Chapter 5
Evolutionary Psychology, Altruism, and Kin Selection

Robert C. Richardson

5.1 The Darwinian Background

Charles Darwin famously wrote in the final chapter of *On the Origin of Species* that the theory of the *Origin* would "open fields for far more important researches. Psychology will be based on a new foundation, that of the necessary acquirement of each mental power and capacity by gradation. Light will be thrown on the origin of man and his history" (Darwin 1859, p. 488). This was his only mention of human evolution in the *Origin*. It is natural to think, as many have, that he meant that *natural selection* would shed light on "the origin of man and his history" and put psychology on a "new foundation." However, that would be wrong. The context for the remark is a discussion of common descent, which meant descent from a common ancestor, and the mutability of species. Darwin sees that embracing "common descent"—one of his more radical departures from his evolutionary predecessors, such as Lamarck and Geoffroy—will result in "a considerable revolution in natural history." In this context, neither natural selection nor sexual selection is even mentioned. He presses, e.g., that living things have much in common "in their chemical composition, their germinal vesicles, their cellular structure, and their laws of growth" (Darwin 1859, p. 484), inferring from this that they all have a common ancestor. This was important to Darwin. He was very conscious that adaptation and, thus, natural selection could disguise common descent rather than reveal it. He knew that selection could yield evolutionary convergence. Indeed, that is the point to thinking about convergence as a mark of adaptation, though Darwin was also conscious that such convergence is imperfect. When natural selection is at work, it is capable of producing the same, or nearly the same, structure in quite different organisms, quite apart from issues of common descent. Wings of bats and birds are a typical example (though both are forelimbs). It is, Darwin thought, *homologies* rather than *analogies*

R. C. Richardson (✉)
Department of Philosophy, University of Cincinnati, Cincinnati, (OH), USA
e-mail: robert.richardson@uc.edu

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that reflect common descent. The forelimbs of bats and birds exhibit parallel bone structures, even though the adaptations that make them effective wings are quite different. So in pressing for common descent, he does not emphasize natural selection, though he never doubts its significance.

In opening his discussion in the *Descent of Man*, some 12 years after the *Origin,* Darwin returned to the topic of *human* evolution:

> He who wishes to decide whether man is the modified descendant of some pre-existing form, would probably first enquire *whether man varies*, however slightly, in bodily structure and in mental faculties; and if so, *whether the variations are transmitted* to his offspring in accordance with the laws which prevail with the lower animals; such as that of the transmission of characters to the same age or sex. Again, are the variations the result, as far as our ignorance permits us to judge, of the same general causes, and are they governed by the same general laws, as in the case of other organisms? (Darwin 1871, p. 9)

Notice that the reference here is to evolution, or descent, and not to natural selection. Also, natural selection (but not sexual selection) plays a much less prominent role in *Descent* as opposed to *Origin.* There is appeal to variations and to inheritance and to the "laws" governing each of them, which includes the "mental faculties," but there is not a hint of competition or the "struggle for existence," much less of natural selection. In *Descent,* he initially recapitulates the argument for common descent from *Origin,* extending it to what he calls the "mental faculties" of man, saying at the outset of Chap. II that his object "is solely to show that there is no fundamental difference between man and the higher mammals in their mental faculties" (Darwin 1871, p. 35).

Darwin is clear that this commitment to evolution is meant to include what he calls the "moral sense." This was crucial for Darwin. It meant, among other things, that our capacities for social interaction were meant to be within the purview of his evolutionary theory. For Darwin, sympathy is not the whole story behind our moral capacities or our social capacities, but it is nevertheless essential for it. Much like David Hume, he thinks that without sympathy, the rest of our moral capacities would have no traction. He therefore conjectures that an animal with "social instincts" would almost certainly acquire something like a developed "moral sense," given even a modicum of intelligence (even though it is not clear to me how he thinks this to be a natural development). The additional capacities that are gained with the acquisition of linguistic skills, he thought, would enhance their responsiveness to social pressures. All of this, though, is laid on the foundation of our natural sympathies, our social responsiveness.

Darwin was not the first to bring evolutionary insights to the discussion of our social sentiments and reasoning, and he was not the last either. Herbert Spencer had placed his discussion of psychology in an explicitly evolutionary setting; William James' psychology is inspired by Darwinian insights, as were many other important psychologists at the turn of the century. There have been other ventures into the evolution of human psychology that are in retrospect less well regarded (be it deservedly or not), such as Desmond Morris' *The Naked Ape* (Morris 1967). With the elaboration of models designed to capture social behavior in the middle of the last century, sociobiology took up the task of capturing animal behavior in evolutionary terms and, almost as an appendix, extended that project to the domain of human social behavior. It is clear that E. O. Wilson thought that human social behavior was, after all, just another form of social behavior (Wilson 1975). He was right. It is also clear that for Wilson, this was initially an afterthought, almost like an appendix to a comprehensive work on social behavior. Work in evolutionary psychology (EP) is the most recent variation in taking up the Darwinian idea that evolution should shed light on human psychology. Unlike Wilson, however, this work is almost exclusively concerned with the human case.

5.2 The Program of Evolutionary Psychology

Contemporary EP is not a homogeneous collection of views, even with respect to its evolutionary commitments, though it is possible to articulate a loose set of claims that are broadly endorsed and typical of contemporary adherents (cf. Barkow et al. 1992; Buss 1995, 2005). In large parts, these commitments are consistent with evolutionary theory as it was articulated during the "evolutionary synthesis" years in the first half of the twentieth century, updated by evolutionary models from the 1960s. Not every advocate of EP is committed to precisely the same set of claims, but it is possible to provide a rough portrait of research interests, which include a number of familiar themes:

- *Psychological mechanisms are the result of natural selection and sexual selection.* While it is generally acknowledged that some outcomes of evolution are due to chance or by-products of selection for other traits, the focus of EP is on traits that are subject to selection, e.g., finding a mate, cooperative activities like hunting, or the raising of offspring. The assumption is that natural selection will tend to efficiently "solve" problems like these. The tendency is to offer only selectionist models without including possible alternatives. In terms of attractiveness, for example, there is a widely touted view about a certain female waist to hip ratio which is supposedly attractive to males, as it is thought to be connected to female fertility; thus, male attraction is "explained" as an adaptation which enhances male fertility.
- *Psychological mechanisms can be thought of as computational mechanisms.* Among psychological mechanisms are narrowly cognitive processes (e.g., probabilistic reasoning or problem solving) and emotional responses (e.g., jealousy or fear). The idea that psychological mechanisms are computational is an assumption common among a range of cognitive scientists, though its prevalence has faded considerably in the last decade. Alternatively, these computational mechanisms can be thought of as exhibited in and causing behavioral *strategies* that respond to environmental challenges. In either case, the psychological mechanisms are supposed to identify risks and benefits of the environment, e.g., strangers pose a risk, thus a fear of strangers is thought to be an evolutionarily favored strategy. Likewise, cooperation within a group, as in sharing of food, tends to enhance fitness over the longer run, therefore being an evolutionarily favored strategy as well.

- *Psychological mechanisms evolved in response to relatively stable features of ancestral environments.* This ancestral environment is often referred to as the environment of evolutionary adaptedness (EEA). EP asserts that most of human evolution took part during the Pleistocene (roughly 2.6 million to 12 thousand years ago), and presumably in the later Pleistocene. Some more ancient adaptations are fundamentally primate, while others are more specifically human. We thus share more ancient adaptations with our primate kin, while more recent adaptions are specifically human. Often, the EEA is identified with the savanna of the African Pleistocene and with a hunter-gatherer lifestyle. Sometimes, the EEA is also identified with a kind of statistical aggregate of the total range of ancestral environments. It is unclear what exactly a statistical aggregate in this case might mean and it is even more unclear how this might play out in an evolutionary scenario.
- *Since psychological mechanisms are adaptations to ancestral environments, there is no reason to assume that they are adaptive in contemporary circumstances.* Social environments are a significant part of the environment and are obviously crucial to human evolution. If we assume within the approach of EP that our ancestral social environment consisted of small, nomadic bands of relatives, then the difference between that and our contemporary culture suggests that whatever strategies were adaptive for our ancestors may not be so for us. Likewise, if we assume that our distant ancestors lived in a sugar-deprived environment, then our fondness for sweets might be “natural,” though no longer adaptive. In general, EP assumes that evolutionary responses are too slow to have had any significant effect in the last 12,000 years, the earlier advent of agriculture and sedentary life. The picture is clear enough. We are adapted for a life in relatively small groups and at least some human adaptations are selected for their usefulness in these small groups.
- *The human mind is a kind of mosaic of mechanisms, each with some specific adaptive function, rather than merely a general purpose learning machine.* Different adaptive problems will require different solutions, or different strategies, in order to be able to deal with them. So, e.g., a mechanism for mate selection, for example, is unlikely to be of much use in foraging. At least some of this machinery must be domain specific, specialized for particular tasks. Some of these may count intuitively as *instincts*. Some advocates of EP treat these mechanisms as *modules,* though others insist that all that is required is distinct domain-specific mechanisms.

5.3 Psychological Evidence

Evolutionary psychologists make use of an array of techniques to evaluate their psychological models, most of which do not specifically depend on the evolutionary assumptions. These methods include the use of questionnaires, controlled experiments, observational methods, and brain imaging, among others. They also make use of a variety of less standardized techniques, including ethnographic records, paleontological information, and life history data. As one would expect, the specific methods and the evidence obtained through them, are sometimes contested; however, this does not seem to be the place to enter into these psychological disputes (cf. Buller 2005; for an in-depth exploration of the psychological issues). Reliance on a broad array of evidence would seem, *prima facie,* to be an epistemic virtue. Evolutionary assumptions are used to advance and formulate hypotheses. Whether they are more than *merely* heuristic is sometimes not clear.

Evolutionary psychologists have articulated and tested a wide array of psychological hypotheses inspired by evolutionary thinking. These include our propensity for aspects such as cooperation, cheater detection, differences in spatial memory, short-term mating preferences, and many others. Some simple examples may be sufficient to illustrate the method. Assume that human memory will be sensitive to items that affected fitness among our ancestors. This might include food items, shelter, or possible mates. The standard memory probes in nineteenth- and twentieth-century psychology relied on random lists, often terms or signs without meaning, to test recall. Using standard memory probes in a test on recall and recognition for lists of words, James Nairne and his collaborators found that recall for survival-oriented terms was significantly better than recall for more neutral words. This suggests that recall and recognition are affected by their felicity towards fitness. Similarly, theories of parental investment, prevalent among sociobiologists and evolutionary psychologists (see Trivers 1974), suggest that females will tend to prefer mates that are more likely to invest in offspring. Males and females also differ in the pattern of jealousy, with females being more sensitive to emotional infidelity (as a risk of abandonment) and males more sensitive to actual sexual infidelity (as a risk to paternity). I do not propose to focus too much on these findings, but to see them as insightful examples on second-generation advantages to fitness. Females are concerned with the fitness of their offspring rather than merely the quantity of offspring, whereas males are more concerned with whether a partner's offspring is his offspring. The predictions obviously concern only average differences: both cues may trigger jealousy, but males and females should differ in their sensitivity to the various cues. These predictions have been supported by straightforward evaluations of preferences using questionnaires, spontaneous recall, and fMRI (functional magnetic resonance imaging).

One of the most striking and prominent examples concerning human judgment focuses on what is known as the "Wason task," a standard tool used by psychologists to study reasoning about conditionals. The initial test was developed by the psychologist Peter Wason in the 1960s, and was subsequently elaborated in conjunction with P. N. Johnson-Laird. The format is familiar and simple. Subjects are given simple conditional rules of the form *If P, then Q,* and are provided four cards with different information. The available values are *P, not-P, Q*, and *not-Q.* The hidden side can contain any of these values as well. The experimental subjects are then asked which of the four cards would need to be turned over in order to be sure that the four cards conform to the generalization. With a formal problem and a variety of informal variants, subjects regularly fail to exhibit the required choices, most often picking *P* and *Q,* despite the fact that the *Q* card is irrelevant; moreover, the *not-Q* card is rarely picked even though it is directly relevant to the task. Falsification is not recognized as immediately relevant. Descriptive and strictly formal rules tend to elicit this "failure" of rationality. It turns out that some variations of this task are considerably easier for subjects to solve, though they are in fact superficially more complicated. More specifically, when the conditional rules explain what is permissible or forbidden, the subjects can systematically elicit more appropriate choices. For example, suppose that subjects are given the rule "If they are drinking beer, they must be 21," and four individuals, one clearly over 21, one under, one drinking Coke, and one drinking beer. The task is to determine whether any of these individuals is violating the rule. Typically, subjects have little difficulty in realizing that they need to check what the person under 21 is drinking, and whether the person drinking beer is 21; they are not inclined to check the one who is clearly 21. The problem is formally identical to the more abstract problem above, but leads to a very different performance.[1]

Cosmides and Tooby (1992) suggest that the differences in performance, despite the formal identity of the problems, are best explained by appealing to *ecological rationality,* a view supported by Gigerenzer and Hug (1992). Within the concept of *ecological rationality,* the human mind has a variety of domain-specific mechanisms governing our inferences that were adaptive in the EEA. When applied to an appropriate content domain, they are both efficient and reliable, yielding the "normatively appropriate" choices. In particular, Cosmides and Tooby (1992) claim that reasoning about social exchange can explain at least a large part of the differences on the Wason selection task, which basically depend on task demands. Social exchange is of course an important part of human social life, and presumably has been so for our hominid ancestors as well. What Cosmides and Tooby call "social contracts" encompasses rules expressing the contingencies of accepting a benefit on some identifiable requirement. In cases of social exchange, reciprocity or status is important, and as a consequence it is advantageous to be able to detect cheaters. There should, in other words, be a "cheater detection algorithm," naturally mobilized in the face of social obligations. It is not necessary here to go into the controversies regarding the psychological data. What is important, however, is that the hypothesis of a cheater detection algorithm is suggested based on a theory of reciprocal altruism, and that the corresponding social contract theory captures significant patterns in the behavioral data. Whether the evolutionary background is supposed to provide additional credentials to the psychological model is not clear in this case. Perhaps the psychological evidence alone would suffice. In other cases, the evolutionary models play a more central role.

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[1] This is not true, though it's often touted as true. It is clear that *deontic* contexts concerned with obligation and permission are logically much more nuanced and complex. These issues are contested. What this means for human performance is unclear.

5.4 Evolutionary Models for Altruism

Relying on work in paleoanthropology and ethnography relating especially to contemporary hunter-gatherers, evolutionary psychologists have elaborated a plausible portrait of ancestral social life (which is however controversial among anthropologists). In the typical case, EP assumes that ancestral hominids lived in relatively compact groups of no more than one hundred. These groups were kin-based and characterized by a sexual division of labor, with males more engaged in hunting and females more engaged with gathering, stable male–female bonds with long periods of biparental care, and cooperative foraging. In addition, much is known about the physical environment. We know, for example, that they were subject to a variety of predators and pathogens and had to deal with a considerable variance in resources. We also know that the range of environments within which ancestral hominids lived and died was quite variable.

This knowledge allows EP to construct a variety of evolutionary scenarios. Depending on the case, they use a variety of resources from evolutionary biology, including theoretical models concerning reciprocal altruism, parental investment, kin selection, and evolutionary game theory. Beginning with the relevant dimensions assumed to be typical in the EEA, evolutionary psychologists construct an account of the adaptive functions that must be satisfied. These can be thought of as a kind of design specification. The psychological task is then to reverse engineer a solution to the adaptive problem. In some crucial cases, the "problem" is the evolutionary source of altruistic tendencies. This is the modern analogue for Darwin's interest in the social instincts such as empathy.

An evolutionary emphasis can lead to problems, especially if the "adaptive problem" is not clear. If the adaptive problem is underspecified, then there are issues over whether the evolutionary solution really is the right one. Underspecification will inevitably lead to underdetermination. It also raises issues for connecting the psychological hypotheses and the evolutionary interpretations. As this concerns a centerpiece of EP relevant to evolutionary biology, and as similar issues affect the use of other evolutionary models within EP, it is worth illustrating in more detail. The following case is built on one of the seminal accomplishments of twentieth-century biology and contains a considerable amount of anthropological evidence and is therefore often appealed to by advocates of EP.

One of the seminal figures in the rise of Darwinism in the mid twentieth century was W. D. Hamilton, who strongly influenced sociobiology and evolutionary psychology. His development of the theory of *inclusive fitness, extended fitness,* or *kin selection* was fundamental to the evolutionary interpretation of a variety of important social phenomena, including not only "altruism" and cooperation, but also selfishness, aggression, and spite. I will focus on altruism, though the extension to other "problems" is very significant as well. The problem is straightforward. We widely observe cooperative behavior: Bats share food; monkeys alert others to predators, even though that draws attention to themselves. Female ants forego reproduction to raise the offspring of their queen. How is this possible in a Darwinian world in which self-interest should be the rule? Hamilton's idea was as simple as it is elegant and developed in exquisite mathematical detail, which will however not be presented here. He essentially proposed a conservative extension of Darwin's insight that variations in fitness, together with inheritance, tend to promote adaptations. In his models, fitness will tend to be optimized over the long run, though we only deal with shorter runs. Darwin originally focused on the individual and the consequences of variations in morphology or behavior for the individual's survival and reproduction. Hamilton extended fitness to include the effects on kin and factored them in organismic fitness. He recognized that it is not *only* the *direct* impact on the individual's fitness that matters for natural selection, but that the *indirect* effects on related individuals also contribute to one's fitness. My overall fitness does not depend exclusively on me, but on my brothers as well, as R. A. Fisher recognized early in the century. Hamilton took this one step further. My fitness does not depend only on me and my offspring but also on the fitness of my brother's offspring. *Inclusive fitness* is just the sum of these various components, suitably weighted by their degree of relatedness to the agent. If b is the benefit a recipient garners from another's behavior, and c is the cost of the behavior to the actor, then Hamilton's rule says that an altruistic behavior with cost c can be favored, provided rb is greater than c, with r being the relatedness coefficient. Thus, I should be willing to consider sacrificing one of my children for two of my brother's. Of course, the benefit may be distributed across a number of individuals (e.g., when an individual emits a warning call), so we need a more generalized rule, which is exactly what Hamilton provided (cf. Hamilton 1964).

When Hamilton originally formulated his account of kin selection, one key problem for evolutionary biologists was the presence of eusociality among the hymenoptera (ants, bees, and wasps). The problem is how sterile castes could possibly evolve when foregoing reproduction should not be favored. We need to explain eusociality in Darwinian terms. The key insight from Hamilton is that asymmetries related to haplodiploid mechanisms of sex determination can facilitate eusociality. Workers are more closely related to their sisters than to their offspring and so kin selection can, under some conditions, make it more advantageous to raise sisters than offspring. Eusociality has arisen numerous times in the hymenoptera as well as in a number of other lineages not characterized by haplodiploidy. This result was seen as a spectacular success for Hamilton's inclusive fitness (cf. Trivers and Hare 1976).

Kin selection and inclusive fitness have become staples for theories in human sociobiology and EP as well as for animal social behavior. They are also staples for evolutionary biology more generally. It is worth noting that, quite recently, evolutionary biologists have raised a number of difficulties in applying kin selection models (cf. Nowak et al. 2010; van Veelen 2010; Gadagkar 2010; Doebeli 2010). The debates arising out of this have been heated (cf. Abbot et al. 2011; Boomsma et al. 2011; Strassman et al. 2011; Ferriere and Michod 2011; Herre and Wcislo 2011; Nowak et al. 2011). These complications do not feature in EP's use of the models, though they are important to contemporary evolutionary biology and should feature in future work by evolutionary psychologists. I do not intend to enter this discussion here and will assume that inclusive fitness theory is on a solid footing (cf. Bourke 2011; for a useful discussion). I have deployed this strategy before (Richardson 2007). Since the use of inclusive fitness assumes the adequacy of the framework, assuming the theory is on a solid footing does not bias my ultimate case. I will suggest that their deployment of the theory is empirically inadequate. I am actually sympathetic with the use of inclusive fitness. But if it should turn out that the critics are right and inclusive fitness cannot even account for the iconic cases, this will hinder rather than help EP.

Let us now turn to a core case, which is a relatively recent application of Hamilton's model that has gained some prominence and that illustrates the use of inclusive fitness within EP. The use of inclusive fitness resembles the application exhibited in Wilson's *On Human Nature* (1978), though with slight variations and amendments. Prohibitions against incest are pervasive features in human cultures. Often, they are cited as cultural universals. Incest is a very interesting case for a social prohibition, since psychological studies show that its disapproval survives even the recognition that it will produce no actual harm. It has been a very significant case for both sociobiologists and evolutionary psychologists. There is a straightforward case against incest from an evolutionary perspective based on the biological costs of inbreeding. It is difficult to assess in detail the implications of inbreeding from a strictly biological perspective, but it is clear that inbreeding does often result in reduced fitness, referred to as *inbreeding depression*. There are different explanations of inbreeding depression. Inbreeding depression is sometimes explained by overdominance, with heterozygote superiority, and sometimes by partial dominance, each with the idea that inbred lines can become fixed for recessive and deleterious alleles. Assuming overdominance, the effects of deleterious alleles are entirely masked; with partial dominance, they are reduced. The former is one important contender and is the one EP appeals to, though either might be mobilized. Assuming recessive alleles are often deleterious, inbreeding would be more likely to couple these deleterious recessives with the consequence of offspring with reduced fitness. Since nearly everyone has some recessives that are likely to be deleterious, incest should lead to reduced fitness among one's offspring. This would be an evolutionary pressure against inbreeding, *which might be called* Fisher's influence: A reduction in my offspring's fitness is a reduction in my own fitness. This much has been recognized, though the exact mechanisms have been disputed for the last century.

The importance of inbreeding depression leads EP advocates to suggest that there is a natural tendency—sometimes a psychological "module"—for incest avoidance. Lieberman, together with Cosmides and Tooby (2003), suggested that humans have a specialized kin recognition system (there are such mechanisms in other mammals) and tries to bring this into line with Hamilton's model for kin selection. They also observe that it could facilitate an avoidance of any deleterious consequences associated with inbreeding depression. The connection to kin selection is indirect. The explanation offered is roughly the following. Aversion to incest, as expressed in incest taboos, encompasses not only oneself but also a negative assessment of third party behavior. This is important, as incest aversion is oriented toward one's own partners, but does not explain or underwrite the more general aversion to incestuous behavior among our kin. The things our relatives do that have a direct impact on their fitness also has an indirect impact on our fitness, given the theory of inclusive fitness. Thus, if incest comes with direct deleterious effects for my relatives, it carries indirect, but nonetheless real, deleterious effects for me. Lieberman et al. (2003) therefore suggest that we should expect a tendency to interfere with sexual unions among close relatives. Since EP assumes our tribe to be composed mostly of relatives, our aversion to incest should extend to them as well. We should have an aversion of incest not only for ourselves but also for our kin. This noticeably neglects the fact that, assuming inbreeding depression, allowing sexual unions among other relatives could actually improve extended fitness. Reducing the fitness of competitors, even relatives, indirectly improves our own since all that matters is *relative* fitness. Further, improving the fitness of some kin, in the presence of other kin, reduces the fitness of those kin and, indirectly, ours. Insofar as this is true, the most one can get is an aversion for ones' own incestuous relations, but not for a competitor's incestuous relations.

The Westermark hypothesis posits a psychological mechanism of the sort Lieberman et al. (2003) predict, suggesting that young children who are raised together develop a sexual disinterest, or even a sexual aversion, to each other. The proper function of this "natural" aversion is to avoid incest, since those who are raised together are most often closely related, or at least would have been in ancestral groups. Lieberman reasonably assumes that co-residence during periods of high parental investment should be a reliable indicator of kinship or at least would have been a reliable indicator in the EEA with small kinship bands. Together with Cosmides and Tooby, Lieberman shows considerable support for the conclusion that duration of co-residence is *psychologically* predictive of sexual avoidance. I do not know of any evidence that this extends to aversion to others' sexual encounters. The evolutionary interpretation above generalizes the aversion to the third person.

Even though this seems to be an attractive view, the evolutionary interpretation is nonetheless problematic. The association cannot be directly tested in ancestral populations, but that is hardly a significant objection. It does fit the patterns of some contemporary "hunter–gatherer" populations, all of which have incest taboos, though with varying scope and severity. It is, of course, true that siblings would typically be associated with one another during childhood; but the proper question is whether those one is typically associated with, once reproductively active, are likely to be siblings, or would have been resident in ancestral groups. This depends on the specific form of social organization that was present in these ancestral groups. We know that our Pleistocene ancestors did not simply have one lifestyle in one region, but lived on the African savannah, in deserts, next to rivers, by oceans, in forests, and even (somewhat later) in the Arctic, employing very different foraging methods, living off diverse diets, with technologies ranging from the simple chopping tools of *Homo habilis* to the rich and sophisticated stone, bone, and antler toolbox of late Pleistocene *Homo sapiens*. There is little reason to think that there was a single form of social structure associated with the full range of human physical environments, or that contemporary "hunter–gatherer" populations exhibit a social structure typical of ancestral groups. It is hard to know whether associations will be limited to siblings or more likely to be with siblings, without a fairly specific account of social organization, including the relative viscosity of the groups and issues such as group size. The application of inclusive fitness theory to the human case depends on knowing what we do not know, assuming without warrant. It is not just a matter of skepticism. It rests on widely accepted and embraced principles.

This concern with the EP model for the evolution of incest avoidance fits with the widely recognized thought among evolutionary biologists that kin selection is more effective within relatively "viscous" populations, i.e., populations that do not involve significant immigration and emigration. This has two underlying theoretical connections. On the one hand, kin selection is more likely to favor altruistic behavior in the presence of kin and social viscosity will tend to increase the number of kin. In this case, one specific concern regards immigration and emigration patterns. In many animal species, there is a tendency for animals to disperse prior to mating, to move away from their familial unit. This clearly has the effect of reducing inbreeding, although there does not seem to be any consensus on whether incest avoidance is particularly significant in supporting dispersal. For example, when male chimpanzees reach reproductive age, they tend to emigrate from the ancestral clan. There is therefore no need for incest aversion, since they move away from their siblings. In order to know how to apply the kin models to ancestral human groups, we would need to know, e.g., whether males and females both remain with the ancestral groups or emigrate. There is some evidence that among early *Homo sapiens,* the males tended to move out of their ancestral groups once they were reproductive, as is the case with chimpanzees. It does not matter whether this is correct. The important point is that without this information, the relevance of the evolutionary models of kin selection to incest aversion is not clear. There are two connections. First, emigration and immigration patterns directly affect the mean relatedness in the group. Mean relatedness impacts directly on the r values involved in inclusive fitness: As relatedness goes down, the corresponding benefit must go up in order to satisfy Hamilton's rule. Likewise, as genetic relatedness goes up, the effect of kin selection may be diluted. Much of this depends on population structure. Here we are in the dark. In addition, emigration and immigration rates are crucial for determining *effective population size*. This is also a key parameter in models of kin selection, rather than simply the size of the local kin group. With relatively low immigration rates, the effective population size increases dramatically. Again we are in the dark.

5.5 Evolutionary Alternatives

The general assumptions above, which form the background for EP, are characteristic for much of the research done in evolutionary biology. However, there is reason to believe that the assumptions are problematic. Recent developments in genetics, evolutionary biology, and in developmental biology suggest that rethinking these assumptions might improve EP considerably, bringing it more in line with more recent evolutionary thinking. Several points can be briefly noted (cf. Bolhuis et al. 2011; Laland and Brown 2011):

- Natural selection and sexual selection are doubtless potent evolutionary forces. There are alterative evolutionary factors that can, and do, affect evolutionary trajectories. EP acknowledges such factors as genetic drift (though it plays no role in their scenarios), but phylogenetic factors play no significant role, such that our primate kin do not typically feature in EP explanations. One salutary change would be to systematically take account of our debt to our primate kin. This would, in particular, downplay the commitment to natural selection acting on specifically human social capacities.
- EP typically assumes that the relevant selection forces are relatively ancient and that recent changes are insignificant. From the perspective of EP, we are as much Pleistocene relics as the condor or the grizzly bear. We do know, however, that there have been substantial changes in the human genome over even the last 10,000 years. Many of these are connected with the adoption of agriculture and the domestication of animals. More generally, evolutionary biologists have found that the rate of evolution can be much faster than EP tends to assume.
- The environment of the Pleistocene is known to have been highly variable, both over time and over space. The environment of the early Pleistocene was very different from, say, the upper Paleolithic. Moreover, humans came to be widely dispersed, occupying a variety of distinctive environments. Given what we know, it would also be reasonable to think that social structures are different in different physical environments; e.g., some would be more conducive to sedentary life styles and others to more mobile ones. Though humans are not as genetically diverse as many other animals, there is sufficient genetic variation to support genetic changes in relatively short amounts of time.
- Human behavior is both adaptive and malleable. When there is variation, a typical assumption of EP is that the strategies are conditional strategies, evoked in different conditions, or that the variants are simply abnormal. More recent developmental biology emphasizing such things as epigenetic inheritance, niche construction, and developmental plasticity, make the assumption of a universal form problematic. It is not that EP assumes some form of genetic determinism; rather, the point is that the kind of interplay we see among genetic factors, epigenetic influences, and learning, makes universals less likely.
- There are significant alternatives to the typical emphasis of EP on individual- and gene-centered models of evolution. This is an issue beyond the problems of applying their preferred modes of analysis. Gene-cultural co-evolution may be an important source of evolutionary changes. This is coming to be a well-developed alternative, emphasizing the role of cultural practices in modifying the human brain. In general, gene-cultural dynamics can enhance and accelerate rates of evolution. Multi-level selection models are also being developed. With distinctive groups, genetically isolated, competing against each other, it is possible to develop models for the evolution of social behavior that do not assume the typically individual- and gene-oriented perspective of EP.

There are alternatives which could enrich the work within EP, but which typically remain beyond its purview. Darwin was right to think that evolution should reshape our understanding of human psychology. There are many avenues to explore in seeing how it might be enriched.

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