only are all aspects of structure and function of organisms to be understood solely as products of selection, but because of their peculiarly direct relationship to the forces of selection, behavior and life history phenomena, long neglected by the evolutionists, may be among the most predictable of all phenotypic attributes.

These ideas have been appreciated by a few biologists for a long time, but they have only recently begun to characterize the science as a whole. Darwin's discussion of sterility between species as an incidental effect of evolutionary adaptation (41, p. 260) and his refusal to deal with sex ratio selection (42, p. 399) suggest an awareness of the difficult problem of determining the levels at which selection is most powerful. Yet significant clarification of this basic issue did not really commence until publication of Wynne-Edwards' massive volume (179) championing group selection and inadvertently exposing its unlikelihood. As late as 1958, Fisher felt constrained to add to the revised edition of his 1929 classic, *The Genetical Theory of Natural Selection,* the admonishment (53, p. 49) that his fundamental theorem and its associated considerations, already misused then by decades of population geneticists dealing (as they saw it) with the fitness of populations, refer strictly to "the progressive modification of structure or function only in so far as variations in these are of advantage to the individual . . . [and afford] no corresponding explanation for any properties of animals and plants . . . supposed to be of service to the species to which they belong." Williams' critique (171) provided a significant turning point. Nevertheless, one has only to pick up any biological journal or attend any biological meeting to realize that this question has not yet been settled for all

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organisms and all situations. The problem may not yet be understood by a majority of biological investigators; its implications have scarcely touched the social sciences, where they are central to the difficult problem of understanding the functions of culture and the origins and sources of cultural rules.

Perhaps more in social life than in any other context it has proven an almost insuperable task for human investigators to think in terms of advantages and disadvantages primarily to individuals. Every thoughtful biologist has to be dismayed at the failure of the social sciences to acknowledge and absorb the principles of biology as the biologists believe they have acknowledged and absorbed the principles of chemistry and physics. Yet the biological principles most significant to the social scientists are the very ones that biology itself has only begun to accept on a wide scale. We can marvel at the boldness of Darwin's challenge (41, p. 201) that "If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory, for such could not have been produced through natural selection." But we should marvel more that in the 115 years since Darwin we have still not clarified all those circumstances in which the structures or functions of one individual may have been formed for the exclusive good of other individuals within its own species. Such clarification will surely go a long way toward constituting a general theory of social behavior.

During the past decade a few investigators, in particular, Hamilton (59–67) and Trivers (155–159), have stirred this field dramatically by specifying and justifying several aspects of such a general theory. A synthesis of the various ideas developed by these investigators remains to be accomplished (but see 67, 169); efforts at reasonably complete evolutionary analyses of social systems are still virtually restricted to the social insects, where they have been both extensive and controversial, with several important theoretical contributions during the past decade (60, 67, 101, 166, 169, 174). Although ten years have passed since Hamilton's landmark papers, apparently only a single social scientist (Campbell, 31) has made a distinct effort to incorporate kin selection into theories of human altruism. (Eleven other papers on altruism in the same issue of the journal containing Campbell's article fail to mention either Hamilton or Trivers or the ideas they have developed.) But so have the biologists, for one reason or another, failed to consider the enormous literature on topics like kinship systems and reciprocity in human behavior.

It seems appropriate that biological and social scientists alike begin to think in terms of a general theory, and that special efforts be made to examine its application to explaining human behavior. My purpose in writing this paper is to outline the components of such a theory, describe their interaction in some circumstances, and attempt to relate certain aspects to a few specific problems, chiefly in the social insects and humans. Most of my ideas on these topics have been generated by considering the arguments of several of the above authors.

WHAT KINDS OF GROUPS FORM AND WHY?

Sociality means group-living. The formulation of any general theory of social behavior begins, therefore, with a description of the selective forces causing and maintaining group-living. Our basic statement must be that, in general, groups form and

persist because all of the individuals involved somehow gain genetically. I will argue that there is one exception: siblings whose group behavior is an aspect of parental investment, and whose altruism toward one another has evolved because it furthers the reproductive interests of the parent(s). Even exclusive of sibling groups, however, this proposition is not a simple one, nor is it commonly accepted among social biologists in the form that I believe it must take.

An individual's gain from remaining in a particular group may be relative to 1. living alone, 2. living in other kinds of groups that may exist within the species, and 3. the risk of changing groups, as a result of either (a) the actual movement between groups, or (b) having to establish social relationships with new individuals. Thus savannah baboons infrequently survive long alone, apparently because of large predators (36, 43). Movements between adjacent troops sometimes occur, often when groups meet at waterholes or along rivers (11, 58, 136). Troops may become large enough for their size to be detrimental to the individuals involved, and may then split (36, 44). Subordinate males may have little chance of breeding in troops with several dominant males, but they may also be injured or killed during efforts to join other troops (11).

Group effects may assist members at the expense of non-members, but coalitions within groups may assist certain individuals at the expense of others. Whenever individuals derive benefits from group functions they may be expected to carry out activities that maintain the group, and thereby serve their own interests as well. Excepting clones and sibling groups, there is, however, no clear evidence that any adaptations have evolved because they assist the group as a whole at the expense of the individuals possessing the adaptations. Yet, with few exceptions (e.g., 37, 38, 57), essentially every effort to analyze or interpret primate social organization assumes that adaptations exist that assist groups and not individuals (e.g. sex ratios have evolved for the good of the troop or population; one-male bands and sexual dimorphism have evolved because they represent efficient distributions of the species biomass; nonbreeding males feed apart at their own expense so as not to compete with females and young; competition for mates is "held in abeyance . . . by a simple reduction in the sex drive"; males are more "biologically expendable" than females; etc). The problem of whether or not such interpretations are correct is especially important because primate social behavior is generally believed to be particularly relevant to efforts at understanding human behavior.

Social groups are not all alike, and many efforts have been made to classify them, especially among the social insects (e.g. 110, 170, 175) and among primates (40, 52, 150). For purposes of discussing the evolution of social organization it seems most useful to begin with five general kinds of groups: 1. groups of unrelated individuals, 2. groups of uniformly related individuals (not siblings), 3. groups of variously close and distant relatives, perhaps containing siblings, 4. groups of siblings (with or without one or both parents), and 5. groups of genetically identical individuals (clones). When several families form a larger group (regardless of breeding system), it will correspond to the third group above. Extended families containing more than two generations of descendants of a single parent (or pair of parents) will also correspond roughly to the third group, and metazoan animals are specializations arising out of or comparable to the fifth group.

The significance of the above groupings only becomes apparent as one considers (see below) the kinds of interactions that may evolve among individuals in each case. Except in clones, the interests of individuals within groups are never identical with those of the group as a whole, and a basic problem in understanding sociality is to specify the conflicts of interest among individuals within groups and their results.

There is no automatic or universal benefit from group living. Indeed, the opposite is true: there are automatic and universal detriments, namely, increased intensity of competition for resources, including mates, and increased likelihood of disease and parasite transmission. Other detriments, such as increased conspicuousness, whether rendering a species less effective as a predator or more vulnerable as prey, may be widespread but are not necessarily universal.

The automatic detriments of group living can be understood only through the interests of the individuals involved. Consider the subordinate male rendered effectively sterile by an aggressive dominant who keeps him from the ovulating females, or the dominant male who is cuckolded by the sneaky subordinate he has not ostracized completely or killed. Consider the female unable to secure all the parental attention of the father of her children because of other females nearby. Consider those gulls, swallows, penguins, or anis who must, for reasons not always clear to us, nest very close to one another with maximal risk of having someone else's eggs deposited in their nests. Consider the individual, whether herbivore or carnivore, who must constantly tolerate other nearby individuals simultaneously seeking the best food or the safest feeding locations.

Group living, then, is like extended juvenile life and lowered clutch or litter sizes; in each case the attribute evolves only because benefits specific to the organism and the situation outweigh what appear as automatic detriments. Longer juvenile life and lowered clutch or litter size both appear to lower reproductive rates (i.e. rates of replications of individuals' genes), but of course they only lower potential reproductive rates that may never be approached in the real environment. The benefit of lengthened juvenile life may be greater adult size, increased time for learning critical to survival or reproduction, better timing of resistant stages with harsh seasons, or conservation of reproductive energy and risk-taking until some optimal time. Lowered clutch or litter sizes are advantageous if they maximize genetic representation at some subsequent time—say at fledging, weaning, or breeding time. What are the benefits of group living that offset its automatic detriments?

An exhaustive list of the selective backgrounds of group living may contain no more than three general items (3): 1. susceptibility to predation may be lowered either because of aggressive group defense, as in savannah baboons (43), or because of the opportunity for individuals to use the group as cover (or to cause other individuals to be more available to predators), as with schooling fish and herds of small ungulates (66); 2. the nature of food sources may make splintering off unprofitable, as with wolves dependent upon large game in certain regions (107) or with (hypothetical) groups dependent upon scattered large supplies of food that individuals locate too infrequently on their own; or 3. there may be an extreme localization of some resource, such as safe sleeping sites for hamadryas baboons (87) or suitable breeding sites for some marine birds and mammals (e.g. 14, 16). The asymmetry in

these three categories points up the difficulty of attempting precise definitions of "social groups" or "group living" (see also 75, 90). In the first two cases the grouped individuals gain because of the presence of the other individuals; in the third they do not, but instead gain solely from the presence of some other resource in the immediate environment (that is, other sources of mortality do not keep the population low enough to prevent extreme competition for the localized resource). In the first two cases, then, one expects individuals to approach or remain near other individuals. In the third case individuals may aggregate around resources but are otherwise expected to avoid one another or to be aggressive, although they may use the presence of other individuals or aggregations as indicators of resource bonanzas. I suggest that group living only appears because one or some combination of these three general extrinsic causative factors at some point enhances the fitnesses of individuals accepting the automatic detriments of group living above the fitnesses of solitary individuals.

It seems impossible to overstress the extent to which the view just outlined contrasts with those prevalent during the past century. The general opinion that group living and cooperativeness are universally and automatically beneficial to all concerned (and indeed that on this account they are basic attributes of all life) can be traced from antagonism to the "nature red in tooth and claw" extensions of Darwinism to include human social behavior (72; see also references in 10, 113, 170). This view has proceeded through reviews and restatements by a succession of such influential writers as Kropotkin (86), Wheeler (170), Allee (9, 10), Montagu (113), and Wynne-Edwards (179) to, at least until a few years ago, a virtually universal assumption throughout social biology. It is difficult to avoid the impression that the tenacity of this view is largely a product of the human way of living and thinking.

Ironically, the argument that man is basically cooperative and altruistic is no less instinctivist than its counterpart that he is basically aggressive and competitive. This fact may not be generally recognized, for opponents of the latter view are usually regarded as staunch anti-instinctivists, regardless of what they say about social tendencies. Furthermore, it is somehow comforting to speak of having built-in tendencies to be cooperative, and disconcerting to speak of having opposite tendencies. Why this should be true becomes an unexpectedly intricate problem. I mention it here for a reason relevant to this essay: The essential consequence of an extreme "basic social instinct" or "innate social appetite" view (see above authors) is that group living, cooperation, and altruism require no (other) special explanation. In the opposing view, just espoused, they always do, and the number of alternatives is small.

WHY DOES SOCIAL BEHAVIOR EVOLVE WITHIN GROUPS?

Once groups form, social behavior evolves within them for three reasons: First, it may enhance the original advantage of group living. Thus, from the individual's point of view, predators may be thwarted further by the tightening of a starling flock, by the alarm notes of cedar waxwings in a feeding group, or by a collective confrontation or attack by the dominant males in a savannah baboon troop; and probably

also by the clustering of baboon females and juveniles near the large males, and by the silence of the play of young baboons (45). Similarly, cooperative hunting techniques of lions (144), wolves (107), and wild dogs (95, 144) increase the nutritional benefits to the individuals involved beyond the simple effect of hunting in groups; so might group defense of clumped resources, as suggested by Brown & Orians (29).

Second, social behavior evolves because it reduces the likelihood of disease and parasite transmission. Although I believe not yet tested, the prediction is compelling that group-living animals will either be plagued more heavily with parasites and diseases than their solitary-living close relatives, or they will be plagued with greater expense of time and energy, and greater risk, in reducing the attacks of such organisms. The record of human migrations and population changes leaves no doubt that in this group-living species one of the most significant kinds of genetic change within historical times has been the development and spread of resistance to various diseases (e.g. 126).

Third, and most important, social behavior evolves because of effects upon the reproductive competition of group members, in relation both to other group members and to the relevant portions of the population at large. Thus the dominant individual in a hierarchy gains because he has used his superior strength, weapons, agility, speed, or cleverness to secure increased access to the resources of reproduction, or even to cause them (as in the case of females) to remain grouped closely around him. The subordinate also gains by his behavior: like the dominant he is informed by the interactions of the hierarchy when and how to display aggression, and when and how to withhold and appease and withdraw, so as to stay alive and remain in the group and be at least potentially reproductive for the longest period. Even if the fitness of a subordinate is lowered greatly relative to that of others in his group, he may still enjoy a fitness higher than the average of the individuals comprising the rest of the population and living either solitarily or in other kinds or sizes of social groups, and, presumably, a higher fitness than he would if, under the circumstances, he made an all-out effort to become the dominant individual.

Behavior that initially evolves because of one effect may acquire another function without losing the first. Primates living in large, tightly cohesive social groups seem to groom almost constantly. Their grooming can be used to predict and interpret social interactions, and evidently influences and reinforces social relationships (139, 148). But, as Sparks in particular points out, it would be inappropriate to oppose these two functions. That parasite-controlling behavior should acquire a social role only illustrates the effects of group living upon the way that selection changes behavior. I suggest a parallel with incest taboos having evidently become vehicles for the formation and maintenance of political alliances between human groups, even though comparative study indicates that such taboos are more anciently related to the genetic effects of outbreeding (1, 5). Neither with grooming nor with incest taboos is the more recent social function entirely opposed to the apparently older one; indeed, in each case it reinforces, and may virtually assure, the earlier function. (Yet it is unlikely that two or more functions can be simultaneously maximized; only by determining which is being maximized can the nature of the relevant selective action be correctly assessed.) In a parallel fashion, post-partum sex taboos reduce

pregnancies during lactation (79), as does inhibition of ovulation during lactation even in the absence of such taboos (23, 55, 112, 121). In this example the taboo reinforces the previously selected function and simultaneously and incidentally relieves the selection that may have been perfecting it. Such relationships between selection and different social functions or effects must be understood if social organization is to be clarified or traced from its beginnings.

PREDATION, GROUP SIZES, AND BREEDING SYSTEMS

The significance of the above arguments can be illustrated by applying them briefly to studies of primate social organization. Primate social groups can for the most part be divided into three major classes: 1. monogamous pairs, 2. single-male polygynous units, and 3. multi-male polygynous units (36, 39, 52, 150).

Both of the latter groups, however, vary in ways significant to the arguments presented here: "Multi-male" groups may contain but a single dominant or breeding male, or be "age-graded" (52). Single-male groups (a) may never join forces, as may sometimes be true of gorilla bands (143), (b) may sometimes fight together or mix in other contexts, but maintain spatial integrity otherwise, as with hamadryas baboons (87), or (c) may mix as individuals to a greater degree, at least sufficiently to confuse observers, as with geladas (35). Monogamous pairs appear to be restricted to forest-dwelling arboreal species. Males in such species enjoy a high confidence of paternity and show more parental behavior than in any other primates; the sexes are relatively monomorphic. Such species are also commonly territorial and non-nomadic, and have probably been consistently more successful at hiding from predators or retreating to inaccessible locations than have their relatives in more open habitats.

All large groups of primates are multi-male, and, in such concentrations of numerous females, the males have apparently evolved to maximize matings, accepting a low confidence of paternity and showing less parental care than in other social groups. (But the actual extent of male parental care, and of tendencies by males to favor offspring of females that were consorts during the releva

yet to be determined for any multi-male primate social group.) Intermediate-sized troops correlate with presence of single-male harems and, when such harems remain in close proximity to one another, with herding of females by males (117). Most highly polygynous species, especially those forming the largest troops, live in open habitats such as grasslands or open forests and are chiefly terrestrial and nomadic. There are exceptions, such as arboreal howler and squirrel monkeys, which, like their savannah-dwelling analogues, may also occur with large predators (possibilities are jaguars, ocelots, monkey-eating eagles, and humans) whose behavior yields benefits to individuals from using the troop for cover or engaging in group defense (see below).

Variations in breeding systems involve dramatic correlations in sexual dimorphism and parental behavior (8). In diverse mammalian groups, monogamous species are less sexually dimorphic in size and time to maturity than polygynous species, and species with large average or maximum harem sizes are more dimorphic than

those in which harems are smaller. In turn, kinds of breeding systems correlate with group sizes. It would appear that, to an extent, breeding systems are imposed by the kinds and sizes of social groups in which the various primates have (on other selective grounds) been caused to evolve. I have suggested (above) only three options to account for the formation and maintenance of social groups.

Except for occasional cooperation in small groups, chiefly in chimpanzees (94, 153), man appears to be the only group-hunting primate. Even including the sleeping cliffs of hamadryas baboons (87), there seems to be no evidence of restrictive localization of critical resources adequate to cause evolution of group living in primates. To explain primate groups above the size of the smallest reproductive units of a single male, his female(s), and their offspring, then we seem to be left with the single causative factor of predation. In primates two effects seem relevant: the troop serving as cover for individuals and the possibility of aggressive defense. Essentially the same classes of social groups exist in ungulates, and similar correlations occur with habitat, breeding systems, paternal behavior, and sexual dimorphism (8, 51).

The idea that variations in the nature and extent of predation (and in the options available for dealing with it) are responsible for the sizes and (secondarily) the compositions of primate bands is probably universally considered an oversimplification, but I believe it will eventually be sustained. This hypothesis proposes predation as the sole factor capable of causing the (evolutionary) formation and maintenance of primate social groups larger than one or both parents and their offspring. All other aspects of social organization are, in this hypothesis, relegated to a secondary role, supposed to have evolved as a result of grouping in response to predation. Hamilton (65) has reviewed the history of this idea as it may apply to animals in general, and carefully developed the theory.

For any particular case it may be extremely difficult to extricate the separate influences of predators, food-finding or food-capturing, and resource localization on the origin or maintenance of group living (54, 73–75, 90, 145, 161, 180). That wolves or African hunting dogs gain by pack-living principally because of their dependence upon big game is relatively easy to defend. That island-nesting seabirds or elephant seals are crowded because breeding space is restricted seems obvious. Less apparent in the latter case is the probability that a history of predation may be responsible for a restriction of breeding to certain islands, and the consequent crowding (90).

Food distribution and abundance have probably been invoked more often than predation to explain both primate troops and colonially nesting or roosting birds. That a basic asymmetry exists between the effects of food and predation on the evolution of sociality may not, however, be widely understood. Consider the frequently discussed question of how predator and food differences may have interacted to result in the remarkable differences in the social structures of the closely related hamadryas and cynocephalus baboons (87, 117). The problem is generally stated as a matter of determining why the hamadryas baboons spread out in one-male groups during the day, and thus has most often been considered essentially a matter of food distribution and availability. In the terms that I have just suggested

for the analysis of group living the more important question seems to be why do both cynocephalus and hamadryas baboons remain as close together as they do. Food scarcity or distribution may provide a pressure for independent dispersal of subgroups of hamadryas baboons even if predation is the same in the habitats of the two species; but the reverse situation of food abundance cannot in itself account for the cohesive, socially complex, multi-male primate troops. Without predators even the cynocephalus baboons, in the midst of plenty, would tend to spread out. How much, then, has predation also influenced the social cohesiveness of hamadryas baboons?

The only situation in which food seems potentially a primary explanation for multi-male primate troops is in the (hypothetical) case of large food sources such as fruit trees, widely spaced and so much more easily located by groups as to cause every individual in a foraging troop to be better off than by going it alone. Even in this hypothetical example a paradox remains. As food sources become more difficult to locate, unless they simultaneously become larger it is difficult to imagine evolution of truly cooperative searches. Instead, one expects a "group" behavior such as may occur sometimes among foraging condors or vultures in which each individual seems to be acting so as to maximize its capability of parasitizing the food finds of others, while simultaneously minimizing behaviors that might alert others to his own successes. Such interactions seem unlikely in themselves to lead to complex sociality, for individuals are not forced to remain in close proximity and gain little if at all from joint efforts or cooperation. If food is abundant there is little gain in being able to count on others sharing small finds; if it is scarce there is little gain in sharing small finds with others.

Yet as food sources become larger, they surely must also become easier, not more difficult, to locate. This change, again, promotes individual, not group, behavior. Perhaps we are often deceived into assigning food a larger role in sociality than it deserves by observing (a) species in which individuals are able to parasitize large food finds of others even without the help of evolved signals (i.e. the parasitized individual does not gain but cannot escape the parasitism), and (b) species in which group-feeding behavior is obvious but the effects of predators actually responsible for grouping are not.

The search for advantages in cooperativeness in regard to food thus leads one to consider parallels with a group-hunting benefit, in which individuals cannot exploit food sources to best advantage without assistance. One possibility in primates is that prey animals such as insects may be stirred up by neighboring individuals in a foraging troop (e.g. squirrel monkeys 154). Chimpanzees are noisy upon locating large food sources, and sometimes hunt or stalk prey animals in pairs or small groups (93, 94, 153). Even in these cases, though, the evolution of complex social structure chiefly or solely as a result of feeding advantages is doubtful. It seems more likely that the feeding behavior, whether competitive or cooperative, is a result of grouping that was originally advantageous for other reasons. I do not believe that a description of the appropriate ecological situation or the predicted troop structure and behavior for social evolution dependent upon foraging benefits has yet been approached for a single primate. What is required is a combination of 1. dependence

upon large, hard to find food sources, or other sources that cannot be exploited to advantage by individuals, and 2: a prevalence of food sharing, with dispersion patterns and signals that maximize utilization of major food sources. Horn (74) and Hoogland & Sherman (73) review the extent to which colonial nesting in birds correlates with food distribution and predation and, utilizing data from Brewer's Blackbirds and Bank Swallows, respectively, arrive at somewhat different conclusions. Zahavi (180) and Ward & Zahavi (161) take the position that predator effects are secondary to those of food in accounting for large roosting aggregations of birds, while Gadgil (54) takes the converse position (see also 145).

We can digress a moment to consider some of the possible consequences of viewing the origin and maintenance of primate bands as a result solely of predator effects. Many investigators of human history have assumed that man evolved his great intelligence and his sociality because of its advantages in obtaining food, especially in connection with hunting large game. But the above arguments suggest that this view virtually requires a dependence upon large game and implies that the genetic changes leading to modern man spread through some (unspecified) kind of peaceful replacement of starved-out, less intelligent groups by better-fed, more intelligent groups. The alternative, if human groups are supposed to have interacted peacefully (or not, as groups, in fashions significantly affecting directions of evolution), is that the genetic changes leading to modern man resulted from selection effective chiefly at the individual level.

Necessarily, such a view reduces the significance of culture as a group phenomenon with a feedback effect upon genetic change. Either intergroup competition was important, or culture as a group phenomenon was not. This problem seems pivotal in the whole effort to unite the approaches of the social and biological sciences, for it involves the unanswered question of how to define and identify function in relation to learned and culturally transmitted behavior, how to determine precisely why certain aspects of culture spread while others disappear, and how to locate the sources and backgrounds of specific cultural rules. Thus, if extrafamilial incest taboos (or marriage rules) are both chiefly functional in alliance formation and wholly cultural, the importance of cultural function at the group level is supported; but so, necessarily, is a human history in which intergroup competition and aggression were instrumental (5). Social scientists almost universally accept the first proposition, while for the most part, paradoxically, rejecting the second one (but see 31, 138).

Whether or not man was initially a primate with a group life derived through antipredator benefits, it seems undeniable that at certain times and in certain places his cooperation in groups both thwarted large predators and allowed successful hunting of large game. But little evidence exists that either function was universal enough to lead us to suppose that his social life evolved or has been maintained—indeed, elaborated into ever more complex stages—on such grounds. Unless man tends to form and maintain social groups solely as a result of possessing the kind of "innate social appetite" attributed to all organisms by early authors, we are left with three alternatives: 1. reject the notion that group living carries automatic disadvantages (at least for man), 2. suppose that man's social history has left him bound inexorably to an innate, individually disadvantageous social existence, or 3.

suppose that modern man has evolved socially around substitute advantages for predation-thwarting or food-obtaining benefits that are no longer present. I can conceive of no reason to accept the first alternative. The second is denied by the extent of man's behavioral plasticity, and in particular by the enormous variability in his social patterns.

But what substitute could have replaced ancient predator or hunting benefits? When man developed his weapons, culture, and population sizes to levels that essentially erased the significance of predators of other species, he simultaneously created a new predator: groups and coalitions within his own species. The fact of widespread and essentially continual intraspecific, intergroup human aggression, the closeness of the parallel to forces most easily postulated to account for group life in other primates, and the arguments presented above and elsewhere (see 3) seem to me inescapable facts leading to the conclusion that much of man's evolution has been guided by the effects of intergroup aggression. (I earlier used the term warfare —illadvisedly because it is too easily dismissed by restricting its definition so as to include only recent phenomena.)

The above idea seems so repugnant that it has often been rejected without reasonable alternatives being offered, and its supporters have frequently been maligned as social darwinists or glorifiers of war. To me, however, the repugnant attitudes are those which tend to deny men the possibility of seeing themselves as they are, and of undertaking the kinds of analyses of themselves whose benefits in regard to understanding other organisms have long been apparent. It is difficult to know how much strife, suffering, and cruelty may be perpetuated by thwarting efforts at reasonably dispassionate examinations of probable sources of our tendencies and motivations in the contexts of group cohesion and intergroup competition [Washburn & Hamburg (164) express a closely parallel opinion].

It seems apparent that the consequence of the seemingly slight difference in viewpoint utilized above, deriving from the realization that group living involves automatic and universal detriments, carries great significance, not only for the analysis of social organization in all primates, but also for attempts to understand human history. If human social organization has for a long time been guided by direct intergroup competition, then we are provided with an adaptive background for increases in group sizes and complexity of social organization, involving a built-in feedback effect of unparalleled explanatory value (3, 7, 29, 66, 82, 176). It is in fact an explanation with a singularity and a potency that I think cannot longer be denied. Simultaneously, it (a) explains culture as a group phenomenon, (b) provides a basis for rapid evolution of intelligence and complex sociality, (c) accounts for the absence of close relatives of man, and (d) accords with recorded human history and human traits and tendencies as we know them today. Almost incidentally, this argument suggests the possibility that the social structure of (at least) all the great apes may have been essentially determined, or at least influenced in very significant fashions, by the activities of predatory or aggressively competitive human groups (Rowell, ref. 137, makes a similar suggestion). Should this hypothesis be relevant, the insight it may provide can scarcely fail to facilitate understanding of both man and the most similar relatives that have managed to survive along with him, and in spite of him.

Table 1 Categories of social behavior. Those categories asterisked will not evolve, and when they appear will tend to be diminished by selection, except when the individuals involved are evolving such actions in the interests of their parents, and as a result of inescapable parental molding. All nonsocial behavior is in the first category; most social behavior is in the second. See also text.

Genotypically	Phenotypically	Examples
selfish	selfish	engagements in reciprocity on average leading to personal gain
selfish	altruistic	ordinary parenthood and nepotism
*altruistic	selfish	foregoing of both parenthood and nepotism
*altruistic	altruistic	adoption of an individual without known relatives by another individual without known relatives (at any time)

WHAT KINDS OF SOCIAL INTERACTIONS EVOLVE?

Social interactions may be classified according to whether they are genotypically or phenotypically selfish or altruistic (Table 1). This perhaps novel classification is useful because it focuses attention on the reproductive consequences of apparently altruistic and selfish acts, and de-emphasizes the complex problem of motivation, which permeates the extensive psychological literature on these topics. According to the scheme in Table 1, it is both genotypically and phenotypically selfish for a small ungulate to leap to the center of the herd upon predator attack, for he is saving his own skin and his own genes at someone else's expense. (Although, in sexual organisms, the compromise of recombination prevents an individual from reproducing intact his own genotype, I assume that selection tends to maximize the extent to which this possibility is realized in each environmental situation; hence, I have purposely used the term "genotypic," which may in general here be translated as "genetic.") Such behavior, characteristic of Hamilton's (65) "selfish herd," does not by itself, however, seem likely to lead to complex social organization. Conversely, it is both genotypically and phenotypically altruistic for a potentially reproductive adult without known relatives (thus, unable to secure genetic benefits through other individuals) to give its life in defense of an unrelated individual. And it is genotypically altruistic but phenotypically selfish for a potentially reproductive adult without known relatives to forego or reduce actual reproduction. In humans the phenotypic reward may be increased wealth or personal freedom, longer life (especially for females), or the gratitude of a society fearing overreproduction. Genetically altruistic behavior (such as adoption of unrelated individuals) will not evolve, although it may recur as an incidental (and negatively selected) result of the evolution of social (in this case, parental) behavior; it may, as in humans, carry personal (phenotypic) benefits to the altruist both as a result of the view of such altruism by society as a whole and because of personal satisfaction to (in the case of adoption, barren)

individuals. It is probably worth remarking that the heritability of such variations in altruistic tendencies under any cultural regime is almost surely so slight as to render trivial the resulting selective trends (119). In other words, for the moment, we are less likely to overpopulate deleteriously if we reward altruistic reductions of reproduction, even though one result is to cause even more favorable selection of non-altruists.

The fabric of complex social organization is woven around three classes of behavior that are genetically selfish in their results, yet appear to involve altruism because they cause their bearers to raise the fitnesses of other individuals either at the expense of the bearer's phenotype or at the expense of the phenotypes and genotypes of some third parties or "manipulated" (exploited) individuals. These three classes of social behavior are *reciprocity* (reciprocal altruism in the sense of Trivers, 155; mutualism in the sense of Lin & Michener, 101); *nepotism* (leading to kin selection, in the sense of Maynard Smith, 105, or to adjustments of inclusive fitness, in the sense of Hamilton, 60, 67); and a phenomenon that I will call *parental manipulation of progeny.* (I use the term "manipulation" here in the dictionary sense of "adroit or skillful management; fraudulent or deceptive treatment," although, of course, without any necessary implication of consciousness or purpose. The appearance of fraud lies in the fact that offspring are, historically, themselves the direct avenues by which a parent reproduces; in the case of manipulation, however, as I shall show, they are treated by parents as parental investment and may not in fact be allowed to maximize their own reproduction or even to reproduce at all. Alternatives to "manipulation" that seem to me slightly less appropriate are parental "molding" or "exploitation" of offspring.)

Reciprocity does not actually involve altruism, except in some temporary sense (155, 169). In systems of reciprocity each individual is in effect gambling that his investments will increase his inclusive fitness, perhaps usually through benefits returned to his own phenotype, but feasibly through benefits "reciprocated" to his offspring or other relatives as well. The individuals in acts of reciprocity need not be related to one another.

Nepotism involves altruism between relatives, the potential for a genetic tendency to spread existing because assisted individuals are likely to be carrying it to the degree that their genotypes are expected to overlap that of the altruist (60, 67). Under nepotism one may thus include parental altruism and the assistance of mates, as well as assistance of relatives not on a direct line of descendance.

Parental manipulation of progeny refers to parents adjusting or manipulating their parental investment, particularly by reducing the reproduction (inclusive fitness) of certain progeny in the interests of increasing their own inclusive fitness via other offspring. It is easy to forget that parental care evolves, not because it increases the reproduction of individual offspring, but because it increases the reproduction of the parent.

Although not previously analyzed in detail as a component of social organization, implication of parental care in sociality dates at least to Darwin (41, pp. 237-38). Fisher (53, pp. 158-60) realized that the sex ratios of broods of offspring will evolve so that the brood will represent the greatest realized reproduction for the parent;

he identified the termination of parental care as that point beyond which the effects of selection on the brood as a whole can no longer adjust the primary sex ratio (see also 156, 159). I believe that in his short passages dealing with sex ratio selection and with sibling altruism in the evolution of aposematic coloration among distasteful insects (53, pp. 177–81), Fisher touched upon a principle of major significance in explaining animal and human behavior: that of social manipulation of offspring by their parents in organisms with extended parental care. Fisher did not connect his two discussions on this topic. He did not expand his treatment of sex ratio selection to include altruism toward siblings in the parents' interest, nor did he discuss variations in the extent and duration of parental care. But there is no obvious reason to restrict parental manipulation of the brood to any particular attributes. Furthermore, the potential significance of parental manipulation may assume remarkable proportions, as when parental care terminates only with the parent's death (e.g. humans), or when the adult life of a parent may totally overlap the adult life of one or more generations of offspring that never escape its influence (e.g. eusocial insects). As a component or concomitant of parental care, social manipulation of offspring may be essentially universal among animals.

Reciprocity, nepotism, and manipulation of descendants, or some combination of these three classes of social behavior, appear to represent our options in explaining how reproductive competition has given rise to any particular case of social organization. An effective theory will first distinguish them, and then specify how each will evolve and how they will interact with one another, given different kinds of initial groups and different selective backgrounds of group living. Such specifications will include: 1. the conditions under which each individual will gain, 2. the conditions under which the reproductive interests of different individuals will coincide or conflict, and 3. the conditions under which (and extent to which) various sorts of asymmetry will enable one or the other individual to win in cases of conflict. Many of these specifications have already been provided, particularly for nepotism and reciprocity (59–67, 155, 168).

The nature and significance of parental manipulation of progeny, the most important example of 3 above, largely remains to be analyzed, although Trivers (156, 157) and Trivers & Willard (159) have initiated this analysis by considering the consequences of increasing parental investment for aspects of sexual selection, sex ratio selection, and parent-offspring competition (see also 4). In the following pages I discuss parental manipulation of offspring in detail, compare the conditions under which the three above classes of social behavior evolve, and describe some aspects of nepotism that I believe represent significant departures or omissions from previously published arguments.

PARENTAL INVESTMENT AND THE MANIPULATION OF PROGENY

Trivers (156) has defined parental investment as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring."

Parental investment, so defined, will increase during evolution whenever a parent thereby improves its overall reproduction. Such increases will generally decrease brood, litter size, or rate of offspring production except when parents somehow increase their overall energy available for parental behavior (e.g. by becoming larger as individuals or by transferring energy from less directly to more directly parental activities).

All parents, in sexual species, have been evolved to produce more than a single offspring in their lifetimes—in fact, more than two. (Hamilton has called to my attention a case in which some aphids produce during their sexual phase a single egg, which, however, later gives rise parthenogenetically to numerous grandchildren.) In consequence the reproductive interests of individual offspring and their parents are always different. The interests of each parent are the same as those of its (lifetime) brood as a whole. The only exception is when all offspring but a parent's last one are beyond its assistance: then the parent's interests will coincide exactly with those of the final offspring, regardless of the genetic relationship between them.

Whenever promiscuity occurs, or any breeding system other than strict lifetime monogamy, conflicts of interest will also arise between parents in regard to the distribution of parental benefits to jointly produced offspring. When nepotism extends outside the parent-offspring relationship, as in humans, the conflict between male and female parents becomes more complex. Specifying the conflicts of interest resulting from variations in genetic overlap among individuals is a fundamental step in assessing the selective backgrounds of behavioral tendencies in all sexually recombining species. Extrafamilial conflicts and coincidences of genetic interest may often have become significant influences on behavioral evolution, partly as extensions or ramifications from a substantial parent-offspring bond, because strong familial bonds provide a basis for subsequent recognition of different classes of relatives. For this and other reasons, an evolutionary theory of family interactions may represent a core item in analyses of all complex social systems.

Trivers (157) has carefully reviewed the nature of parent-offspring conflict and discussed its various ramifications. No author, however, has considered in detail the problem of who wins in cases of conflicts of interest between parent and offspring, although Williams (171) and Alexander (4) have each provided brief suggestions. This problem is of particular significance because of both the centrality of parent-offspring interactions in the evolution of sociality and the peculiar asymmetries of the parent-offspring interaction. Trivers (157) suggests that the usual or "classical" view is that the parent wins, simply because of physical superiority, and he suggests further that offspring may often win by "psychological" means. Except for statements by Alexander (4), however, no suggestion of asymmetry in this regard seems yet to have been incorporated into kin selection theory.

In my experience biologists do not find it easy to understand that genes which *reduce the mother's reproduction* by causing competitive interactions among embryos in the uterus cannot spread regardless of their advantage to the embryos possessing them. It is even less obvious whether the same will be true for siblings no longer inside the uterus, or even for progeny no longer receiving parental care. Nor is it obvious whether genes that reduce the mother's reproduction by inhibiting

aggressive or competitive interactions among siblings will be disfavored in the same fashion. It is not obvious how to determine the effects of genes carried by the male parent, which will compete with those of the mother in this context whenever she mates with more than one male. Finally, it is not clear when and how this kind of selection ceases to be effective in different kinds of families (e.g. polygynous versus monogamous) and different ecological situations (e.g. more or less predictable environments). In other words, it is not clear how and when offspring will, in different circumstances, finally become "free agents"—that is, independent of particular kinds of continuing parental influences. All of these problems must be clarified if we are to understand how natural selection operates within and between families. Siblings are often the closest relatives within a population, and they are often one another's most direct competitors as well. Thus the extremes of cooperation and competition may both be represented in their interactions. It will be useful to know when these interactions evolved because they increased the reproduction of the involved individuals and when they evolved because they increased the reproduction of their parents.

The parent-offspring interaction is unlike most other kin selection situations for several reasons. First, the parent is usually bigger and stronger than the offspring, hence in a better position to impose its will. Second, the offspring is always in a position of benefiting from parental attention, and in some circumstances is wholly dependent upon the parent even for survival. Third, the entire parent-offspring interaction has evolved because it benefited one of the two individuals—the parent. No organism can evolve parental behavior, or extend its parental care, unless its own reproduction is thereby enhanced. As a result, when a parental benefit is used by an offspring to increase its own inclusive fitness at the expense of that of the parent, selection will favor either retraction of the benefit or elimination of the "misuse." This effect can be realized from at least two kinds of selection.

First, as pointed out by Williams (171), the same genes will be operative in the adult offspring as in its parent. Consider a female parent, evolved to divide her parental benefits so as to maximize the reproductive success of her brood as a whole. Suppose that a juvenile mutates in such fashion as to cause an uneven distribution of parental benefits in its own favor, thereby reducing the mother's overall reproduction. A gene which in this fashion improves an individual's fitness when it is a juvenile cannot fail to lower its fitness more when it is an adult, for such mutant genes will be present in an increased proportion of the mutant individual's offspring. Thus no individual can receive a net benefit from possessing such an allele, and genetic lines will win that lack alleles disrupting in this fashion the parent–offspring interaction (see also Figure 1). Furthermore, offspring should on this account evolve tendencies to accede to parental discipline.

Second, the parent will win so long as the withholding of parental care or the imposition of parental punishment gives to it a net reproductive gain; that is, so long as the detriments to the competing offspring as a result of parental actions and the energy and risk involved in taking such actions do not exceed, in their effects upon the parent's reproduction, detriments to the parent from whatever competitive or adversary behavior by the offspring is being thwarted. Assuming that cheating is
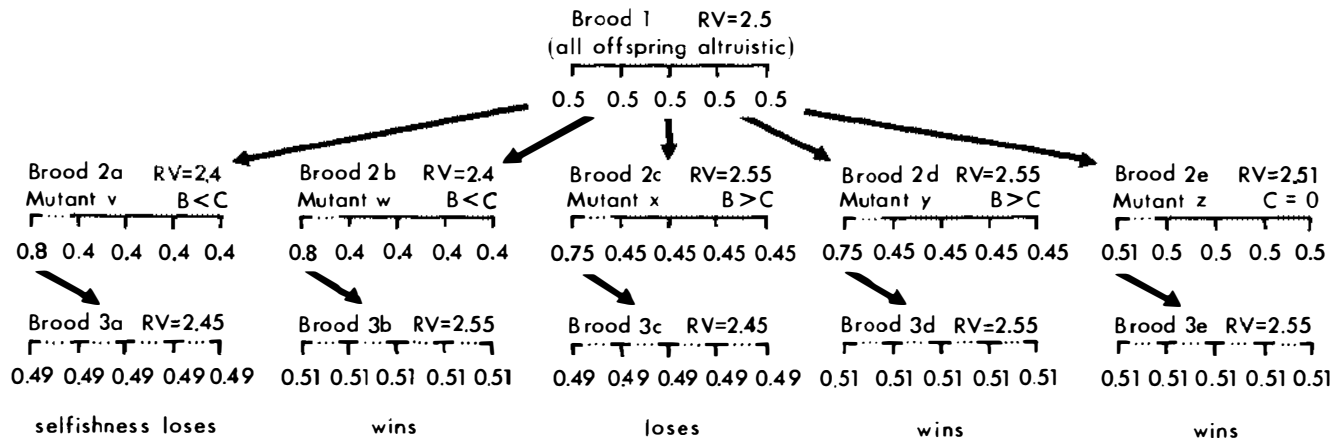
Brood 1   RV=2.5
(all offspring altruistic)

0.5 0.5 0.5 0.5 0.5

Brood 2a RV=2.4	Brood 2b RV=2.4	Brood 2c RV=2.55	Brood 2d RV=2.55	Brood 2e RV=2.51
Mutant v $B<C$	Mutant w $B<C$	Mutant x $B>C$	Mutant y $B>C$	Mutant z $C=0$
0.8 0.4 0.4 0.4 0.4	0.8 0.4 0.4 0.4 0.4	0.75 0.45 0.45 0.45 0.45	0.75 0.45 0.45 0.45 0.45	0.51 0.5 0.5 0.5 0.5

Brood 3a RV=2.45	Brood 3b RV=2.55	Brood 3c RV=2.45	Brood 3d RV=2.55	Brood 3e RV=2.55
0.49 0.49 0.49 0.49 0.49	0.51 0.51 0.51 0.51 0.51	0.49 0.49 0.49 0.49 0.49	0.51 0.51 0.51 0.51 0.51	0.51 0.51 0.51 0.51 0.51

selfishness loses   wins   loses   wins   wins

Figure 1   Outcomes of various combinations of selfishness and altruism among siblings in a series of simplified cases (see text as well for explanation). Numbers represent reproductive values of individual brood members, for convenience here considered only in terms of likelihood of survival to reproduction. "RV" in each case represents the collective reproductive value of each brood to the parent, measured in the same terms. The letters $v-z$ represent five different mutations, each leading to selfish behavior having the particular effects indicated in each case; the same effects could be postulated on a single mutation in five different environments. The sequence Broods 1-2b-3b shows that selfish behavior by an offspring can win, and can improve its parent's reproduction in the long run, even if it depresses the parent's reproduction in mixed broods of altruists and nonaltruists. Likewise, the sequence Broods 1-2c-3c shows that selfish offspring can win as individuals in a mixed brood but reduce the parent's reproduction in the long run and lose as altruistic offspring from which to derive benefits disappear. Parental genes suppressing effects of mutants v and x will win, except that maintenance of the mixed brood effect of x will benefit the parent (see text).

A more realistic (and complicated) example would consider that the reproductive values of different offspring will differ, and altruism will evolve so as to be dispensed unevenly within the brood, maximizing benefit/cost, and thereby the parent's total reproduction. Additional complications reducing the likelihood of altruism winning will be: 1. likelihood of nonsibling interlopers and 2. changing values of altruism deriving from other kinds of environmental uncertainties.

only trivially effective, the parent will actually win even more emphatically, for individual offspring should evolve to allow the parent to win whenever the parent's response to competition from the offspring is more detrimental to that particular offspring's inclusive fitness than are the advantages the offspring would gain through performing an act detrimental to the parent. A parent may gain from destroying an offspring or reducing its reproduction when the result is but the slightest gain in the reproduction of the parent's brood as a whole; but an offspring gains reproductively by a personal reproductive deficit only if the effect on its siblings (and on other contemporary relatives whose reproduction it can affect), as a factor of their genetic overlap with it, yields greater reproduction than the destroyed or hampered off-spring would have effected without the personal loss. This means that selfishness in an offspring, relative to its siblings, has to help the selfish offspring directly; even the slightest diminution of its personal fitness (e.g. by parental punishment) as a result of a selfish act will inevitably reduce its inclusive fitness as well.

Two points are emphasized by these arguments: 1. the importance of a parent's influence on its offspring's phenotype during ontogeny and 2. the likelihood of asymmetry in the way that an individual responds to conflicts of interest with its own individual progeny and with its parents. Responses to offspring will clearly evolve to be in one's own interests, while responses to parents may not.

If parental investment in individual offspring increases during evolution because it improves a parent's reproduction, then it follows that a parent may not only use any part of its available energy in the care of any particular offspring to improve its reproduction via others, but also any part of its investment in any existing offspring. Behavior of this general sort may be described in five categories:

1. limiting the amount of parental care given to each offspring such that all survive and reproduce
2. restricting parental care or withholding it entirely from some offspring when resources become insufficient for an entire brood
3. killing some offspring or feeding some offspring to others
4. causing some offspring to be temporarily or facultatively sterile helpers at the nest
5. causing some offspring to become permanent (obligately sterile) workers or soldiers

The above manipulations include adjustments of sex ratios within broods by: (a) differential investments of a direct sort between offspring of the different sexes, (b) discarding offspring of one or the other sex before termination of parental care when that sex is unlikely to be successful at breeding, and (c) differential invest-ments via altruism in progeny of one sex directed toward the other (see below, and 159). The last two manipulations can be effected by dispensing parental benefits so as to produce some offspring incapable of maximizing their own inclusive fitnesses except by helping their parents or other relatives to reproduce (see also below).

If individual offspring cannot evolve to secure a disproportionate share of parental benefits—a share that in the long run reduces the parent's reproduction—then the behavior of offspring in the instances in which they appear to be doing this must actually represent incidental effects of advantages to the parent, although to identify this advantage to the parent it may be necessary to measure the effects of selection

one or more generations after the appearance of selfishness (Figure 1). This problem is the same whether one considers sequentially produced offspring or offspring produced simultaneously in a brood.

If the selfish departure of a subordinate offspring from a brood does not alter the average reproduction of brood members and does increase his own reproduction (Figure 1, Brood 2e), the selfish individual obviously will only have to beat the average of the altruistic brood members (e.g. Brood 1) to win; this effect, in other words, will be in the parent's best interests too. If his departure (or other selfish behavior) reduces the average reproduction of the other brood members (Broods 2a–d), then to avoid adverse effects from selection among parents, he will have to beat the average that prevails in broods lacking selfish members, or that which would have prevailed in his own brood had he not departed (Brood 1). In both of these cases the selfish offspring will by its selfishness eventually increase the parent's reproduction (Broods 3b, 3d). This benefit, however, may not be evident until the selfish descendants achieve a number which together with the original parent's remaining altruistic descendants causes the reproductive value of descendants (i.e. their worth in terms of genetic contribution to subsequent generations) to exceed the value of descendants from parents having only altruistic offspring (e.g. sequence from Broods 1–2b–3b). To say it another way, a brood that is wholly selfish (e.g. Brood 3b) may outreproduce both mixed broods (Brood 2b) and broods that are wholly altruistic (Brood 1). In effect, a selfish gene in an offspring can win, and can thus benefit the parent, even if it depresses the parent's reproduction in the initial generations. This curious fact makes one wonder about the possibility of the evolution of a tolerance by parents for very successful selfish offspring.

The fate of mutant x in Figure 1 is instructive in regard to the effects of parental manipulation. Parents gain whose broods contain some proportion of selfish (x-bearing) offspring but whose members are not all selfish. So long as the difference between selfishness and altruism depends upon a genetic difference it may be difficult for parents reliably to achieve the most beneficial proportions of selfish and altruistic offspring in a brood. The parent who is able to produce the effect of a mixed brood through phenotypic influences on its offspring, however, can produce this effect more reliably, and one predicts that, for reasons given above, when this kind of control appears it will supercede; i.e. the parental phenotype will be extended to include this attribute of the brood.

In general, learning, plasticity, and phenotypes as such evolve because environmental alternatives are not entirely predictable. Parental behavior is an aspect of phenotypic plasticity, and the environmental uncertainties in response to which it evolves include not only the physical and social environments of offspring but their genetic environments as well. If certain kinds of intrabrood cooperativeness maximize a parent's reproduction, and these behaviors conflict with the interests of individual offspring or of the other parents (e.g. in nonmonogamous systems), then the parent will evolve to effect appropriate cooperation by parental influence in response to tendencies of genes to spread because they further the interests of individual offspring or of mates. In this context, genetic diversity within a cooperative brood tends to increase environmental uncertainty.

In those instances in which it appears that offspring have evolved to compete with their parents, alternative explanations must first be eliminated. There will be two such general classes of interactions: those which seem to be terminated by the parent and those which seem to be terminated by the offspring. Both are predictable results of parental manipulation. In the first case, as with weaning in mammals, parents may have been favored whose offspring both actively (and honestly) seek parental benefits, thus both informing the parent of the extent of their needs and affording the parent control over the termination of the benefit. If the offspring needs are great, the parent may gain by giving more benefits; in any case the offspring's active seeking of benefits will enable the parent better to judge the cost-benefit ratio.

When a parent-offspring interaction appears to be terminated by the offspring, in terms of evolved adaptations, the offspring is probably in a better position to adjust its behavior to the parent's advantage than is the parent itself. Mate selection may be a frequent example. Such conditions are obviously likely when the parent is dead or absent, but they do not automatically accrue in such situations, and are not restricted to them. This situation may appear as a conflict, for even if offspring are evolving so as to maximize their parent's reproduction, this circumstance evidently specifies that the parent knows less about its own best interests than does the offspring, hence is also unlikely to be able to assess its judgment relative to that of the offspring. Even if it is to the parent's advantage for the offspring to become a free agent, sometimes a parent may be favored who acts as though this is not true, thus causing the offspring to be the active terminator of the interactions, and perhaps as well testing the offspring's "judgment" of the situation.

These hypotheses and predictions are testable. To the extent that offspring evolve to compete with their parents, greater strife at weaning termination, including, perhaps, longer weaning periods, is predicted in multi-male bands of primates (such as chimpanzees and cynocephalus baboons) than in hamadryas baboons, patas monkeys, and monogamous species, for in the latter groups successive offspring of a single mother are more likely to have the same father. Existing evidence is scanty, but that available does not seem to support the prediction that offspring compete with their siblings more in regard to weaning when their mothers are promiscuous. Thus Lawick-Goodall (92–94) indicates that chimpanzee females are more promiscuous than those of any other primate, yet weaning is so remarkably gentle that she ". . . originally thought that mothers played no active role . . ." Weaning may extend across one or two years. Interpretation of both of these facts is complicated by the continued close association between a mother and her offspring long after weaning. It would seem that weaning should be more traumatic when it represents a more complete termination of the parent-offspring relationship. Nevertheless, the considerable evidence of cooperation between siblings in chimpanzees, and of adoption of younger siblings—evidently more pronounced than reported for any other primate—does not seem to accord with the prediction that offspring evolve to compete with their parents. Various authors (43, 71, 77) report aggressive weaning in both multi-male and single-male bands of primates, but the data are too scanty for any comparisons to carry much weight. Interpretations of these data also await careful analysis of the actual degree of promiscuity in the involved species. Ransom & Ransom (133), for example, state that in anubis baboons they observed

". . . repetitive preferences for sexual partners," sibling bonds "which will probably last into adulthood," and four different kinds of special adult male–infant relationships, one of which, at least, was definitely associated with a male–female pair bond.

In an evolutionary sense, then, the interests of an individual offspring still under parental care seem likely to prevail only when the offspring is consistently in a better position than the parent to judge how best to improve the parent's reproduction. Cheating, which can evolve to extreme complexity in systems of reciprocity (155), can evolve only briefly and in limited fashions in offspring's interactions with their parents—i.e. until parental responses stifle or erase its effects. Between the parents, that sex with the greater parental investment will have the greater ability to manipulate its progeny in its own interests when the interests of the two parents conflict.

Competition between siblings need not disappear abruptly with termination of parental presence: a parent may influence whether its offspring disperse sooner or later. The amount of dispersal will in turn affect potential for competition and cooperation among siblings. As soon as a brood breaks up, the only way an offspring can improve its parent's reproduction is by improving its own, though it may still do so to the parent's disadvantage by failing to avoid competition with siblings. What is emphasized is the difficulty of determining when parental care terminates; the importance of that event is not diminished by the difficulty in identifying it. If an offspring begins to divorce itself prematurely from parental care the parent may be expected to resist 1. when it possesses information the offspring does not possess that tells the parent that departure will reduce the parent's reproduction and 2. when the offspring's continued presence will assist the parent by assisting its other offspring. If individual offspring behave selfishly at termination of parental care so as to reduce the parent's reproduction, extensions of parental influence will be favored that encompass the detrimental situation, if they protect the brood from the selfish offspring or suppress the selfish behavior.

As a result of environmental uncertainties, circumstances will exist in which parents are favored who reduce the tendencies of their offspring to dispense altruism because the parents cannot entirely prevent dispersal or infiltration, and the resulting likelihood that altruism among their offspring will sometimes be directed at nonsiblings. In other circumstances parents will be favored who disperse their broods even though such dispersal reduces the potential for intrabrood altruism that might increase the reproduction of the brood as a whole. These circumstances will involve such things as advantages of outbreeding (see below), advantages of multiple efforts at colonization of new habitat, avoidance of predators [for example, white-tailed deer and pronghorn antelope bed their twin fawns separately (84); also D. Hirth, personal communication], size of overwintering sites [sibling paper wasps that will nest together in the spring may be forced to overwinter separately (168)], and various results of environmental uncertainties. Environmental uncertainties may be the only factors preventing indefinite prolongation of reproductive "linkages" through altruism, thus favoring separate and independent individual descendants.

Reproductive linkage through altruism, which could develop only in stable environments, to some degree parallels asexuality. In asexual clones, altruism between individuals (phenotypic altruism) should be especially evident; both genetic simi-

larity and environmental predictability should increase the tendency of clones to function as units. In this tendency surely lies the selective background for the evolution of metazoans. What I am suggesting here is that in the appropriate environments parents can to some degree cause broods of offspring to behave like asexual clones. Precisely to what extent this tendency can evolve is uncertain. A useful comparison would involve regularly monozygotic or polyzygotic litters in mammals. To the degree that parents can cause their litters to resemble clones, members of long-evolved polyzygotic litters (e.g. most mammals) should behave toward one another in intrauterine competition essentially as do monozygotic embryos (e.g. North American armadillos) and should be no less alike in regard to nutrition when born. This prediction does not exclude the possibility that under some circumstances parental manipulation may result in production of distinct "runts," since 1. uneven partition of finite parental benefits may sometimes maximize reproduction, and 2. some offspring may be physiologically "identifiable" to the parent as representing poor investments (61, 159; see also below).

It is instructive to review those cases in which the reproductive interests of different individuals overlap most. Monozygotic individuals have completely overlapping interests, as do obligate parasites and their hosts if the parasites never leave the cells of the hosts (hence, possibly, plastids, mitochondria, and some viral particles). In species with characteristic lifetime monogamy, as with some penguins in which offspring cannot be reared by a single parent (147), the reproductive interests of the parents overlap almost completely, though not completely since either may be able to take another mate should its current mate be sterile or become inferior as a result of age or injury. When parental investments of the two sexes are identical, reproductive interests of monogamous mates may overlap completely in regard to any brood of offspring they may have produced together.

To the extent that intergenerational reproductive linkages already exist in sexual organisms, and are variable (that is, to the extent that cooperation exists among all or parts of broods or later descendants as a result of selection among parents), they may represent the chief confounding element in our efforts to identify precisely what it is that selection is maximizing; in other words, they may help us know what to measure, and what generation to measure it in, to determine which genetic line is winning (or what in fact constitutes "winning"). The other problem is that of deciding what constitutes the effective population: Against which individuals and against how many do we compare an organism's reproduction to determine which genetic lines are winning? These problems are exemplified and discussed below.

The principle of parental manipulation of progeny is thus involved in most reductions of clutch size whether behavioral or physiological, and indeed it operates even before zygote formation (apparently universally) during oögenesis when females combine cytoplasm into some of their genetically different gametes and consign others to extinction as polar bodies. The trophic eggs of crickets (167) and ants (175), fed by the mothers to their offspring, represent sacrifices of some gametes or zygotes to assist others. Hamilton (61), in noting that the theory of Williams (172) that senescence is a result of pleiotropy fails to account for high juvenile mortality, suggests that parents in species with extended parental care benefit from early

mortality of inferior or inviable offspring. A slight extension of this idea leads to the implication that in cases of heterozygote superiority, early lethality of one or both homozygotes may be a product of selection, a part of what Hamilton terms "infant replacement."

Parents may thus improve their reproduction either by altruism or by even fatal competition and cannibalism among their offspring, beginning in the uterus. In this light it will be useful to re-examine the reported cases of cannibalism or fatal competition among embryos (or juveniles still inside the mother) in animals as widely different as salamanders (12) and pronghorn antelopes (122). Cannibalism among juvenile salamanders may reflect an environment sufficiently unpredictable that it disfavors the evolution of a stable litter size. The pronghorn starts 3–7 embryos but produces two offspring; the proximal two embryos form necrotic tips that pierce the membranes of distal embryos at an early stage, suggesting occasional loss of the proximal embryos, unfortunately not yet observed.

Ingram (76) describes in detail the behavior of hawks and owls which lay their eggs at 1–3 day intervals and begin incubating when the first egg is laid. The result is hatchlings of staggered sizes, which may be easier to feed, but in such broods the larger offspring appear rather regularly to eat the smaller ones if food shortages arise. Ingram is probably right in referring to this phenomenon as controlled cannibalism, in which the parent, who evidently cannot predict the optimal clutch size in time to lay the appropriate number of eggs, uses some offspring to increase its reproduction via others. It is at least possible that consistent early abundance of food, followed by consistent lower supplies, may have caused the evolution of a tendency to use smaller offspring as food supplies for older offspring; this possibility exists whenever there is no easy way for a parent to convert its own body resources directly into food for its offspring in the way that, say, pigeons or female mammals do. As Lack (88, 89) has noted, brood reductions, whether or not they involve cannibalism, appear to be widespread among birds, are associated with asynchronous hatching, and probably function generally to increase parental reproduction.

Ability of parents to gain from redirecting their investments in some offspring so as to maximize the investment in others will result in new forms of manipulation as parental investment in each offspring increases. When parental investment is very great, this redirection may even include sacrifice of whole offspring, not only through killing and cannibalism when food is scarce (and historically unpredictable), but also through redirecting the parental behavior of adult offspring so as to render them obligately or facultatively sterile workers (or helpers at the nest). A parent may dramatically increase the effective amount of parental behavior for its reproducing descendants either by causing some of its offspring to behave parentally toward others or by causing members of one sex (or both sexes) in its brood to cooperate as parents to its grandchildren. This suggestion raises a whole series of interesting questions. Thus to what extent do the following situations represent decreases in clutch size or reproductive rate favored because of the value of increases in parental investment in individual descendants beyond the effects of kin selection in the Hamilton sense (i.e. involving reductions of inclusive fitness of some offspring)?

1. polyandry in certain birds involving cooperation between male siblings with a single female (106, 134)
2. similar polyandry in humans evidently functioning, partly through primogeniture, to retain in the family a critical heritable resource (the farm) (19, 56, 97, 129, 142)
3. restriction of reproduction to one male and female in packs of adult canines including (mostly?) siblings (94, 107, 130, 131), although many or all behave as parents
4. restriction of mating to a single male in groups of brothers, and his protection during mating by his brothers, in turkeys (162, 163) and in wolves (131)
5. helpers at the nest in various birds (27, 28, 70, 146)
6. obligate sterility in workers and soldiers of sterile insects

If the individuals in these cases are not receiving genetic benefits overcompensating their altruism to siblings, then the genetic relatedness of the siblings may be incidental to their altruism, since they are all similarly related to the individual being helped, i.e. the mother. For example, several factors other than kin selection may operate to produce tendencies of females to mate only once or twice per batch of eggs (156, see also below). The best reproductive strategy of a female with some sperm available (as compared to none) will always be adjusted in favor of oviposition when oviposition conflicts with further mating. A relevant comparison for this question would be the degree to which ovipositions occur between matings in, say, butterflies and moths with aposematic, distasteful offspring that move in close-knit groups and those whose offspring depend on cryptic coloration and move about singly. Parents are largely confined to "responding" (in an evolutionary as well as individually adaptive sense) to the appearance of competitive genes active in offspring (as metazoans "respond" to the appearance of cancerous changes among the descendant "nurse" cells comprising their bodies.). One way may be to reduce genetic uncertainty within the brood (e.g. through monogamy or oviposition between matings); another may be to impose control over brood altruism phenotypically. Thus a theory of parental manipulation as well as one of kin selection predicts greater tendencies to monogamy and inbreeding in parents who will not be present to mediate phenotypically their brood's altruism, as with aposematic or distasteful caterpillars, parasitic wasps, and *Polistes* wasps (see below); but the reasons are different. Such possibilities emphasize the difficulty of determining unequivocally when parental influence terminates.

PARENT MANIPULATION OF PROGENY AND OUTBREEDING

An obvious possibility of conflict exists between parental gains from cooperation among offspring within broods and the apparent advantages of outbreeding. Three alternative strategies can be suggested: First, in some cases parents may be favored who disperse their broods before they reach reproductive age, even though continued cooperativeness might otherwise have been valuable. Second, cooperation among adult siblings may often involve unisexual groupings. And third, cooperation in bisexual groups of adult (breeding) siblings may be concentrated in organisms like

humans in which behavioral ontogeny is so complex as to provide multiple possibilities for safeguarding against incest.

The significance of incest avoidance among siblings suggests the likelihood that cooperating siblings will be of a single sex, as already reported for turkeys in Texas (162, 163) (actually it remains to be demonstrated that cooperating males are always siblings), native hens in Tasmania (106), and polyandrous human societies (19, 129). The question is raised whether coincident selection favoring intense sociality and outbreeding might not lead to the production of unisexual broods in some cases; most theories of sex ratio selection require no particular relationships between sex ratios in the population as a whole and those within individual broods (Williams, 171, p. 153, may be the only exception, arguing that broods containing equal numbers of males and females may be advantageous because of effects of maximizing genetic diversity). Schaller (144) reports an apparent disproportion of all-male or near all-male litters in African hunting dogs. The frequency with which dominant (or breeding) females in canine packs seem to pair with other than the dominant male raises the question whether under usual conditions the result would be avoidance of breeding with a dominant brother (107 summarizes references for wolves; see also 94, 130, 131).

Monozygosity in twinning and in the case of armadillo quadruplets may often lead to maximally cooperative broods or extension of cooperativeness into adulthood, because of unisexuality as well as genetic overlap. Whatever the specific reason, the consistent monozygosity of littermates in North American armadillos predicts a greater degree of altruism than exists between individuals in other vertebrates in which genetically identical individuals are not consistently produced; and it is truly a prediction, for essentially nothing is known of the social behavior of armadillos. The same prediction would not be made for monozygotic twins in cases such as in humans, where twins are rare and apparently were even more rarely allowed to live during most of human history; in such cases monozygotic individuals should behave toward one another in the same fashion as ordinary siblings close together in age (incidentally, also evidently a rarity in pretechnological human societies). The precise degree of difference in altruism between monozygotic armadillo littermates and polyzygotic littermates of other mammals should correlate inversely with the effectiveness of parental manipulation, given similar ecological conditions and similar abilities by littermates to assist one another reproductively.

EVOLUTION OF SOCIAL INTERACTIONS IN DIFFERENT KINDS OF SOCIAL GROUPS

The evolutionary consequences of reciprocity, nepotism, and parental manipulation of offspring can be illustrated in two ways: 1. by comparing their evolutionary effects in the kinds of social groups in which each will evolve, and 2. by comparing the predictions deriving from models utilizing each, or some combination of the three, to explain aspects of existing social systems. I now attempt these two kinds of comparisons. I first utilize a hypothetical group, greatly simplified and as similar as possible for all cases. Then I consider (a) the evolution of sterile castes in social

insects and (*b*) certain aspects of human social behavior, particularly those which seem to involve parental manipulation of offspring.

Reciprocity in Groups of Unrelated Individuals

Consider a herd of five unrelated male deer forming a hierarchy in which their respective reproductive (or fitness) values on some arbitrary scale are 0.5, 0.4, 0.3, 0.2, and 0.1. For simplicity assume that such herds form only outside the breeding season and their significance lies only in improved predator detection. The fitness differences of the individuals may be solely a matter of likelihood of survival to the breeding season, and can be considered to result from differential access to the safest feeding positions. (I have purposely not followed the convention of assigning a fitness of 1.0 to the most fit individual because of the difficulty in comparing fitness changes in different situations; see below.)

Assume now that the fitness of lone individuals, less likely to attract predators, averages 0.13. The subordinate male in the five-male group will thus gain by leaving the group. In a smaller group, however, the other males will be more vulnerable, their fitnesses dropping, say, to 0.4, 0.3, 0.2, 0.1. Now the new subordinate male should also leave, and in such cases group living will not be maintained. It is possible, however, that the higher-ranking males can gain by yielding sufficient proportions of their fitnesses to the subordinate to raise his fitness above that of solitary individuals, thus, 0.49, 0.39, 0.29, 0.19, 0.14, if we assume that the subordinate's gains equal the other individuals' losses (that is, benefit = cost, or $B = C$). These fitness shifts can be accomplished merely by giving the subordinate individual slightly less vulnerable positions in the herd. In any group in which the individuals cannot (for whatever reason) identify or respond differentially to closer and more distant relatives, the social system will evolve according to pure reciprocity. (Note that whether or not dominant individuals gain by the joining of a subordinate, or the subordinate chiefly gains, may depend upon the kind of responses appropriate to the significant predators: if large males either singly or in coalitions defend against predators, subordinates may never gain by leaving a group, and dominants may gain little by their presence.)

Suppose that in the above case when an individual gives up a unit of fitness to another individual the beneficiary gains not one but two units ($B = 2C$). In a system of pure reciprocity each individual will still gain from maximizing his own fitness relative to those of other group members and the rest of the population. Since within the group each act of beneficence will now assist the recipient more than it will cost the actor, a system of reciprocity could raise the fitnesses of group members relative to those of individuals outside the group. If, for convenience, we now assume that each group member in the original example (0.5, 0.4, 0.3, 0.2, 0.1) could dispense the equivalent of its reproductive value in beneficent acts (this reducing its fitness to zero in the absence of incoming benefits), and that every individual did so without showing preference within the group, the new fitnesses of group members would be 0.50, 0.55, 0.60, 0.65, 0.70 (each individual receiving one fourth of twice the reproductive values of the other four combined). In this situation the fitnesses of the different individuals relative to one another is no longer the same; within the group the dominant has lost the most and the subordinate has gained the most. Because

$B = 2C$ all but the dominant have increased fitnesses. If, say, $B = 3C$, all would gain with respect to the population at large; if $B = C$, only the two subordinates would gain; etc. Because fitnesses are relative, the significance of such changes can only be evaluated in terms of the directness of competition among groups and among different individuals but the evolutionary significance of reciprocity is clear. As Trivers (155) and Hamilton (66, 67) point out, in such a system individuals will gain who can take advantage of opportunities to minimize beneficence and maximize returns, or to cheat without being detected; thus, ability to recognize cheating, and even (in certain kinds of animals) tendencies to cheat by falsely accusing others of cheating, may also increase.

Reciprocity and Nepotism in Groups of Uniformly Related Individuals

Now consider the same herd but suppose that the males are all related to one another by 1/4 (an equivalent evolutionary situation prevails if they are only on the average 1/4 related but cannot react differentially to closer and more distant relatives within the group). Their fitnesses at the outset are still 0.5, 0.4, 0.3, 0.2, 0.1. Considering the first situation described above, it will now pay the subordinate individual (genetically) to remain in the group with his fitness lower than that of a solitary individual (0.13), for merely by so doing he raises the fitness of his close relatives from 0.4, 0.3, 0.2, 0.1 to 0.5, 0.4, 0.3, 0.2, a collective total of 0.4 units. This is greater than 4 times the increase of his fitness (0.03) if he becomes solitary. Genes causing this amount of helping of relatives will spread (i.e. nepotism in this case will lead to kin selection), and if the selection continues, sooner or later each individual will be tested for whether or not it carries such a helper gene (60, 67). To simplify the example we may consider that only in subordinates is the helper gene actually expressed (in this case its expression involves merely staying in the herd). This is commensurate with earlier predictions about systems of reciprocity involving individuals engaged in dominance-subordinance relations; on the other hand phenotypic dominants may sometimes be in a better position to give benefits at small loss, and phenotypic subordinates in a better position to profit greatly as beneficiary (both situations leading to $B > C$). Thus, for a dominant social donor, perhaps, $B > 2C$ and for a subordinate donor $B < 2C$. In such cases dominants will be able to raise their own fitnesses by maintaining the herd through small investments with great value to other herd numbers.

In a group of related individuals, then, inclusive fitness (60) becomes involved in the extent to which beneficence will be expressed because fitnesses of individuals are relative to the population outside the group. Nevertheless, to the extent that an individual's fitness is most relevant to that of other individuals within his immediate group, reciprocity and the attendant tendencies to cheat can also evolve in groups of equally related individuals, or groups in which closer and more distant relatives cannot be distinguished.

Reciprocity and Nepotism in Groups of Variously Related Individuals

Now consider the same herd but suppose that the α (0.5) and β (0.4) males are monozygotic twins and they behave as if they know it; that is, monozygosity has happened frequently enough for the behavioral responses genetically appropriate to

it to evolve. (We can assume, for this example, that the fitness difference of the twins resulted from an effect, such as differential nutrition, on their phenotypes.) The other individuals are unrelated to one another or to the α and β males. If each beneficent act raises the fitness of its recipient as much as it costs the actor ($B = C$), then the herd will evolve much as it would in a system of pure reciprocity: each individual will give up only enough to keep the subordinate in the herd. But if $B > C$, say, $B = 1.1C$, then the α and β males should give all of their benefits (in excess of any required to retain the subordinate in the herd) to one another. If the other males still dispense their beneficence randomly, the fitnesses of the members should become 0.66, 0.77, 0.0825, 0.11, 0.1375.

This picture is much oversimplified and not realistic, since we would expect unrelated individuals grouped as above with related individuals not only to exclude the "clannish" twins from receiving their benefits but to dispense benefits among themselves only on a reciprocal basis, such that their relative fitnesses would not shift as much as in the example. What actual shifts would give each the greatest benefits again depends on how important are comparisons inside and outside the group.

In any case the significance of variations in genetic relatedness within groups is clear. The important point here is that the monozygosity of α and β means that the genes of each are maximized by complete beneficence, even though the relative fitnesses of the two individuals reverse in the process. The same would not be true of the three unrelated individuals, for whom the above example is unrealistic; they should behave so as to minimize fitness shifts among themselves.

The examples given so far point up two problems that deserve mention. First, because of variations in social circumstances, nepotism may be expected to assume two different forms. If different associates are consistently likely to bear similar genetic relationships to one another, one expects more or less indiscriminate tendencies to be altruistic or benevolent toward associates. Such tendencies will be reinforced by fluid or inconsistent social situations that reduce the likelihood of successful capitalization upon abilities to remember or recognize individuals of differing relatedness. This kind of nepotism is that most frequently implied in discussions of kin selection (27, 28, 50, 60–67, 131). An obvious reason is that in most vertebrates, except for humans, genetic relationships of individuals are poorly known.

The second form of nepotism occurs whenever the variance in relatedness among close associates is high, and means exist by which different relatives can be identified. In such cases altruism or benevolence should be distributed discriminately, favoring close relatives. This second form of nepotism may become extremely complex.

These two expressions of nepotism may both occur in humans for reasons that can be understood from reflecting upon effects within different sectors of so-called "primitive" societies, for example, as distinguished by Sahlins (141). Consider any individual within a household, and the variance in relatedness to him that would be shown among individuals with whom he might associate, chosen at random from 1. the same household, 2. the same lineage but different households, 3. the same village but different lineages, 4. different villages, and 5. different tribes. It will be

seen that the lowest variances will occur 1. within the same household, where all relationships will be high, and 2. between villages or tribes, where all relationships will be low. The highest variances will probably exist at intermediate distances, as between households within the same lineage.

From these observations we predict a relatively consistent, indiscriminate response to opportunities for altruism toward members of the same household or of different tribes, but a highly discriminative kind of nepotism at intermediate levels, perhaps most exaggerated within lineages. Discriminatory nepotism within groups has rarely been analyzed genetically, except in Hamilton's (60) argument that male workers are absent in Hymenoptera because of their low relatedness to their sisters (see below for an alternative explanation). Commonly, groups of related animals have been considered as uniformly related and the only question raised is their "average" relationship. A good example is Hamilton's statement (60, p. 20) that "the average relationship within a rabbit-warren is probably quite sufficient to account for their 'thumping habit' . . ." But nepotism and reciprocity will evolve differently when relatedness varies and the individuals can somehow respond to the variations. The above comparisons indicate that thumping could evolve among unrelated rabbits if $B > C$, and that Hamilton's statement does not consider the problem of differences in genetic relationships and degrees of competitiveness among individuals within (and between) groups (see below).

Hamilton's development of the concept of inclusive fitness began with the argument that the reproductive success of an individual organism cannot be measured by alone considering the effects on the number and quality of direct descendants. Also involved are effects on the reproduction of genetic relatives. But, since both of these effects can only be measured in a comparative sense, there are always other individuals involved, and they are the reproductive competitors of the individuals and genetic elements being considered. In Hamilton's equations they are the population at large, an average of the rest of the species. Hamilton's arguments thus seem only to consider the detriments of altruism in terms of energy expenditure and risk-taking in the act itself, and to omit or at least not specify the problem of subsequent detriment to the altruist (or its descendants) owing to the presence of the recipient (or its descendants). But all of the members of the species, or population, will not compete equally directly with any given individual. Nearby individuals are more direct competitors. This would not affect Hamilton's calculations unless nearby individuals also have a greater likelihood of being closer genetic relatives. That such a correlation generally exists is obvious, and is acknowledged by Hamilton (67). I believe this factor modifies every consideration of whether or not, and how, nepotism will actually evolve. The following examples illustrate its significance and applicability. Note that the first three cases refer to what might be called, respectively, ecological, sexual, and genetic competition; but all such categories may be combined under the term reproductive competition, and all are ultimately significant only in genetic terms.

1. Whenever a resource is adequate for a single individual only, and no substitute is available, any two individuals except monozygotic twins should fight to the death for it. Thus queen honeybees may have evolved stings solely in the context of killing

their closest relatives, competing sisters; trees may kill their own offspring germinating beneath them (see below).

2. When two individuals are equally related to a third, and are also (a) equally available for the reception of altruism and (b) equally needy, the altruist should help which ever one of the two is less competitive. Thus an individual should be more willing to assist a very close relative (i.e. too close to be a suitable mate) (a) if it is greatly different in age and (b) if it is of the opposite sex. Identically related individuals of the same age and sex will be more direct competitors in the latter case for quality mates, a resource that, for males at least, is nearly always in short supply. This argument does not necessarily conflict with cases such as brother-alliances in chimpanzees (94), since the above conditions may not be met.

3. If an altruistic act favors two relatives, say, 1/4 like the actor, and another altruistic act equally expensive favors just as much four relatives 1/8 like the actor, the first act will be favored in evolution because it assists fewer competing genetic elements.

4. If degree of genetic relationship and directness of competitive effects diminish together in certain, not necessarily unlikely fashions with increasing distance from any given individual in a population, then nepotism cannot evolve.

An approach that ignores the correlation between directness of competition and degree of genetic overlap between genotypes leads to the argument that inbred species (and presumably, as well, asexual species or species that have "given up" part of their sexuality, e.g. those with haploid males, polyembryony, frequent parthenogenesis or self-fertilization, or consistent matings between siblings) should show more altruism because of the greater average genetic relationships between individuals. If, however, members of inbred species were automatically more altruistic than members of outbred species, then it should follow that any given individual would be more altruistic toward his most distant relative within his species than toward any member of any other species (excluding those with which mutualistic interactions have evolved independently of kin selection) with which he would presumably share fewer genes. But species boundaries represent diminishments in overlaps of resource utilization as well as in genetic overlap, and the two changes are not necessarily quantitatively correlated. Any conspecific individual may represent a greater competitive threat than any nonconspecific individual, in which case one's most distant relative within his species may be a more appropriate object of aggression or interference than either closer relatives or members of other species.

I suspect that field evidence will demonstrate that members of inbred species (and others which have reduced the impact of sexual recombination in other fashions) do indeed display more tolerance and cooperativeness than those of outbred species; but I suggest that the cause–effect relationship is reversed, with the inbreeding (and reduced sexuality) sometimes an "acceptable" detriment deriving incidentally from group living and cooperativeness and sometimes advantageous because of environmental stability.

The second problem which must be considered in groups of variously related individuals (above) is illustrated by the fact that in all cases mentioned so far, shifts in fitness occur both among the individuals in the group and between group mem-

bers and the population at large (whatever that may be). Nothing has yet been said of the relative importance of these two categories of relative fitness estimates, nor of the effect of subgroups within the herd; nor are these questions generally raised in such considerations. How does one judge what amount of fitness loss within a group, as a whole or compared to individuals or subgroups within the group, overbalances a fitness gain relative to the population at large; or vice versa, what fitness loss relative to the population at large is overbalanced by fitness shifts of various sorts relative to the rest of the group? What, in fact, is the relevant "population at large"?

Suppose that in the same herd above the α and β males are related by 1/2 (but for purposes of this example are not siblings), the others by something less. Again, they should restrict their beneficence to one another so long as the subordinate receives enough benefits to stay in the group. Now, however, the related males, not being identical, are also genetic competitors, and it will matter in selection how their fitnesses change relative to one another. Four different levels of fitness shifts are thus involved in any estimate of the significance of an act or event to any individual's reproduction: 1. his fitness relative to his genetic relatives in the group, 2. his fitness relative to nonrelatives within the group, 3. his fitness relative to the mean of all the other individuals in the group, and 4. his fitness relative to the mean of individuals in the population at large. Again, the last is itself a problem of multiple subgroups that may or may not be relevant to any particular fitness estimate. How do we decide what combinations of fitness shifts relative to one another are most important?

For this question, suppose first that in the same herd as above only the fitnesses of group members are relevant (i.e. there is only one herd in the species). Then the individuals will gain only by elevating their fitnesses proportionally within the group. Accordingly, any individual destined to remain the subordinate should leave, except, of course, that considering only the fitnesses of group members as being important implies that this is the only group, that these males belong to a closed group and never compete directly with any other males. Such a situation will occur only if a permanent barrier appears within the range of a species, isolating a population containing only enough males to make up one social group of the sort being considered here.

If only relative fitnesses within the group are relevant, then no individual should initiate reciprocity when $B = C$, and only individuals related by more than 1/2 and subordinates should do so when $B = 2C$ (excluding reciprocity initiated in relation to a likelihood of gaining by cheating). Each individual should act only so as to increase its total proportion of the reproductivity of the immediate group. Thus, by giving benefits exclusively to one another, when $B = 2C$ monozygotic α and β males increase their combined fitnesses from 60 to 80% of that of the entire group if the other males do not engage in beneficence. But if the other three males withhold benefits from α and β and dispense them fully among themselves then in this example α and β will not be able to increase their combined fitnesses above 60% of the total value of the group.

When individuals are not genetically identical but overlap genetically to different degrees within the group, then the related individuals can also maximize genetic

fitness through their relatives. Thus, if α and β are 1/2 alike, when α's fitness rises in relation to all group members, β's fitness rises by 1/2 as much in the same comparison. So α is interested in maximizing his own original five units and he is half as much interested in maximizing the five units of β. But contributions to the other's fitness also assist the competing half of the other male's genotype and, if fitnesses are compared only within the group, unless $B > 2C$ in the above case, then acts of beneficence will not assist the altruist. Since the beneficence of α and β in itself (independent of reciprocation) will hurt them when it is applied to the three lowest-ranking males but will have no effect when applied to the relative (because in within-group comparisons, the 50% genetic overlap leads to $B = C$, in terms of the interests of the altruist), all beneficence either individual dispenses should be to the other. α and β can elevate their fitnesses relative to the other three group members by engaging in reciprocity between themselves, but if each dispenses all its beneficence to the other, β will gain in relation to both α and the rest of the group, while α will gain only in relation to the rest of the group. Thus β will gain from maximal exchange but α cannot even gain from a symmetrical exchange: if α yields 0.4 units of beneficence to β and β yields 0.4 units to α (and $B = 2C$), then α (retaining 0.1 units) = 0.9 and β = 0.8. Thus, unless a more fit individual can, in this sense, secure greater benefits from a subordinate than he gives up in a reciprocal engagement, he should avoid such engagements when only fitnesses within the group are relevant. Both dominant and subordinate, however, can gain in relation to other individuals by a reciprocal interaction in which neither loses relative to the other whenever $B > C$.

Interactions of Nepotism and Reciprocity

Nepotism implies that benefits are given by one individual to another without reciprocation, the gain to the first individual resulting from the genetic overlap between the two.

Reciprocity implies that benefits are only given when there is a high likelihood of a compensating return to the phenotype of the benefit-giver (but, conceivably, the return could be to the phenotypes of relatives of the benefit-giver). Only reciprocity can evolve within groups of unrelated individuals. In groups of equally related individuals (or individuals who cannot respond to differences in degrees of relatedness and can only evolve to respond in terms of average relatedness), nepotism will also evolve such that only two kinds of individuals will be distinguished: group members and nongroup members. Reciprocity can also evolve in such groups. One can imagine an equal tendency to engage in acts, the returns from which must accrue from reciprocity with different individuals in the group, beyond the limits of beneficence from which gains through nepotism are possible.

What happens in groups of variously related individuals, within which the individuals can respond to the differences in relationships? Obviously, when reciprocity is unlikely, closer relatives should be favored in beneficence. But so should they if there is any doubt about reciprocity, as there must always be. One can better afford to lose, and less afford to cheat, in reciprocity with a relative, and more so with a closer relative than with a more distant one. If all acts of nepotism should always

be directed at one's closest relative, should not all acts of reciprocity as well (assuming no variation in cost–benefit ratios)? If so, then in groups of variously related individuals, nepotism and reciprocity will always tend to be intricated. Thus, reciprocity can evolve alone, but only in groups of unrelated individuals; but nepotism evidently cannot evolve independently of reciprocity because reciprocity will always be potentially a factor in the social interactions of groups within which nepotism can evolve. A good illustration is the example above in which monozygotic twins in a group of five individuals cannot elevate their total combined fitness within the group by dispensing all their benefits to one another if by so doing they cause the other three males to exclude them from their altruistic interactions. This fact may be responsible for many of the confusing aspects of human systems of kinship cooperation and altruism that have led social scientists to doubt their derivation from a history of differential reproduction.

Parental Manipulation of Groups of Siblings

Now suppose that the same herd of five males is composed of siblings. Their genetic relationships may average ½ (one father), ¼ (all different fathers), etc. Regardless of their degree of relationship, or variations in degree of relationship, their maximal value as a collective whole will represent the greatest fitness for the mother, or both parents if they are monogamous. Even if that total fitness is raised so little that the subordinate does not increase his genetic fitness by remaining in the group, parents with altruistic subordinate offspring will outreproduce other parents. If, in such a case, subordinance is genetically determined at the outset, the gene may be lost; however, phenotypic subordinates will still be expected to behave altruistically. As with recessive genes for aposematic coloration that help dull-colored siblings but hurt individuals in which they are expressed, genes for altruistic subordinance can be favored if individuals heterozygous for the gene are favored because they are likely to have an altruistic sibling homozygous for altruism.

If $B > C$, then if the sibling group members act strictly in their parents' interest they should dispense all their benefits, for only in that way can the total reproductive value of the group be maximized. They should do this even if some individuals lose in relative fitness within the group and each group member is unlikely to compete directly with any individuals outside the group. In other words, as suggested earlier, if they evolve so as to maximize their parent's reproduction, siblings should behave like members of an asexual clone or a group of monozygotic individuals.

Let us now attempt to apply these considerations in the analysis of some real cases.

EVOLUTION OF SOCIALITY IN INSECTS

The social insects have been a central theme in every major publication on natural selection for one important reason: they are apparently alone among all organisms in having evolved obligately sterile individuals. Darwin (41, p. 236) referred to the sterile castes of insects as the "one special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory." Darwin effectively solved the

problem of how different kinds of sterile castes can evolve within a single species by realizing that selection can operate through the "family." As he put it (41, p. 238) ". . . a breed of cattle, always yielding oxen with extraordinarily long horns, could be slowly formed by carefully watching which individual bulls and cows, when matched, produced oxen with the longest horns; and yet no one ox could ever have propagated its kind."

Nevertheless, as Hamilton (67) indicates, the problem of precisely how obligate sterility has evolved in the various social insects is still with us. As the most extreme form of altruism known, its relationship to everything said about social behavior up to this moment is obvious. Indeed, the social insects are probably the best example available for distinguishing the predictions and correlates of the three general systems of selection in social groups.

Several lengthy and detailed discussions of the probable selective backgrounds of insect sociality have been published recently (11, 50, 60, 67, 101, 109, 110, 166, 168, 169, 171, 173–175). The following account is by comparison a brief and sketchy effort in which I shall attempt to distinguish in certain specific regards the predictions and correlates of theories principally invoking 1. reciprocity, 2. kin selection, and 3. parental manipulation of progeny.

Since Hamilton's (60) paper, with the principal exception of Michener (110) and Lin & Michener (101), only kin selection, in which each individual worker or soldier caste is expected to secure an overcompensating genetic return for its altruism, has been invoked to explain altruism in eusocial insects. Across the past several years, however, I have become convinced that kin selection is not a sufficient explanation for such behavior in insects, and that it may be only feebly and infrequently involved. Kin selection, I suggest, will prove ultimately to be most relevant to the kinship and breeding systems of primate and human societies, for only there does clear evidence exist of keen ability to discriminate among many different relatives within social groups. [Curiously, Hamilton (67) makes the same suggestion for reciprocity.] The broad applicability of Hamilton's (60, 67) papers, and the changes in approach that they have caused, place them among the most important theoretical contributions to evolutionary biology since Fisher. But I believe that in some respects Darwin was more nearly correct than Hamilton, and that a form of parental manipulation of progeny in the interests of the parent best explains the sterile castes of insects. The difference between these two arguments can be clarified by referring to Hamilton's (60) summary statement (p. 29) "If a [hymenopteran] female is fertilized by only one male all the sperm she receives is genetically identical. Thus, although the relationship of a mother to her daughters has the normal value of ½, the relationship between daughters is ¾. . . . other things being equal, [a newly adult daughter would prefer] returning to her mother's [nest] and provisioning a cell for the rearing of an extra sister to provisioning a cell for a daughter of her own. From this point of view therefore it seems not surprising that social life appears to have had several independent origins in this group of insects . . ."

If, however, other things are indeed equal, then queen offspring of the above monogamous female cannot maximize their inclusive fitnesses by their devotion to producing offspring only half like themselves. Only if we assume that the parent has

evolved to mold or manipulate her offspring phenotypically so as to maximize her own reproduction can both worker and queen offspring maximize their respective inclusive fitnesses. This they can do because of the particular phenotypes with which the mother endows each of them as a result of the distribution of parental benefits and influences. Such an idea does not detract from the underlying significance of kin selection in sexual organisms. The amount of genetic overlap of different individuals must still determine the amount of parental molding necessary to effect cooperation. Nevertheless, it is clear that individual offspring consistently appearing in the same situations are unlikely on the basis of kin selection alone to evolve dramatically different roles in which one is a sterile helper at the nest and one reproduces in the normal fashion. Furthermore, so long as it is parental manipulation that brings about sibling cooperation, genetic relationships among siblings indicate only the amount of parental molding necessary, not whether or not it will be able to yield a given result. Alternative explanations for the prevalence of eusociality among Hymenoptera, and for its presence in male-diploid termites, are thus given more credibility.

The eusocial insects actually have two distinctive attributes: sterile castes and overlap of the mother's reproductive life with that of her offspring. Social groups with these attributes appear to derive from two different precursors: 1. groupings of subsocial (parental) females (eventually including their offspring) and 2. extended families of single mothers. In either case extended parental care precedes eusociality and sterile castes. This apparent dichotomy has long puzzled students of insect social behavior, and is in fact responsible for much of the disagreement in recent theoretical arguments (101, 109, 110). The similarity of the two groups is greatest if the groups of subsocial females, in cases that lead to eusociality, are always sibling groups. Then, as Lin & Michener (101) note, the only difference would be that in one case the mother is present and in the other she is not. As a result, the problems of selection during evolution of sterile castes become essentially the same in the two cases. Because (a) single-queen colonies are vastly preponderant in eusocial insects, (b) facultative sterility has not been unequivocally demonstrated among nonsiblings, and (c) for reasons already indicated it is much easier to evolve sterile castes among siblings. I here suggest that the burden of proof may be upon the investigator who argues that sterile castes have evolved other than within broods of single mothers.

In this light we can begin our comparison by considering Michener's (109) proposal that groups of cooperating unrelated female bees evolved through stages in which differences in reproduction among them came to be actual division of labor in reproduction, and then led directly to the evolution of sterility in some of the females. Lin & Michener (101) defended this idea, but with the critical modification that the cooperating females may (sometimes!) be siblings.

As was shown above, in systems of reciprocity, each individual is continually gambling that his investment will improve both his phenotypic and his genotypic fitness; indeed, what is going on is a form of mutual exploitation under the benefits of group living. There is in fact no altruism except in a temporary sense that benefits may be given at one time and received only at a later time. Should systems of pure

reciprocity exist, evolution will tend to reduce fitness shifts to zero–that is, to equalize investments and benefits to individuals. There is no alternative, and this is the precise opposite of what has to happen in the evolution of obligate sterility. As a result we can dismiss reciprocity as being the central factor in the evolution of sterile castes.

Bees or other parental insects may have interacted reciprocally in groups prior to the evolution of sterile castes, and they may have done so subsequent to the evolution of sterile castes. Different families of social insects in a single large group of the sort that are sometimes called "multiple-queen colonies" may even use sterile individuals now as their social donations, or their contributions to reciprocity in the maintenance of the entire group of families, as can also be proposed for facultatively sterile individuals in human religious sects. Group living among competing reproductives may have evolved among subsocial bees for any of the reasons for group living given earlier, and such group living may have [as Lin & Michener (101) suggest] somehow "primed" siblings in the direction of forming groups within which sterile castes could evolve. When such groups are composed of closely related nonsiblings, eusociality could feasibly evolve through kin selection; but this route seems less likely than the route of parental manipulation, for reasons outlined below. In no other sense can the interactions of unrelated competing reproductive females lead to evolved sterility.

In distinguishing the predictions and the correlates of kin selection and parental manipulation in accounting for sterile insect castes let us first consider the genetic relationship of altruist and beneficiary.

A principal difference between kin selection and parental manipulation is that kin selection, as formulated by Hamilton (60), requires that each individual secure genetic returns for its altruism greater than the cost of the altruism to its own personal reproduction, this return deriving from the likelihood that given relatives will carry a gene for altruism carried by the altruist. To the extent that the evolution of parental care has placed parents in the position of being able to use their investments in some offspring to increase their total reproduction via other offspring, this requirement is nullified.

Genes for altruism among siblings that benefit the parent can spread regardless of their distribution in the brood with respect to dispensation of altruism. I believe that this fact may largely solve the problem of initially saving and spreading genes causing their bearers to be altruistic, advantages to parents thus perhaps providing a major source of genes leading to altruism in all contexts (including the temporary altruism of reciprocity). The significance of this explanation in accounting for phenomena such as aposematic coloration is obvious (see also 53). Thus the parent with a few brightly-colored offspring in a poisonous brood may be both more likely to lose the brightly colored offspring and more likely to produce a bigger brood after predation. The allele for brighter color, assumed for this example to be recessive and present in other individuals in broods having a few homozygous bright individuals, may as a result be selected downward within broods while simultaneously being selected either downward or upward in the species or population as a whole. (See also Figure 1, Broods 1-2c-3c.)

While this situation continues (meaning until the alleles for aposematic coloration have spread widely), the selection that is going on will favor the parent who produces at least a few homozygous bright offspring, disfavor homozygous bright offspring, and either favor or disfavor alleles for brightness, depending upon the intensity and kind of selection. It may also favor parents whose offspring tend to cluster around the few bright offspring, probably to the added detriment of those individuals since they will likely be more obvious to predators in the middle of a group of moving caterpillars than when alone. If a mutant for brightness is not entirely recessive then its initial spread may be inhibited more than in the above example, except that a heterozygous parent will produce an entire partly bright brood. This example purposely omits the possibility of predators with a generalized ability (of whatever origin) to avoid brightly colored potential prey. In such cases alleles for brightness will be favored in all circumstances.

Let us now consider the genetic relationships of altruists and beneficiaries among social insects. Hamilton and others have emphasized the ¾ average genetic relationship of sisters in a hymenopteran social colony, given the haplo-diploid sex-determining mechanisms of all Hymenoptera and a monogamous mother. This emphasis is misleading for three reasons. First, the termites, which have also evolved eusociality, have normal diploid males. Second, as pointed out by Trivers (158), only the females are considered but brothers are also reared by workers, and in haplo-diploid species they are only ¼ like [and ¼ unlike!] their sisters. Third, eusocial hymenopteran queens at least frequently mate with more than one male. Considering its importance, relatively little attention has been paid to the mating of social Hymenoptera. Astonishingly, it was only recently discovered (Parker, ref. 124, lists references) that multiple inseminations (as many as 7–12 per queen) are evidently the rule in honeybees (each male can mate only once). Single mating has been established for few social hymenopteran females, but multiple insemination is apparently common (101, p. 141; 124; 175, p. 330).

There is no evident correlation between monogamy and eusociality or tendencies toward eusociality. It is possible, but not convincing in view of the generally polygynous or promiscuous hymenopteran background, to postulate 1. brief periods of monogamy in each line that became eusocial and 2. that once sterile castes had evolved, multiple matings could become the rule even if monogamy were critical in the appearance of sterility. Wilson (75, p. 33), after noting that multiple insemination ". . . is not favorable to Hamilton's thesis, . . ." suggests 1. the above explanations and 2. the possibility that males are often closely related. But the necessarily dangerous mating flights of queen honeybees (compared to mating on the comb), even though drones have access to hive interiors, suggests selection favoring outbreeding; the appearance under inbreeding of useless diploid males that are killed in the pupal stage by the workers (83, 135, 178) suggests a long history of outbreeding. Hymenopteran siblings may average a closer relationship than siblings in species with diploid sexually produced males, but a 3/4 average relationship is yet to be demonstrated. A point which detracts from the hypothesis suggested here is the tendency of the sperm of different honeybee males to clump inside the queen (152). This phenomenon reduces the variation in genetic relationships among the hive

members at most times. But this phenomenon may be widespread (124), and there seems to be no evidence that it has been elaborated in honeybees because of a value in regard to kin selection (also, see below).

Monogamy in termites probably long preceded eusociality coinciding with extended parental care and ensconcement in burrows or crevices. Such behavior is widespread among orthopteroid insects; Alexander (2) has provided a hypothetical scheme indicating some of the steps by which this behavior could lead to eusociality. The nesting cavity of termites (as well as the nests of wasps and bees) is a resource possibly of value to breeding offspring. Parents could gain if adult offspring sometimes remained in the cavity because of the opportunity of taking it over from the parents when they died. Parents could gain further by 1. keeping such offspring from engaging in deleterious competition over the nest resource and 2. causing them to use their parental behavior in the parent's interest when healthy parents and adult offspring overlap. Long-lasting nests and overlap of parents and offspring serving as facultative workers would in turn select for longer parental life, and ultimately, perhaps, for obligately sterile offspring. Abilities of parents to make their offspring helpers would often tend to increase the duration of the nest as a reproductive resource and reinforce the entire process. I believe that this hypothetical scheme may be generally applicable in accounting for insect eusociality, and for at least some cases of extended families in vertebrates.

The central role of the duration of the nest resource in the above hypothesis focuses interest on the manner in which nests are founded or pass from one generation to another. In this connection, West-Eberhard (168, pp. 66–67) has described a series of intense conflicts across several weeks among potential queens of the tropical paper wasp, *Polistes canadensis*, for possession of a 22-cell nest that had five foundresses when first observed. These queens may or may not have been sisters. Likewise, West-Eberhard describes as "offspring" three queens that fought for the nest for three weeks after the dominant queen was removed; she does not term them sisters, although they likely were. The evolutionary background of this kind of conflict can only be understood through knowledge of the frequency with which *P. canadensis* nests are usurped by nonsibling queens. West-Eberhard describes several usurpations, but with little knowledge of the relationships of the contending queens.

A parallel to the parent–offspring interactions in the above evolutionary situation can be drawn with long-lived trees. So long as the insect nest, as a reproductive resource, persists longer than the incipiently social queen, there will be selection for longer adult life; with trees, a similar effect accrues from persistence of the resource of a place in the sun and soil. Both the tree and the insect are then in competition with offspring for the resource, but the evolution of offspring that compete with a healthy parent will be thwarted in either case. One predicts, as a result, that seedlings will be less able to grow up under their own parents (e.g. 165) than will seedlings of other species, which can evolve to compete; and within-species allelopathy should be viewed as a parent–offspring interaction, rather than simply intraspecific competition leading (for example) to some kind of population regulation.

A healthy tree with a long life ahead of it gains only from offspring that germinate somewhere other than beneath it, and it loses from those that germinate beneath it. The extent to which parental poisoning of young will evolve, if it is not genotype-specific within species, will be determined by the frequency with which seedlings germinating beneath conspecific adult trees do so beneath their own parents; if the adult is often enough a nonparent, competitive ability will evolve in the seedlings too.

Trees should also evolve so as to maximize their likelihood of replacement by an offspring, however, and with certain combinations of lengths and predictabilities of juvenile and adult life, the result will be greater likelihood, at least at certain times, of seedlings succeeding under their own parents. The production of suckers or sprouts from roots of dying or afflicted trees must reflect a history of success in trees replacing themselves, in this case by genetically identical offspring.

With trees there is no obvious capability of evolving to use some juvenile seedlings to produce and rear others, so the competition can be clarified (partly) in terms of Hamiltonian kin selection: The tree is more interested in producing further offspring of its own (1/2 like it) than in giving up the resource to its offspring so that they can produce grandchildren (1/4 like it), particularly if the replacement is likely to be a single offspring. The same is true of the insect (and it is particularly important that in each case the resource is suitable for a single reproductive individual). But this description does not specify why the parent wins in the competition, nor does it explain the evident "altruism" of the offspring. The social insect differs from the tree in that, being already parental and with parentally inclined offspring ready to assume ownership of the next resource, it is evidently only small steps away from the capability of using those offspring as effective parental investment contributing to the reproduction of other offspring. Once assistance of parents is seen in this light, the step to obligate sterility in some offspring is easy to envision. It is possible that, in explaining insect eusociality, more attention should be given to the effects of evolving the potential for producing a reliable and persistent (homeostatic) environment useful to a single adult, which in turn selects for longer adult life (as in trees), causing particular kinds of parent–offspring competition.

The hypothesis that sterile insect castes evolved in the context of assisting the reproduction of their parents thus leads to predictions somewhat different from those of Hamiltonian kin selection. Sterile offspring may in this hypothesis be totally altruistic, for no genetic return is required except to the parent (or, to say it another way, to the brood as a whole). The sterile offspring are only a part of the mother's parental investment, and genetic relationships among the brood, sex determining mechanisms, and numbers of matings by the mother may all be more or less irrelevant. The reason is that the correlation is not with altruism being directed at close relatives, but with altruism being directed at siblings, whose relationships to the mother (for each sex) are always the same.

Supporting the hypothesis that eusociality in the Hymenoptera derives from the prevalence of extensive parental care, which has no great relevance in itself to male haploidy, is the fact that parasitic Hymenoptera and the plant feeders of the subor-

der Symphyta possess the male-haploid system of sex determination, no extensive parental care, and no social behavior. Likewise the termites evolved eusociality without male haploidy.

It appears that the critical factor in the evolution of eusociality is overlap of breeding parents with adult offspring or extensive parental care of siblings in an environment favoring cooperative nest-founding (therefore genes in the parent causing sibling offspring to cooperate in the parent's interests whether or not the parent is present). One of the difficulties experienced by entomologists in applying their usual precise definitions has involved the question of whether or not "true" social life (eusociality) should require only that parents tend their offspring to adulthood or that there be in addition sterile castes. The reason the problem has existed is that no parental insects are known to tend their offspring to adulthood, and overlap with them, without having sterile castes. The closest, perhaps, is *Halictus quadricinctus,* in which the mother remains in the nest "and is still present when the first of her offspring emerge" (175; see 101, pp. 146–47, for other doubtful cases). This virtual absence of parents in the same nest overlapping adult offspring without sterile workers further argues that it is parent-offspring interactions and not selection on sibling interactions as such that is involved in eusociality. Eusocial insects are unusual in having parents that overlap the total adult life of some offspring, even of successions of offspring.

Regarding the relationships of sister workers in the Hymenoptera it is also relevant that with, say, two matings by the mothers the sisters may average 50% genetic overlap (or more: see 67), but with two haploid fathers their relationships actually vary more than they would with a single diploid father because the haploid sperm contributions of two different fathers cannot recombine. Some pairs of workers will overlap genetically much more than others; this point has never been made clear, and one result is that efforts to apply kin selection (e.g. 27, 28, 50) have considered only average relationships and thus between-group selection. The lack of evidence of within-colony discrimination in single-queen species, even given two or more fathers, calls forth the spectacle of nurse bees sometimes tending young queens with whom they share relatively few genes. Again, it is to the mother's advantage (although not to the fathers', in the case of multiple mating) that sisters treat each other alike. Although Hamilton (60, 67) believes that worker laying indicates worker reluctance to raise the queen's male offspring, discrimination by workers against the queen's male offspring has apparently not been reported, and other explanations for worker laying are likely (see below). If bees and other social insects can discriminate offspring of different mothers within multiple-queen colonies (evidence of aggression among workers in multiple-queen colonies would represent the critical datum), and if kin selection is the main force in the evolution and maintenance of worker altruism, it is legitimate to wonder why workers with different fathers have not evolved the ability to discriminate full and half siblings. If altruism is a matter of queens manipulating their parental investments, this problem ceases to exist.

A second problem involves the question of why there are no male workers in the Hymenoptera. The kin selection argument is that, because of their haploidy, they are less closely related to one another and to their sisters, hence have less stake in

the colony (60). But there is another much more compelling explanation. First, males are rarely parental in the Hymenoptera, social or not (see 175 for the possibility of specialized exceptions among ants), although the females are more parental than perhaps any other insects. More importantly, the hymenopteran female controls the sex ratio of her brood by fertilizing or not fertilizing her eggs. As a parent she can therefore produce whatever proportion of females (thus, whatever proportion of workers) is most advantageous to her in the immediate situation. Under these conditions it is scarcely necessary to invoke kin selection to explain the absence of the genetic revolution necessary to make hymenopteran males parents. As Trivers & Willard (159) point out, the altruism from female progeny toward male progeny, in this case without compensating genetic return, will favor parents able to produce appropriately greater proportions of the more altruistic sex; Michener (110) has compiled sex ratios for social bees that seem to support this argument. Such altruism could not affect primary sex ratios if it occurred beyond the period of parental care (53), and were thus solely a matter of kin selection.

The history of the situation in regard to sex of workers (and soldiers) is again quite different in termites. Young termites are not helpless maggot-like offspring tended from hatching to adulthood in cells as hymenopteran offspring were before social behavior; termite sterility was not preceded by such extreme parental behavior. And termite females evidently do not have the kind of immediate and precise control over the sex ratio of their broods possessed by hymenopteran females. Thus, to the extent that they are now extremely parental, male and female termite workers probably became so more or less together.

A third point involves the production of males parthenogenetically by the worker females. Some consider this tendency support for kin selection (60, p. 31), some have considered it evidence against kin selection (101, pp. 153–55), and some consider it evidence that offspring may evolve so as to compete directly against their parents—in other words, they may "break out" of the clutches of manipulative parents. But there are other ways to view this phenomenon, at least in some cases. When a queen dies or is lost for whatever reason she has only one way to reproduce further if there are no larvae that can still be made into queens. Her final blaze of reproductive glory will be to have her workers make as many males as they can before the colony is dead. I suggest that queens have been favored whose workers begin frantically to make males with the slightest waning of her influence. (Hamilton, 67, refers to such behavior by workers as "selfish," apparently referring to the "race" by the workers to see which will reproduce most. But such behavior matches the mother's wishes, and in some eusocial insects leads to the production of a new queen, whereupon the workers "altruistically" kill the incipient queens that didn't make it.)

The above explanation is insufficient to account for all of the varying reports on the phenomenon of male production by workers (67, 101, 175); but, perhaps owing to the fragmentary nature of current information, so is every other single explanation.

Perhaps more relevant than parent–offspring competition in the problem of male production by workers is father–mother competition. Since all males are produced parthenogenetically, fathers will gain from producing both worker daughters that

make males in competition with their mothers, and, paradoxically, queen daughters that do so while suppressing their worker daughters' male production; the effect through a male's worker daughters is perhaps more immediate (see also 101). Queens, on the other hand, will gain from worker daughters that do not make males and queen daughters that do and that suppress male production by their worker daughters. When the queen is alive and healthy it is solely in the male's interest that worker females make sons, and this may be the only clear competition between male and female-parents in colonies of social Hymenoptera. Coupling this conflict with the value to the queen of her daughters making males when she is dead or waning may provide explanations for many of the confusing variations reported in this phenomenon. Moreover, a mechanism can be postulated whereby the male may to some extent compete successfully against his mate in this regard; this by constantly evolving sperm that are somehow able to thwart tendencies by the queen to lay unfertilized eggs, while producing daughters that tend to lay if they are phenotypically channeled into becoming workers.

The three points outlined above all seem to support the idea that the parents of sterile insects have made them so in their own interests, and have made them altruistic beyond the possibilities of kin selection as so far formulated. This theory, which has not previously been proposed, is also supported by the fact that the pheromonal influence of the queen is in every case either directly, or indirectly through the existing castes, the determiner of sterility. And, as noted earlier, it provides a solution to the question of why the queen honeybee has evolved a special sting apparently used only against her sexual sister. Hamilton (67) was so puzzled over this phenomenon as to suggest that *Apis* queens return from their nuptial flight into strange colonies often enough for the queen's sting to evolve as a result. If the colony is largely a manipulation of the queen's parental investment, then both extremely altruistic and extremely selfish adaptations among offspring are easily explained so long as they contribute to the queen's reproduction. Not only could a sting evolve solely because it efficiently dispatched the closest relative of the stinging individual at appropriate times, but the "quacking" of young queens still in pupal cells, in answer to the "piping" of an emerged sister queen whose response may be to sting them to death (68), can also be understood in this light.

The queen's sting, then, may be analogous to the necrotic tip of the proximal embryo of the pronghorn, the graded sizes of owl nestlings, and the various other determiners of clutch or litter size in different animals: it is a device that prevents partitioning of the parental investment (measured in honeybees largely in terms of available workers) beyond the point at which it is maximally reproductive to the parent. That this circumstance is not clear from the arguments so far provided on this topic (as Hamilton's puzzlement would imply) indicates that it is insufficient to argue that k in Hamilton's (60) formula somehow includes variations in intensity or directness of reproductive competition.

Obviously parental manipulation of progeny is not restricted to physical coercion or pheromonal control. It means chiefly that parents with one kind of offspring outreproduce those with another. Whether the offspring are selfish or altruistic, and the exact manner in which they are caused to be selfish or altruistic, is another problem. A good example with which to illustrate these points is the paper wasp,

Polistes fuscatus (68), often considered to represent an intermediate stage in the evolution of sociality in insects because founding females are facultatively sterile. One reason for its illustrative value is that founding females, which sometimes cooperate and may (frequently or always) be siblings, begin reproduction long after their mother's death.

Queens of *P. fuscatus* begin nests in spring, build up a population of workers during the summer, and in fall produce new queens and males. The new queens both mate and overwinter apart from the old nest site. In spring they found nests singly or in groups. When they found nests in groups only one queen lays, the others serving as workers for her even though they too are fertilized. West-Eberhard considered that the individual subordinates may gain genetically by cooperating to help their most fit sister, but at least two potentially alternative explanations exist and have not previously been discussed.

First, subordinate females may get to take over the nest (because the original queen is somehow lost) often enough before the reproductive brood is produced. (Production of queen daughters only near the end of summer after producing solely diploid worker females also raises interesting questions about the fate of sperm provided by different males.) Second, queens may gain by producing daughters that sometimes cooperate at the individual expense of all but the dominant, actual queen and thus build fewer nests more swiftly. Obviously the old queen need not be present at nest-founding for this altruistic tendency to evolve. Whether such altruism evolves depends solely on whether the parents carrying the genes responsible for it outreproduce. This outcome in turn will depend chiefly on two things: 1. Is it more reproductive to build fewer nests more swiftly? or 2. Is there a high likelihood that subordinates will accidentally direct their altruism at nonsiblings? If new queens tend to return to the old nest site to start nests, altruism may rarely be misdirected. If they generally nest in new sites the possibility for error may be increased. A testable difference in predictions is thus provided between the behavior of individuals either of the same species or of different species with different dispersing tendencies; unfortunately, without consistent differences in inbreeding coefficients or number of matings per queen between populations it will not help us in this case to distinguish between kin selection and parental manipulation.

We may ask, finally, why the sterility of subordinate *Polistes* queens remains facultative. If the old queen is really producing, in effect, a brood of queens and workers, why not obligate sterility? Three categories of environmental uncertainty may combine to help explain this situation: 1. varying queen mortality or incapacity before production of the sexual brood in autumn, 2. varying availability of nest sites, and 3. varying likelihood of siblings reliably nesting together without interlopers. Sometimes, apparently, the queen gains if all her surviving daughters found nests alone.

PARENTAL MANIPULATION AND INFANTICIDE IN HUMAN SOCIETIES

Among vertebrates, at least, humans are parental manipulators par excellence. Their parental investment is enormous, and their generational overlap is extreme. Except

for the particular eusocial insects in which new queens are never without workers, humans may be unique among all organisms in that under normal circumstances a human offspring is never entirely without parental care, even if it has itself become a grandparent; even if its parents are dead, it will only rarely be without some direct benefits of parental care since heritable resources include land, wealth, and privileges of many sorts. This multigenerational extension of parenthood has enormous significance in many regards—for example, in complicating the effects of sex ratio selection. Since there is no obvious time at which parental care terminates, Fisher's (53) argument that differential mortality past termination of parental care will not affect primary sex ratios is difficult to apply. Here I chiefly discuss one example of possible parental manipulation in humans: infanticide.

The killing, and sometimes cannibalism, of human babies has been a widespread practice and is still frequent in many parts of the world. Four contexts of infanticide are particularly interesting in connection with parental manipulation of offspring: twinning, closely spaced babies, babies arriving during harsh times such as severe droughts, and sex-preferential infanticide.

First, in the case of twins, one or both may be killed. Data from the Human Relations Area File indicate that in over 50% of 160 societies for which there are data on treatment of twins, one or both of the twins have characteristically been either killed or neglected and left to die (difficulties of interpretation and dubious interpretations make it difficult to give exact numbers). Second, babies born during lactation are in many cases killed or aborted. Chagnon (33) cites such cases from his studies of the Yanomamö Indians of South America, and he includes the fact that in one case the mother stated that it was done to protect the two-year-old child she was still nursing. Third, babies born during famines or droughts are often killed, with perhaps the most notable cases reported from the deserts of Australia, where aboriginal babies were said to be regularly killed during droughts and also regularly eaten or fed to other siblings (17, 18).

These three kinds of infanticide suggest that man's rate of offspring production has been selected downward from its current physiological maximum (meaning the maximum rate at which females can actually produce babies). When they are considered together with post-partum sex taboos that frequently coincide roughly or precisely with lactation, and with the post-partum inhibition of ovulation that has been demonstrated to be extended by lactation (55), our confidence in this conclusion is greatly strengthened, despite the essentially universal argument that the significant effect is population regulation, therefore a reduced rate of actual increase (e.g. 46, 47, 116, 118, 127). In the above senses, then, human parents have evidently been sacrificing or using part of their offspring to increase their reproduction via others. Furthermore, they have been doing so by cultural practices. In this case, and as it turns out in many others as well, it is difficult to deny the correlation between the physiological and the cultural phenomenon, suggesting that man's cultural history and his reproductive history are by no means independent of one another.

Indeed, we may be able to use such physiological indicators to determine the degree to which cultural practices represent maximizers of reproduction in the

environment in which man has been evolving. To the extent that it can be demon-strated that infanticide, abortion, and coital taboos were actually employed in the interests of the groups for the purpose of population control, the notion can be refuted that man is bound to his biological reproductive history. To the extent that such behaviors were significant in serving the interests of individuals or families, that is, in increasing their reproduction at the expense of the remaining individuals or families in the group, they suggest a close correlation between the history of repro-ductive success of individuals and families and the nature of cultural practices.

The fourth category of infanticide that I mention is sex-preferential infanticide, a widely reported phenomenon (13, 15, 32, 123; and many others). If infanticide tends to increase the reproduction of its practitioners, how can tendencies to destroy more of one or the other sex enhance this effect? Killing of a newborn baby returns the mother both behaviorally and physiologically to reproductive condition as much as 1–3 years sooner. Such effects may partly account for the tendency to kill infants by male langurs that have just taken over a troop (111, 151); they may also account for male chimpanzees attacking a new female and killing her infant offspring, presumably conceived by a male in a foreign group from which she had come (30).

Offspring of one or the other sex may vary in reproductive value simply because of local variations in sex ratio, sometimes themselves stemming from variable effects of cultural practices such as wars. Variations in the value of the two sexes may also occur as a result of other considerations. For example, most human societies allow polygynous units, and even if they do not they develop polygynous breeding systems, meaning that fewer men than women contribute to each generation of offspring. It follows that the reproductive variance among men is increased over that of women (see also 156). As many as one fourth of the mature men may lack mates (33, 34, 108). The powerful men not only secure the most women, but their sons are also favored. In one case of 61 men in four villages of Yanomamö Indians (104) four men had 41, 42, 46, and 62 grandchildren, respectively, while no female had more than 31 grandchildren. Moreover, two of the four men were sons of the other two.

Under such circumstances advantage is generally gained from emphasizing one's male ancestors, and we are led to a comparison with domestic animals. Animal breeders not only pay many times more for males because they will sire the offspring of many females, but they trace lineages through the male side as well, often completely ignoring the female side. Furthermore, a breeder often pays as much as he does for a female simply because he might obtain from her a valuable son. Breeders with top-grade stock are pleased to obtain male offspring because of their potentially great value; breeders with relatively low-grade stock on the other hand prefer female offspring because low-quality males are worthless as breeding stock. When these considerations are applied to polygynous human societies they generate among others the obvious prediction that female-preferential infanticide is more likely among women married to high-ranking men and less likely among women married to low-ranking men or not legitimately married at all. Unfortunately, the published data generally fail to deal with variations within societies, partly because of the levels at which culture has generally been supposed to function and partly because the kinds of questions raised here have rarely been posed. As a result recent

eliminations or reductions of infanticide may have rendered these predictions untestable. (All of these predictions will obviously be enormously complicated by local or temporary variations in the usefulness of sex-influenced altruistic roles such as able-bodied hunters or warriors, or women to carry out household chores.) (See also 159.)

A last prediction for polygynous societies is that infanticide will more often be practiced on first babies when they are daughters. Broods of offspring in polygynous societies benefit greatly by the presence of an oldest son: he may both protect his younger sisters and arrange their marriages; he may pass extra wives to his younger brothers before they are able to secure and hold them on their own (33); and he may through primogeniture function as the agent of his parents' interests. Female-preferential infanticide of first babies in such societies is well known, and a remarkable correlation exists in the documentation of significant male bias in first babies and in the babies of very young mothers (120, 128, 149). Again, physiology and culture appear to coincide, suggesting a close relationship between man's reproductive history and his cultural practices.

PARENTAL MANIPULATION AND THE EVOLUTION OF MENOPAUSE

An additional question relating to parental manipulation of offspring in polygynous societies concerns the evolution of menopause. It is reasonable to suppose that menopause evolved because women were repeatedly achieving ages at which it became more profitable for them to tend the offspring they had already produced than to add more. (This argument holds even if part of the reason for the change should be some kind of irreducible increase in likelihood of malformed offspring from "old" eggs. The widespread assumption that menopause is only a matter of exhaustion of egg supply is evolutionarily untenable unless one assumes that during human history no significant proportions of women were achieving menopause age. The other widespread assumption that disappearance of reproductive ability assists the population because it reduces the likelihood of malformed babies is also unsupportable because of the necessity of invoking altruism, as noted earlier.)

There is a possible intriguing reinforcer to the above hypothesis. To the extent that human mothers are able to influence significantly the mating success of their offspring (for example, if by political maneuvering they are able to increase materially the likelihood of their sons entering the breeding population), then women of menopause age in polygynous societies may become capable of adjusting their reproduction along a scale of variance approaching that of the men, and in a fashion not available to them at earlier ages. This effect on numbers and quality of grandchildren places an enormous premium on a shift in the nature of reproductive effort by middle-aged females. An expected correlate is unusually prominent hierarchies among older females in highly polygynous societies, in which a male's rank and mating success correlate significantly with his mother's rank. Such correlations are known in some polygynous primate societies, particularly, as one would predict, those in which paternity is uncertain and paternal behavior is minimal (thus, those

living in multi-male bands) (80, 81, 85, 140). If true equivalents of menopause have indeed evolved in primates, they are most likely in such societies.

Similarly, in elephants, in which nonbreeding old females may be common (96), the value of the old female to her descendants as a repository of environmental information (Eisenberg, personal communication) could cause her reproductive success to be enhanced by eliminating the risk associated with further production of offspring. Note that the preceding discussions suggest how either patrilinearity or matrilinearity might come to be emphasized within polygynous human societies, with interactions between confidence of paternity and power differentials among males the chief significant variables. This fact is relevant to the efforts of anthropologists (leading to confusion and disagreement—e.g. 100, 132) to correlate the importance of the avunculate (mother's brother) with patrilinearity or matrilinearity; the above remarks suggest that it may predictably correlate with either.

PARENTAL MANIPULATION AND POLYANDRY

Polyandry in humans, as a consistent marriage system, involves correlates that make it potentially interesting in the context of parental manipulation of progeny and of kin selection. Although rare, polyandry is prevalent or the rule in a number of Asian peoples (19, 56, 123, 129, 142). The two major systems are: 1. brother-husbands of single wives (or wives fewer in number than husbands) with inheritance, lineage tracing, and place of residence generally relating to husbands, and 2. unrelated husbands of a single wife with property and lineage and residence usually relating to the wife. The first case is more strictly polyandrous, much more prevalent, and more interesting to the question at issue here. The second situation may actually yield a polygynous breeding system if men are sufficiently free to attend different females; this system seems more closely related to a polygynous history with minimal male parental behavior. A similar division may account for some difficulties in interpreting polyandry among birds; for example, compare fraternal polyandry in Tasmanian native hens (106) and nonfraternal polyandry in tinamous (91, 125) and jacanas (78; Jenni, personal communication).

Some reported correlates of fraternal polyandry in various groups of humans are: 1. a history of female infanticide (123), 2. sex ratios unbalanced in favor of men (apparently even in the absence of female infanticide) (e.g. 19, 142), 3. early marriages arranged by the parents (early teens or even sooner), 4. eldest son with first rights to both property and wife (56), 5. consignment of "extra" offspring to religious careers, often as celibates (56), and 6. subsistence agriculture with all arable land divided in family holdings so small as to "barely suffice to support a conjugal group" (102, p. 183). (In some societies in which the peasants live in this fashion, more well-to-do men are monogamous and wealthy men are polygynous.)

Polyandry in such societies is easily related to the low *and* reliable productivity of farms, with the result that additional labor without additional children (thus, more than a single male per family) has come to be the best route to long-term maximization of reproduction because of the necessity of retaining the minimal acceptable plot of land (see also 97); this argument is not contradicted because the

necessity, in some cases, of paying taxes to lords to an extent favors larger land holdings (56). That the "hired hand" is generally a brother (or brothers) and that limited access to the wife of the older male (even, sometimes, the father when a wife dies early) has become part of the inducement to cooperativeness in parental behavior, is obviously commensurate with predictions from kin selection and parental manipulation. In this sense cooperation by brother-husbands can be viewed as a reduction in reproductive rate accompanying increased parental investment, in effect by the grandparents. Although data on primary and secondary sex ratios are not entirely satisfactory (see above references), if the occasional reported heavy bias in favor of males ($\sim$ 125: 100) in populations as a whole is reflected at birth, support is generated for the notion that effective parental care (and thus manipulation) extends through much of each individual's life, and, as Trivers & Willard (159) have put it, when altruism is directed toward siblings parents may be selected to invest more than 50% of their resources in producing offspring of the more altruistic sex.

Such differential investment can result from cultural practices (e.g. infanticide) as well as physiological tendencies. Such circumstances may better account for the behavior of some birds such as the Tasmanian native hen than the combination of kin selection and a meiotic-drive-induced sex ratio distortion proposed by Maynard Smith & Ridpath (106). In effect a parent may dramatically increase the parental care available to its grandchildren by adding parents in the form of nonbreeding offspring. A parallel circumstance may exist in jays and other group-living birds with helpers at the nest (27, 28) and in packs of canines dependent upon large game (94, 95, 107, 144) in which frequently only one or two females breed while numerous individuals (older offspring? siblings?) share in parental duties. Schaller's (144) reports of disproportionate numbers of males in Serengeti hunting dogs, and an apparently disproportionate number of nearly all-male litters is relevant, since more than two adults tend each litter (see also 107). Essential and still unanswered questions for these hypotheses are the extents to which offspring presumed to be altruistic are 1. actually helping siblings and 2. still receiving parental benefits.

NEPOTISM AND THE REPRODUCTIVE HISTORY OF HUMANS

Although human societies are groups of variously related individuals within which genetic relationships are universally rather well understood, a more or less general rejection by social scientists of the idea that nepotism is related to the reproductive history of humans has stifled attention to the correlations between genetic relationship and likelihood of altruism. Nevertheless, some correlations are so appropriate, once breeding systems and other necessary modifiers are taken into account (5, 6), that it seems astonishing that social scientists, impressed with the extraordinary knowledge of kinship details in all societies, did not develop and apply the theory of inclusive fitness before the biologists did so.

Two examples may be useful here. First, it is commonly argued that the frequent use of the term "sibling" for cousins as well as for true siblings, and the widespread asymmetry of marriage rules allowing (or even favoring) cross-cousin marriages, while forbidding parallel-cousin marriages, indicates discordance with the idea that

kinship systems and incest avoidance are related to reproductive history (e.g. 99, pp. 280–81). Cross and parallel cousins, it is pointed out, are similarly related, and neither should represent greater inbreeding. This is true in monogamous societies with excellent records and great fidelity among wives. But most societies have permitted polygynous marriages, and in such marriages: 1. sororal polygyny (sister-wives), and responsibility for a brother's wife and family if he dies or is incapacitated, are common and 2. older successful men often secure "extra" wives and pass them to younger brothers before the latter could secure and hold them on their own (e.g. 33, 103). Both of these phenomena, in themselves, obviously accord with the concepts of kin selection and evolved nepotism. Further, in the circumstances just described, parallel cousins, but not cross cousins, may indeed be (half) siblings and not cousins at all; as a result this particular asymmetry in marriage rules, despite numerous disclaimers in the literature, must be re-examined as potentially related historically to incest avoidance.

Similarly, the phenomenon of "mother's brother" (132) as the adult male responsible in certain ways for some children is at least sometimes prominent in polygynous societies in which confidence of paternity is quite low. Low confidence of paternity may result from (for example) living arrangements; as an extreme case, wives may live separately from their husbands, and as groups of sisters within houses, with each male allowed only visiting privileges and only one wife per house. Genetically speaking, a man's sister's offspring are on the average 1/8–1/4 like him; only by a remote accident of meiosis or an almost equally remote (in nontechnological societies) mistake in maternity can they be totally unlike him. His spouse's offspring, on the other hand, may be 1/2 like him or (depending on her fidelity) totally unlike him. As confidence of paternity diminishes, therefore, a man's sister's offspring become relatively more important to his reproduction, and a woman's brother becomes a more likely candidate for parental behavior for her offspring that may otherwise suffer from a lack of paternal assistance. Indeed, a man's sister's offspring, because of the high confidence of maternity, will be his closest relatives in the next generation whenever confidence of paternity is very low. Thus, if paternity is correctly ascertained only 1/4 of the time, then a man's spouse's offspring will average 1/8 like him (and 3 of 4 will be totally unlike him), while his sister's offspring will average 5/32 like him, and all will approach this degree of overlap. The behavioral (selective) outcome of the persistence of this situation will not be easy to assess, since the frequent lack of genetic overlap between a man and his spouse's offspring will place a premium on accurate assessment of likelihood of paternity by analysis of the phenotypic attributes of the spouse's offspring. If a man rejects some of his spouse's offspring in such a situation, and is right 3/4 of the time, he increases the average relatedness between himself and his spouse's (accepted) offspring from 1/8 to 3/8. In inbred populations one may not achieve such reliability, but in an outbred, variable population he might be right even more frequently.

These correlations, and many others like them, have never been adequately examined in light of modern social theory; they must be taken into account before a biological background for kinship and breeding systems in humans can be dismissed. Above all, such considerations must not be taken as merely alternative or

adversary to other functions, such as the establishment of alliances or coalitions among families or groups at various levels; nor should such complications be allowed to confuse the effort to unravel the functional basis of kinship and marriage patterns. To avoid being killed out by marrying out (160) (in other words, by establishing mutually beneficial systems of reciprocity) is a biological effect too. What must be understood is that combining the modern concepts of kin selection, reciprocity, and parental manipulation in the analysis of the fabric of human society is not merely the revival of an old argument, refutable from examples and exceptions already used to that purpose, but the application of a new, basic, and comprehensive theory.

WHAT, AFTER ALL, IS SELECTION MAXIMIZING?

Now let us return to a problem repeatedly raised in all of the above examples: How can the significance of fitness shifts be measured or judged? This problem could scarcely be pointed up better than by the difficulty in deciding whether a particular aspect of human culture is increasing or decreasing the reproduction of its bearers. In societies permitting polygyny, wives of polygynous men have fewer babies than wives of monogamous men (26, 46, 114), but they may have many more grandchildren (104, 118). The same is very likely true in at least many cases of those practicing conception control, abortion, infanticide, and post-partum abstinence from coition. Most such behaviors have been interpreted as population-regulating devices, developed and maintained because they help the entire group, as their correlates in other animals were widely interpreted by zoologists until recently (21, 46, 47, 118, 126, 127). How can we determine what is really happening?

There are two major problems in defining a population meaningfully when relative fitnesses of individuals are to be estimated: 1. What is to be measured and when should it be measured? Should we measure numbers of offspring produced, numbers reared, numbers breeding, numbers of grandchildren produced, reared, breeding, etc? 2. How many individuals, and which ones, are to be included in the comparison? How does one decide what constitutes the effective population when he is attempting to measure the effect of a given act or event upon the fitness of an individual? The farther one projects into the future, on the average, the larger will be the group of individuals that must be compared if relative fitnesses are to be meaningful. I suggest that these are the two main aspects of the problem alluded to by Hamilton (63) when he referred to the difficulty of discerning what it is, after all, that selection is maximizing (see also 24, 25, 98, 177). Both questions involve environmental stability, or predictability, and family structure; the evolution of family structure in turn is partly a function of the stability of the environment. Thus the social insect queen who invests totally in sterile workers for what amounts to several generations (e.g. *Polistes*) has evolved a strategy that involves stabilizing the immediate environment (the hive or nest) and reinvesting repeatedly until an optimal time for actual use of some maximized parental investment to produce reproductive descendants. The alternative strategy is to generate the same buildup, without generational overlap and parental control, through descending generations of independent reproductives.

It is in this sense that the eusocial insects parallel the metazoan organism. They may as well be described as a kind of ultimate achievement in what is commonly called "k selection," and the correlate is environmental certainty created in part by the organism itself.

When likelihood of genetic representation in some subsequent generation correlates most closely with ability to retain some heritable resource, such as a superior nest site, cavity, or structure (in eusocial insects), a superior territory (in birds or mammals) or farm (in Tibetan peasants), or even a royal title and the privileges accompanying it, dynasties may best be perpetuated (genetically as well as otherwise) by high investments in small numbers of offspring, including such practices as fraternal polyandry, helpers at the nest, primogeniture, and unbalanced sex ratios within broods.

In the problem of identifying the population that is significant when trying to assess changes in an individual's fitness, one wishes to determine some kind of long-term effect of an act or an event upon an individual's likelihood of having its genes represented, or maximized, at any particular later time that the population is examined. If population structure is simple, with all individuals responding to the environment and to one another similarly (the usual model of population genetics), then the problem is reduced to a measurement of dispersion in relation to interbreeding capacity. The significant population for determining an individual's fitness, or shifts in its fitness, will be that group of potentially interbreeding individuals which will actually interbreed or function as a breeding unit in the span of time prior to the point at which the individual's fitness is to be measured. Thus, if a population is more or less evenly distributed across a radius of 100 miles and the genes of individuals move approximately one mile per generation, then if one estimates fitness across ten years, the effective population insofar as effects of acts or events upon an individual's fitness are concerned will be a population within a 10 mile radius. Perhaps most of the time we behave as though the effective population, when the distribution of individuals is roughly even, is the entire population; that is, we measure the effect of an act or an event by its result at some point more distant in time than the time required for the effect to spread throughout the population.

Such simple situations are unlikely to prevail in any species. They are chiefly complicated by two phenomena: 1. partial or complete barriers to dispersal within the range of a population of potentially interbreeding individuals, and 2. social behavior, including, in particular, family structure.

The effects of dispersal barriers may be understood if one considers first an essentially complete barrier that prevents for an indefinitely long time the passage of genes throughout the entire "population." Obviously, in considering fitness shifts one will no longer wish to consider that part of the population beyond the barrier as a set of individuals to be compared with the individuals in question. Now it can be seen that any barrier of a less permanent nature than the one just postulated will create really complex problems.

One of the relevant effects of social behavior is that it tends to create barriers to dispersal, or to gene flow, of just the intermediate sorts that cause the greatest difficulty. The second relevant effect is that individuals will tend as a result of

evolution to respond differentially to one another, depending upon their degree of genetic relatedness or overlap.

To understand the extent to which dispersal and social behavior complicate the problem of assessing effects upon fitness, consider a social group containing several breeding units (families), variously related to one another at the outset. This group of families functions as a single social unit, cooperating in some fashion, having little interaction (except perhaps of a hostile nature) with other such groups, and inter-breeding only infrequently with other such groups. We realize that fitness shifts among individuals in the population of such groups of family units can be measured within: 1. whatever is generally considered to be the entire species, or entire set of potentially interbreeding populations, 2. any "local" population composed of several or many groups of breeding units, 3. the individuals of the particular group of family units in which the event or act has taken place, or 4. family units. In the long run the first or second measure may be the most important. But degree of relatedness and intensity of reproductive competition both diminish more or less gradually with increasing distance from any selected individual within a reasonably viscous population, and we have not acquired the kinds of demographic data that will tell us, in any general sense, how to determine the limits of the effective units of evolution in natural populations. The significance of this problem can scarcely be exemplified better than by a point made earlier—that if degrees of relatedness and intensity of competition among individuals diminish together in certain, not unlikely fashions with distance from any given individual in a population, then nepotism cannot evolve.

CONCLUDING REMARKS

I began with a denial of any great significance for the phenomenon of group selection. It is appropriate, perhaps, to finish with a caveat. For two reasons human social groups represent an almost ideal model for potent selection at the group level. First, the human species is (and possibly always has been) composed of competing and essentially hostile groups that frequently have not only behaved toward one another in the manner of different species, but also have been able quickly to develop enormous differences in reproductive and competitive ability because of cultural innovation and its cumulative effects. Second, human groups are uniquely able to plan and act as units, to look ahead and purposely carry out actions designed to sustain the group and improve its competitive position. These features may actually represent an exhaustive list of the precise attributes of a species that would maximize its likelihood of significant group selection, or evolution by differential extinction of groups. Thus group selection involves the paradox that competing populations must be sufficiently isolated to become different in ways that may lead to their differential extinction yet close enough together that they can replace one another. This condition is obviously fulfilled with sympatric competing species, which are intrinsically isolated. So, to some extent, are hostile neighboring populations of humans.

It is an important result of the above considerations that in seeking to define the adaptiveness of culture, to analyze directions of cultural change, and to identify

sources of cultural rules, we cannot ignore or downplay effects significant at the group level (e.g. 3, 7, 20, 22, 48, 49, 69, 83, 115). On the other hand existence of group functions does not erase functions at individual and family levels, and therefore does not preclude significant within-group reproductive competition.

It has been the hallmark of psychology and psychiatry (and even of zoological ethology) to seek basic conflict situations in behavioral ontogeny. I suggest that if such conflicts are to be sought, an appropriate focus is on the basic dichotomy between personally or directly selfish (or reproductive) actions and group-sustaining or indirectly selfish actions; for it is combinations of these often conflicting tendencies that will lead their bearers to maximal reproduction in the long run. In human societies there is the additional problem of what motivations one communicates to his fellows, who should view with favor any evidently altruistic actions, including group-sustaining behavior, even if such actions are in reality ultimately selfish to the actor because of their group-maintaining aspects. It is not necessary that an appropriately selfish (i.e. maximally reproductive) individual be aware either of his motivations or of all of the consequences of his actions. Indeed, we frequently exhort our children to be (consciously) unselfish altruists, even though such tendencies would consistently be selected out of human populations, except for one paradoxical and crucial fact—that actions which would otherwise be truly altruistic may increase the reproduction of their bearer if they are viewed as true altruism by his fellows. If it is reasoned that parental exhortations to unselfish altruism have during human history led human progeny to reproductive success, then it might be argued that sincerity represents a valuable social asset even when it derives from a real failure to recognize the reproductively selfish background and effects of one's own behavior.

In other words, in within-group social interactions, selection may have consistently favored tendencies for humans not to be aware of what they are really doing or why they are doing it. In this complex of conflicts, it strikes me, lies a truly basic and difficult set of problems in the analysis of human behavior. Yet to the extent that we continue to deny a relationship between man's reproductive history and his social behavior (and by extension the structure of his culture) we are simultaneously denying to ourselves the possibility of even defining these problems.

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