EVOLUTIONARY THEORY AND THE HUMAN FAMILY

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ABSTRACT

Emlen's (1995) paper "An evolutionary theory of the family" reviewed existing ideas about the nature of family systems and the reasons why they have evolved in certain animal species. His theorizing led him to propose 15 predictions about how family systems function, based on favorable evidence from various species, mostly birds. While he suggested that these predictions can be applied to the human case, he himself did not attempt to do so. We consider the applicability of Emlen's 15 predictions to the study of human family systems, and find that several aspects of the life history and ecology of Homo sapiens require that they be modified. These considerations include: (1) the importance of intragroup solidarity in the context of intergroup competition: unlike in many other species where dispersal constraints arise from food or breeding site shortages, the primary pressure driving human sociality seems to be competition from other human groups; (2) the complex nature of exchange and reciprocity in human society: reciprocal altruism in particular is integral to human social interaction and leads to a particularly high degree of non-nepotistic helping behavior; and (3) the implications of menopause and the existence of potentially dominant, postreproductive helpers: helpers of this sort have little incentive to disperse or to encourage offspring to disperse, thus greatly increasing family stability.

INTRODUCTION

HUMAN SOCIAL DYNAMICS are exceedingly complex, governed by intricate systems of nepotism and reciprocal exchange. Much of sociology, anthropology, psychology and economics is centrally concerned with the explication of these dynamics. Recent advances in evolutionary biology may contribute additional insight into the forces governing human social systems. Application of evolutionary theory to the study of human affairs is not new, and has already inspired discoveries in many domains of human social behavior (e.g., see Barkow et al. 1992; Betzig 1997). Evolutionary theory and research on the factors governing the stability of family systems, in which multiple individuals cooperate in the rearing of young, promises to be another such domain. Analyses of the inclusive fitness costs and benefits of the choices available to an individual at a given time may elucidate the mechanisms governing human family dynamics (Emlen 1995).

Emlen’s approach to these issues invokes Hamilton’s (1964) inclusive fitness theory, and the extensions entailed by the ecological constraints theory (Koenig and Pitelka 1981; Emlen 1982a,b, 1991; Stacy and Ligon 1991; Koenig et al. 1992) and reproductive skew theory (Vehrencamp 1980, 1983a,b; Emlen and Vehrencamp 1983; Reeve and Ratnieks 1993; Keller and
Reeve 1994), in order to address the issues of (1) when individuals may be expected to stay and help rather than to disperse and attempt independent reproduction, and (2) how much conflict should be exhibited over the partitioning of reproduction among members of a group. A basic proposition is that an individual is expected to remain in a family group and assist in the rearing of others’ offspring when the expected inclusive fitness benefits of such a philopatric strategy outweigh those to be had by attempting to disperse and breed. The central proposition of ecological constraints theory is that such a situation is most likely to arise when ecological factors place severe limits on one’s ability to survive alone or to find suitable breeding habitats or mates. Skew theory then focuses on the division of reproduction within an established group, and proposes that dominant group members may share reproduction with subordinates if doing so will either prevent the subordinates from dispersing or reduce the competition between dominants and subordinates for reproductive status. Again, the existence and magnitude of this sharing are expected to be governed by the inclusive fitness payoffs for dominants of giving up more or less reproduction in order to entice subordinates to remain. These theoretical propositions provide a potential starting point for understanding the evolution of family systems, and Emlen (1995) proposes that together they provide “a general evolutionary framework for understanding biological families” (p 8092).

From these ideas, he derives 15 predictions about family living, which he claims “should generalize across all taxa, to all species that live in family groups, including humans” (p 8092); these predictions are listed in Table 1.

In this article, we assess Emlen’s claim that his unified theory should apply to the human animal. We attempt to take this analysis further by considering not only the functional significance of decision-making in the familial domain but also the sorts of psychological adaptations that may have evolved to bring about adaptive decisions with respect to allocations of nepotistic and reproductive effort. As we shall demonstrate, the predictions in Table 1 are often contradicted by the available human evidence, and we attribute these departures from general expectation to certain aspects of human life history and ecology. The details of these discrepancies and the proposed reasons for them suggest ways in which the predictions can be reformulated to apply more broadly across species.

Emlen draws most of his examples from avian systems. Among cooperatively breeding birds, males are generally the more philopatric sex, and thus more likely to be helpers. Evidence about human social and family systems, however, indicates that in Homo sapiens, it is females who assume greater responsibility for the maintenance of social ties and the provisioning of social support both within the family and among friends. This is true not only in the novel environment of the modern West (Oliveri and Reiss 1987; House et al. 1988; Salmon and Daly 1996), where actual exchange of support is more likely to flow between families that are related through females than through male lines (Mutran 1985; Chatters et al. 1986; Hogan and Eggebeen 1995), but also in hunter-gatherer societies (van den Berghe 1979). Hunter-gatherers live in conditions closer to those that existed during much of our evolutionary past. They are generally not as patrilineal as agricultural peoples and maintain strong matrilineal ties. Thus, we stress women’s reproductive decisions and nepotistic helping at least as much if not more than men’s, although we include data about family relations for both sexes where possible.

The evidence we present is drawn from a variety of sources, including ethnographic accounts of particular societies, cross-cultural analyses, and demographic and survey data from the modern West. Each of these sources of evidence can illuminate the evolved nature of human family relations. Ethnographic accounts and cross-cultural data serve primarily to provide us with some idea about the flexibility of human behavioral strategies across different ecological and social contexts within and between cultures. We interpret the range of behavioral variation as indicative of the flexibility of relevant human psychological adaptations, rather than as indicative of local adaptations.

A search for the behavioral decision-making rules that govern family relations is actually a search for psychological adaptations to changes in our environments. Studies of
**TABLE 1**

*Emlen's (1995) 15 predictions about the nature of family interactions*

<table>
<thead>
<tr>
<th>Number</th>
<th>Prediction</th>
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<tbody>
<tr>
<td>1</td>
<td>Family groupings will be inherently unstable. They will form and expand when there is a shortage of acceptable reproductive opportunities for mature offspring, and they will diminish in size or dissolve (break up) as acceptable opportunities become available.</td>
</tr>
<tr>
<td>2</td>
<td>Families that control high quality resources will be more stable than those with lower quality resources. Some resource-rich areas will support dynasties in which one genetic lineage continuously occupies the same area over many successive generations.</td>
</tr>
<tr>
<td>3</td>
<td>Assistance in rearing offspring (cooperative breeding) will be more prevalent in family groups than in otherwise comparable groups composed of nonrelatives.</td>
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<tr>
<td>4</td>
<td>Assistance in rearing offspring (cooperative breeding) will be expressed to the greatest extent between those family members that are the closest genetic relatives.</td>
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<tr>
<td>5</td>
<td>Sexually related aggression will be less prevalent in family groups than in otherwise comparable groups composed of nonrelatives. This is because opposite-sex close genetic relatives will avoid incestuously mating with one another.</td>
</tr>
<tr>
<td>6</td>
<td>Breeding males will invest less in offspring as their certainty of paternity decreases.</td>
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<tr>
<td>7</td>
<td>The loss of a breeder will result in family conflict over the filling of the resulting reproductive vacancy. In the specific case of simple conjugal families, the surviving parent and its mature opposite-sex offspring will now compete for breeder status. The conflict will be especially severe when offspring are of the dominant sex and when resources controlled by the family are of high quality.</td>
</tr>
<tr>
<td>8</td>
<td>Sexually related aggression will increase after the re-pairing of a parent. In the specific case of simple conjugal families, the surviving parent and its mature same-sex offspring will now compete for sexual access to the replacement mate (stepparent). This conflict will be especially severe when the asymmetry in dominance between the surviving breeder and its same-sex offspring is small.</td>
</tr>
<tr>
<td>9</td>
<td>Replacement breeders (stepparents) will invest less in existing offspring than will biological parents. They may infanticidally kill current young when such action speeds the occurrence, or otherwise increases the success, of their own reproduction. This will be more likely when the replacement mate is of the dominant sex.</td>
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<tr>
<td>10</td>
<td>Nonreproductive family members will reduce their investment in future offspring after the replacement of a closely related breeder by a more distantly or unrelated individual.</td>
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<tr>
<td>11</td>
<td>Replacement (step-) families will be inherently less stable than biologically intact families. This will be especially true when offspring from the originally intact family are of the same sex as the stepparent.</td>
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<tr>
<td>12</td>
<td>Reproduction within a family will become increasingly shared as the severity of ecological constraints decreases, that is, as the expected profitability of the subordinate's option of dispersal and independent reproduction increases.</td>
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<tr>
<td>13</td>
<td>Reproduction within a family will become increasingly shared as the asymmetry in social dominance between potential cobreeders decreases.</td>
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<tr>
<td>14</td>
<td>Reproduction within a family will be shared more equitably when the potential cobreeders consist of siblings than when they consist of parent(s) and grown offspring.</td>
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<tr>
<td>15</td>
<td>Reproduction will be shared most with those family members to whom the dominant breeders are least closely related. In species in which dominants actively suppress reproduction by subordinates, such suppression will be greatest in those subordinates to whom the dominant is most closely related.</td>
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Modern hunter-gatherers may thus be especially informative in understanding how human adaptations functioned in ancestral environments, but studies of people in any society, including our own, can provide insights about the nature of psychological adaptations. When behavior fails to promote expected fitness, the detailed departures from theoretical expectations often reveal the decision and selective processes that led to their evolution (e.g., Daly and Wilson 1986; Tooby and Cosmides 1990). This point is not peculiar to the human case; behavioral ecologists draw similar inferences from nonhuman animals' failures to max-
imize fitness (e.g., Semel et al. 1988). Our aim in reviewing the evidence for and against Emlen’s predictions is not to demonstrate whether familial behavior is presently adaptive, but rather to gain greater insight into the psychological adaptations that govern family interactions. For each prediction, then, we have tried to suggest what relevant adaptations might look like and how they might function, not necessarily adaptively, in a modern environment.

**Definition of a Family**

Emlen (1995) defines a family as an assemblage of relatives who interact regularly, but do not necessarily share residence (although they typically do so). Since coresidency, or shared territory, is not essential, this definition clearly encompasses human family groups whose members may occupy more than one residence, as long as they interact regularly. For modern humans, regular family interaction can in principle include additional forms of communication, such as phone calls, e-mail, and faxes, and it is less clear whether Emlen’s definition encompasses these cases, too. It seems evident, however, that Emlen’s emphasis on sustained interaction is not intended to limit the definition of an active family to any particular kind of contact, at least not so much as to distinguish among alternative, effectively reproductive and nepotistic allocations of time, attention, and benevolence. Accordingly, and to be as fair as possible in testing the predictions, we consider data from both sustained coresidence and the maintenance of some form of contact.

Emlen’s discussion and most of his predictions deal specifically with situations where offspring who are old enough to reproduce remain celibate on their parents’ territory and assist in rearing siblings. This is a common scenario in nonhuman species with helpers, but it is not the only type of family. Emlen certainly means for these predictions to be easily extended to relatives other than parents and offspring. Similarly, in humans, parent-offspring relationships are not the only family ties, although they are certainly central to family interaction. Wherever data on extended family relations are available, we have attempted to include them in our discussion; data on parent-offspring interactions are the most numerous. Our emphasis on this relationship is thus a result of the relative availability of information, and not of a lack of interest in extended family relations.

**Coresidency Among Relatives**

Since families have been defined as groups of individuals that either share residence or remain in contact, it is important to know what range of opportunities exists for the maintenance of such contact in humans. In a cross-cultural study of adolescence, Schlegel and Barry (1991) quantified relevant data about human coresidency patterns, at least with reference to the parent-offspring relationship. Their analyses show that in many cultures children continue to reside with their parents after puberty, but this pattern is far from universal. Women typically married within two years of menarche in 112 of 178 societies (63%), and of the remainder, most married within five years. Thus, one may say that in the majority of preindustrial, face-to-face societies, like those in which the human psyche evolved and to which it is presumably adapted, daughters do not often linger prolongedly on parental property after reproductive maturity. Since there is at least a year of adolescent subfecundity after menarche (Wood 1994), young women residing at home for a short time after puberty begins are not necessarily foregoing reproductive opportunity.

The residency patterns of young adolescent males exhibit greater cross-cultural variability, but the general tendency seems to be for sons to remain slightly longer after puberty than daughters, although the difference is not great (Schlegel and Barry 1991; Davis 1996). Presumably this indeed reflects greater limitation and delay of marital and reproductive opportunities for sons than for daughters, but, contrary to what one might expect on the basis of Emlen’s analysis, adolescent sons typically direct less nepotistic effort toward their natal families than adolescent daughters (Kaplan 1996). Moreover, if marriage means the beginning of a reproductive career, it does not necessarily imply emigration from the parental community, and by the criterion of regular interaction into adulthood, human beings in all societies seem to be intensely familial.

Later, we will further consider the implica-
tions of continued residence in the parental community, as well as how lifelong nepotistic interactions with natal family members are common features of human social life. For the moment, we wish to stress that the modern Western practice of prolonged postpubertal, premarital residence in the parental home is not species-typical. Moreover, continued residence in the parental community does not imply reproductive competition between mother and daughter, not even in matrilocal societies. This needs to be emphasized since Emlen’s discussion may imply that reproductive gains are necessarily attained at the expense of same-sex individuals who maintain familial ties with the reproducer; in fact, sustaining familial ties need not mean fewer resources and reproductive opportunity per capita. In a review of the data on reproductive success in cooperatively breeding birds, Koenig (1981) has shown just this: not only does the total reproductive output of a breeding group generally increase with group size but the per capita reproductive output often increases as well. Similarly, human cooperative ingenuity is surely such that the reproduction of both mother and daughter can often be facilitated by their continuing proximity.

DOMINANCE AND CAREGIVING

Another point that complicates the application of Emlen’s theory to the human case concerns the generational direction of “helping at the nest.” Human females are unusual, perhaps unique among mammals, in that they undergo reproductive cessation (menopause) often well in advance of any serious impairments in other body systems. Even in traditional societies a woman’s reproductive career ends by the time she is 45, and yet she may survive for another 20 years or more (Hill and Hurtado 1991). Thus, there is an extended period in which a woman cannot make a situationally contingent decision between personal reproduction and nepotistic effort, but can promote her inclusive fitness only by promoting the reproduction of others. In fact, the most popular explanation for the evolution of menopause is based on the assumption that postmenopausal women become helpers (e.g., Williams 1957; Hamilton 1966; Alexander 1974), although other possibilities remain tenable, including that menopause is not an adaptation at all (Hill and Hurtado 1991). Furthermore, these older, nonreproductive family members may often remain socially dominant to their adult children, even if physically weaker. Such retention of rank is fairly common in apes and monkeys (Byrne 1995), where the most dominant female in a matrilineal kinship group is typically the oldest female (Cheney and Seyfarth 1990), and it is common in people, too (Brown 1982).

Emlen’s 15 predictions are based on comparative evidence from nonhuman species, and several follow from assumptions that (1) breeders are dominant to helpers, and (2) helpers have the option of breeding independently, even if their likelihood of success is very small. But if postmenopausal women remain socially dominant to their adult daughters, then the first of Emlen’s assumptions will be violated when such women provide grandmaternal care. The second assumption is also inapplicable insofar as the grandmother can no longer reallocate her efforts to personal reproduction. These considerations may have a substantial effect on the cost-benefit structure of dispersal and competition within family groups, as will be explained later.

Of course, the breeders in human families are not always subordinate and junior to their nonreproductive helpers. In some societies prereproductive children contribute significantly to family subsistence or assist in caring for younger siblings (Weisner 1982; Turke 1988; Schlegel and Barry 1991; Seginer 1992), and they may even incur a decrease in their personal reproduction by so doing (Turke 1988), although this does not seem to hold for modern Western society (Spitze and Ward 1995). But when children help raise siblings while still subordinate to their parents, the situation still does not quite fit the assumptions on which Emlen’s theory is based, insofar as the prepubertal and adolescent helpers do not have the option of independent reproduction.

An inexplicit assumption of Emlen’s model violated here is that the dependent lifestage in which one consumes rather than produces familial resources is followed immediately by reproductive maturity. In other words, personal reproduction and nepotistic assistance of reproducing relatives become available as
alternatives at one and the same lifestage. This occurs in seasonally breeding birds that must choose between helping and reproducing at one year of age. In humans, however, it is not unusual to have nepotistic investment in younger siblings available as an option well before sexual maturity; a similar situation has been described in some cooperatively breeding fish (Taborsky 1994).

Of course, many men are capable of reproduction throughout life, although their fertility (and perhaps more importantly their prowess in intrasexual reproductive competition) declines with advanced age, and perhaps in keeping with their more prolonged possibility of personal reproduction, men do not seem to engage in as much familial nepotism as women. For these and other reasons, some of Emlen's predictions may be more applicable to one sex than to the other, although they were formulated in a sexually neutral fashion. In the analyses that follow we include data about both men's and women's familial relationships, when possible. With these ideas in mind, we will now consider in detail Emlen's 15 predictions (see Table 1).

**Family Formation and Stability**

**Prediction 1.** Family groupings will be inherently unstable. They will form and expand when there is a shortage of acceptable reproductive opportunities for mature offspring, and they will diminish in size or dissolve (break up) as acceptable opportunities become available (Emlen 1995:8094).

If psychological mechanisms that govern the stability of family groups under various levels of ecological constraints have evolved, then the appropriate evolutionary processes had to be there to shape them. Therefore, before inquiring into the possible nature of the adaptations underlying human family formation, it is important to consider what sort of processes are likely to have guided their evolution. For humans, there are several good reasons to doubt that families have been selected to be “inherently unstable.” We would argue instead that human beings are likely to have been selected to try to maintain family ties under all ecological circumstances.

Emlen's prediction is derived from theories of delayed dispersal (Emlen 1982a,b, 1991; Stacey and Ligon 1991; Koenig et al. 1992) that place strong emphasis on the effects of environmental constraints on breeding opportunities. In a cross-cultural analysis, however, Low (1989) could find no significant relationships between human group size and any ecological variables such as the availability of water or the variability, predictability or extremes of temperature, nor was she able to detect any correlation between group size and pathogen pressure, starvation risk or protein deficiency. She concluded that human groupings appear not to be limited by extremes of environmental variation in the same way as other species.

Consistent with this conclusion is Alexander's (1990) proposal that the social environment has been of greater selective relevance in the evolution of human sociality than physical factors, and that it was specifically between-group competition that drove the evolution of large familial and suprafamilial groupings and clan group solidarity. If Alexander is correct that human groups have been the predominant environmental force acting on their own evolution, then it is unlikely that ecological constraints were ever such as to favor environmentally contingent decisions to disperse in order to reproduce away from kin. Thus, rather than being the nonpreferred result of temporary shortages, familial affiliation and cooperation are human universals (Brown 1991).

The relevance of Prediction 1 to the human case is also limited by the fact that helpers may not always be capable of independent breeding, as noted above. Obviously, family members who perceive themselves as incapable of independent reproduction should not abandon the helper role when a breeding vacancy arises. This proposition may be violated and Emlen's expectation upheld, however, when a prepubertal potential helper's chance of attaining breeding status is diminished in proportion to the amount of help presently provided, and there is some evidence that this may be the case in humans, at least in some circumstances (Turke 1988). Postreproductive helpers, such as menopausal women, by contrast, have presumably been selected to channel their efforts into grandmaternal and other nepotistic investments, more or less regardless of ecological conditions.

According to these arguments, natural se-
lection has not shaped humans to be familially fickle such that families "dissolve" when favorable conditions for dispersal arise, but rather to maintain strong kin bonds. One element of the evolved psychological underpinnings of persistent, loyal familial affiliations must be love. Emotions are powerful motivators that normally function to guide behavior adaptively (Nesse 1990). The primary function of love is arguably to cause a desire to invest in, or make sacrifices for, the love object. If this view is correct, and if humans are, indeed, obligately familial, then people should be predisposed to love others who exhibit cues of being family members (Williams 1997). These cues are likely to include things like phenotypic resemblance and other cues of paternity certainty, as well as presumptive genealogical links to other relatives. There is little reason to expect that cues of environmental richness will affect familial love in the way that Prediction 1 implies, such that the affective bonds of kinship are strong when food, shelter and potential mates are scarce, and weak when they are abundant. It is at least as plausible to argue the reverse, that familial love will fail when the resource circumstance is desperate, as Turnbull (1972) claimed of the Ik of east Africa.

If Prediction 1 were sound, we might expect families to be especially prone to dissolution in the modern industrial world, where dispersal opportunities are abundant. In recent tribal societies, and presumably in ancestral societies as well, dispersal distances were usually short enough to allow kin to see and help each other frequently, reinforcing familial feeling. But what happens to family stability when planes, trains and automobiles make long-distance dispersal easier, and distances between family members increase? In this environment of long-distance dispersal opportunities and resultant costs of maintaining family ties, do family ties dissolve, or is this dispersal instead a product of our modern contact maintenance technology? And most important, with respect to the validity of Prediction 1, is the establishment of mature reproductive status associated with a reallocation of sentiment and effort away from natal family members, as the prediction implies, or is it instead associated with sustained or even enhanced contacts?

Using Canada’s General Social Survey (GSS), we can examine the relationship between marital status and the frequency of contact (by letter, phone and actual visits) between respondents and their parents, grandparents and siblings. According to the above interpretation of Prediction 1’s implications about familial attachments, married respondents (i.e., those who have found and moved into a potential “breeding vacancy”) should maintain less contact with their natal families than same-age respondents who remain unmarried.

METHODS

The 1990 GSS Cycle 5 on family and friends was a telephone survey of a stratified random sample of all persons 15 years of age or older in Canada, except for residents of the Yukon and Northwest Territories and full-time residents in institutions, with supplementary samples of the elderly and Ontario residents (Statistics Canada 1991). The survey had a 75% response rate, and data were obtained from 13,495 households.

For the present analyses respondents were divided into the following six categories: men ages 15–24, 25–34, and 35–44, women ages 15–24, 25–34, and 35–44. Thus each analysis was performed six times, once for each group. \( \chi^2 \) tests were performed to determine whether a relationship existed between marital status (never married vs. married or common-law) and frequency of contact with relatives; formerly married but currently single respondents were not included in the analyses. Two different measures of contact were used: frequency of face-to-face contact with a particular relative and frequency of contact by letter/ phone. Three different types of relatives were considered: parents (or mother if parents did not live together), grandparents and siblings. Frequency of contact was coded into five levels: daily, at least once a week, at least once a month, less than once a month, and never. When an analysis reached significance, the \( \chi^2 \) table was partitioned to determine where the significance actually lay. Analyses of the frequency of contact were confined to respondents who had living relatives in the category under consideration, but did not currently reside with the respondent. A second set of \( \chi^2 \) tests was performed to examine the relationship between marital status and whether the respondents resided with his or her mother.
RESULTS AND DISCUSSION

If one defines a “family” in terms of coresidence, then modern Canadian families do indeed break up as “breeding opportunities” become available: in all six age-sex groups, married respondents were significantly and substantially less likely to live with their parents than single respondents (N ranges from 746 to 1470, χ² ranges from 82.09 to 369.71, for all df = 1 and p < 0.00001). For the vast majority of respondents, however, contact with family members did not end with the cessation of coresidence. Among those not living at their parental home, there was no clear relationship between maintenance of parental contact and marital status. In fact, the analyses suggest that for men, being married is associated with more frequent contact with parents (Figure 1): married men ages 15-24 and 25-34 visited their parents significantly more often than same-age single men (N = 444, χ² = 25.54, df = 4, p < 0.00004 and N = 1108, χ² = 13.58, df = 4, p < 0.009, respectively). There was also a significant difference between married and single men ages 25-34 in the amount of contact they had with their parents by letter/phone; however, partitioning revealed no consistent trend of greater contact for one group or the other. There was no difference between married and single men ages 35-44 for either measure of contact with parents, nor for women of any age group.

Of course, it is possible that single individuals living away from home had a specific reason for doing so; perhaps they left because they did not get along with their parents. There is a positive relationship between parent-child affection and both frequency of association and coresidence in the U.S. (Aquilino and Supple 1991; Bengtson and Roberts 1991). This, however, is an inappropriate argument to salvage the original prediction, since it is not known why there was parent-child conflict. One might expect that family discord would be associated with the activation of those evolved psychological mechanisms that function to bring about family dissolution, while a harmonious affect would be associated with the activation of those functioning to maintain cohesion.

In contrast to the case of contact with parents, both single men and women, at least when younger, seem to have more contact with grandparents than do same-age married persons, although the results were not consistent across all analyses (Figure 2). This is superficially consistent with Prediction 1, but presumably this contact does not represent prereproductive helping of senior kin who are still reproducing; on the contrary, this is evidence for the role of grandparents as postreproductive helpers, as discussed above.

Single men maintained more frequent contact than married men with their grandparents by both measures (15-25: visits N = 833, χ² = 18.53, df = 4, p < 0.001; letter/phone N = 833, χ² = 14.68, df = 4, p < 0.005; 25-34: visits N = 590, χ² = 13.17, df = 4, p < 0.01; letter/phone N = 589, χ² = 13.11, df = 4, p < 0.01). In the case of contact by letter/phone, however, single men between 25-34 compared to married men were also more likely not to be in contact at all (χ² = 5.948, df = 1, p < 0.05). The same pattern appeared for men ages 15-24 in the frequency with which they visited grandparents (χ² = 4.59, df = 1, p < 0.05). Single women ages 15-24 visited their grandparents more and kept in contact with them by letter/phone more frequently than did married women (N = 975 and 974, χ² = 29.22 and 29.57, respectively, df = 1 and p < 0.00001 for both). There was no difference between single and married women ages 25-34 with re-
FIG. 2. FREQUENCY OF CONTACT WITH GRANDPARENTS IN RELATION TO MARITAL STATUS AND SEX OF RESPONDENTS

Single respondents reported more frequent contact than married respondents (Statistics Canada 1991).

spect to either type of contact. Since $\chi^2$ analysis requires an expected value of at least 5 in each cell, and there were not enough respondents in the sample between the ages of 35 and 44 with living grandparents to meet this criterion for all cells, so it was not possible to carry out analyses for this group.

There seems to be no significant differences between married and single men or women in the frequency of contact they have with siblings, which again contradicts the sustained-contact interpretation of Prediction 1, with two exceptions. The first exception occurred for married men ages 15–24, who had more contact with their siblings than their single counterparts ($N = 697$, $\chi^2 = 7.72$, $df = 1$, $p < 0.05$); the second exception was for married women ages 25–34, who had less contact with their siblings than single women ($N = 1554$, $\chi^2 = 18.87$, $df = 4$, $p < 0.0008$).

These results are consistent with previous work on intrafamilial exchange. Eggebeen and Hogan (1990) looked at patterns of exchange in American families, and found, after partialling out effects of such variables as income and presence of children, that married persons exchanged goods and labor with their parents neither more nor less than single, separated, divorced and widowed persons. Persons with young children, however, were much more involved in exchange with their parents, and were, as a group, the recipients of the largest amount of aid from them. This increase was primarily accounted for by childcare, which suggests that the slight tendency we observed towards increase in contact with relatives for “mated” respondents might be even greater if we had limited our analyses to couples with children.

Thus, at best Emlen’s first prediction holds only for some demographic groups with some types of relatives. There is no indication that mature offspring maintain contact with parents and siblings only until, or unless, they can assume reproductive status. On the contrary, the results reported by Eggebeen and Hogan (1990) support our notion of parents as post-reproductive helpers of their children, an option which is not obviously contingent on ecological circumstances. It should also be noted
that almost everybody in the sample main-
tained some form of contact, even if very infre-
quent, with their living relatives, another hint
of our consistently familial nature. Of course,
the relationship between ecological constraints
and family stability in pretechnological cul-
tures is still unknown, but on the basis of the
theoretical arguments we have presented, we
suspect that Prediction 1 will not hold with
them either.

**Prediction 2.** Families that control high quality
resources will be more stable than those with lower
quality resources. Some resource-rich areas will sup-
port dynasties in which one genetic lineage continu-
ously occupies the same area over many successive
generations (Emlen 1995:8094).

According to ecological constraints and
benefit-of-philopatry models, an available breed-
ing vacancy should only be acceptable if its ex-
pected fitness payoff is at least as high as the
expected payoff for remaining at home. Em-
len (1995) argues that individuals reared in
high-quality environments should therefore
be choosier in evaluating dispersal opportuni-
ties than those from low-quality natal environ-
ments. In the human case, well-to-do families
should be more stable than poor ones.

This prediction is really an extension of the
one that preceded it, and like Prediction 1, it
suffers from a lack of explicit attention to the
expected adaptation. If *Homo sapiens* tend to
be obligately rather than facultatively familial,
as argued above, then dynastic continuity is
unlikely to be a simple function of environ-
mentally contingent dispersal decisions. If we
again suppose that familial affection is the
evolved psychological mediator of family co-
hesion, then Prediction 2 suggests that famil-
ial love should be dependent not only on cues
of the quality of available dispersal opportuni-
ties but also on their quality in relation to that
of the natal environment. We know of no pub-
lished research bearing directly on this predic-
tion, but there are both theoretical and empir-
ical reasons to doubt it. Again, if a helper is
incapable of independent reproduction, there is
little reason to expect it to make its help con-
tagious on the economic circumstances of its
natal family; unless helping influences the
likelihood of acquiring a breeding opportu-
nity, a prepubertal helper ought to benefit by
helping to rear relatives regardless of the (rel-
ative) quality of the available breeding vacan-
cies, and the same is true for postreproduc-
tive helpers.

Moreover, even if a potential helper is capa-
ble of independent reproduction, other con-
siderations constrain the relevance of the
quality of available territories in determining
how one allocates effort between nepotism and
reproduction. Alexander’s (1990) argument is
again relevant here: the evolution of the hu-
man capacity to form large, solidary social
groups was primarily a response to between-
group competition. If family and clan solidar-
ity and strength have long been crucial deter-
minants of an individual’s expected genetic
posterity, as Alexander proposes, then it is pos-
sible, even probable, that individual reproduc-
tive decisions have been shaped by selection
to be responsive to the effects of these deci-
sions on social standing. In other words,
whereas there might have been little reason
for our ancestors to make continued family
relations contingent on available reproductive
opportunities relative to natal conditions,
there may have been good reason to adjust
reproductive and social decision-making ac-
cording to the impact of these decisions on
one’s social standing. This is true not only for
the potential reproductives but also, and per-
haps especially, for kin, who may stand to ben-
fit from an individual’s social alliances. Un-
der this view, family interactions should
depend greatly on their economic and social
implications; both familial affection and other
social sentiments should be sensitive to cues
of a target person’s abilities to affect one’s own
social standing. This suggests that familial loy-
alty and affection may be felt most strongly
toward those relatives who are in the position
to provide the greatest benefit, and this will
often mean those who are the highest in stand-
ing themselves. With this in mind we will now
review the evidence bearing on Emlen’s sec-
ond prediction.

What constitutes a test of Prediction 2 again
hinges on what is meant by a stable family. If
the criterion of stability is sustained coresi-
dence, then Prediction 2 is not supported.
White (1994), for example, reviews evidence
from the modern west, indicating that young
adults from relatively resource-rich natal fami-
lies are less likely to reside with parents than
same-age persons from poorer families, and are less likely to return to the parental home once they have left. Schlegel and Barry’s (1991) cross-cultural study of adolescence includes an analysis of the factors affecting age at marriage, which we can use as a rough indicator of the cessation of coresidence in most traditional societies. Across cultures, marriage is often under the control of kin: males are described as free to make their own decisions about whom to marry in only 18% of 141 cultures surveyed, and females in only 13% of 131 (Schlegel and Barry 1991). Although it should be noted that the bride’s and groom’s preferences are perhaps seldom completely ignored (Harris 1995), Schlegel and Barry (1991) appropriately stress the element of economic exchange in marriage negotiations conducted by self-interested parties, usually parents. Early marriage of daughters is most common in societies with bride service or bridewealth, which brings goods or labor into the parents’ household. In dowry-giving societies, on the other hand, where marrying of daughters is costly, female age at marriage tends to be older. There are several exceptions to this rule, however, and it is Schlegel and Barry’s (1991) analysis of these exceptions that provides the strongest evidence against Prediction 2, yet supports our argument for sensitivity to social benefits. In such dowry-giving societies as those in India, ancient Rome and preindustrial Europe, age at marriage varied according to parental status: high-status families married off their daughters at an early age, while low-status families married them off late, an opposite pattern to that which might be inferred from Prediction 2. According to Schlegel and Barry (1991), delaying a daughter’s marriage in such societies is especially tempting for a family of limited means, because the family will lose not only part of its wealth but also her labor when she weds. In a wealthy family, on the other hand, female domestic labor is augmented by that of slaves and servants; the family has adequate resources for a dowry, and can use resources so acquired to “buy” a son-in-law that improves the family’s own social position. There is no advantage to delaying marriage when daughters can function as social capital.

Schlegel and Barry’s (1991) account suggests that in societies where children provide labor and/or where it is expensive to marry them off, their dispersal could affect the “territory quality” of their parents. If marriage transactions are manipulated to improve social standing, then this would also have an effect on Prediction 2. Instead of high-status children leaving later because they have higher standards for what constitutes a suitable opportunity, low-status children may wind up leaving later because their departure significantly decreases the resource capital of their parents. In other words, dispersal age is complicated, and may be affected more by status considerations and the adaptations driving them than by a simple accounting of territory quality. If the human psyche has in fact evolved to be concerned with maintenance of status, then to the extent that parental resources can finance dispersal, high-resource holdings could make it easier for offspring to disperse, and disperse at an earlier age, without great loss to parental standards of living. To the extent that familial resources are non-partible in a given human society, high-resource holdings may delay dispersal.

Alternatively, stable families can be defined as those whose members maintain contact with each other in adulthood. Unfortunately, tests of Prediction 2 under this criterion must be limited to modern western data. Published evidence supports the prediction that although people maintain kin ties no matter what their socioeconomic status (SES), the ties appear to be stronger the wealthier the family. Taylor (1986), for example, found that low income was associated with reduced support from kin among black Americans, despite their greater need. Similarly, White and Reidmann (1992) report that people with lower levels of education and family income are less likely to receive social support from their adult siblings (White and Reidmann 1992), while Eggebeen and Hogan (1990) found that high SES was associated with greater intergenerational exchange within families in the U.S.

These published studies address only the presence or absence of familial support and exchange, without presenting evidence on its frequency. We can again use data from Canada’s GSS to test whether contact with kin is more frequent, and not just more likely, among wealthier families.
METHOD

These analyses used the same data set described above, and each analysis was conducted separately for the same six age-sex groups of respondents; frequency of contact was coded as before. Analyses were conducted on the relationship between the respondent's total annual household income versus frequency of contact by letter/phone or face-to-face with parents, grandparents and siblings, respectively. (The relationship between a respondent's contact with kin and natal family income might provide a better test of Prediction 2, but this information was unavailable; if offspring income is substantially correlated with parental income, then these analyses should exhibit similar trends to those that would be obtained with natal family income.) Total annual household income was divided into four groups: $0–$19,999, $20,000–$39,999, $40,000–$59,999, and $60,000 and up; all analyses were χ².

Each analysis yielded a 4×5 contingency table, so that when one reached significance it was necessary to partition it to determine where the significant differences lay and whether they were along dimensions relevant to the hypothesis being tested. Each significant analysis was partitioned in the following manner: income groups were combined to yield two groups, those that earned less than $40,000 a year and those that earned $40,000 or more. This allowed us to see if the existing trend was consistent with our prediction, and to be certain, for example, that the observed significance was not owing to both the lowest and highest income families engaging in more contact than middle income families. The next partitioning tested whether they kept in any contact with relatives. The final partitioning looked only at those respondents who kept in at least some contact with the relevant family member, and tested whether respondents in one of the two income groups were more likely to maintain daily contact than the other.

RESULTS AND DISCUSSION

Although not all analyses and partitions were significant, all showed the same pattern: high-income respondents were more likely to maintain some sort of contact than low-income respondents; this result is consistent with previous studies on familial social ties and exchange. Among those who did maintain contact with their families, however, low-income respondents were in more frequent contact with family members than wealthy ones (Figure 3).

For male respondents ages 15–24, there was no significant relationship between income and frequency of face-to-face contact with parents, grandparents or siblings, nor was there any effect of income on frequency of contact with parents by letter/phone. There was, however, a significant relationship between income and frequency of contact by letter/phone with grandparents (N = 541, χ² = 40.63, df = 12,
p < 0.00006) and with siblings (N = 438, $\chi^2 = 27.30$, df = 12, p < 0.007) for this group. Respondents in the low-income group were more likely not to be in contact with their grandparents at all ($\chi^2 = 14.85$, df = 1, p < 0.05), although this was not true for siblings. Among respondents who maintained at least some contact, those in the low-income group were significantly more likely to be in daily contact, while those in the high-income group were significantly more likely to be in less frequent contact (grandparents: $\chi^2 = 6.98$, df = 1, p < 0.05; siblings: $\chi^2 = 9.15$, df = 1, p < 0.05). There were no significant relationships between income and frequency of contact for any of the analyses carried out for female respondents ages 15–24.

For males ages 25–34 there was no effect of income group on the frequency of contact by letter/phone with parents or the frequency of face-to-face contact with grandparents. There was a significant relationship between income and frequency of face-to-face contact with parents (N = 987, $\chi^2 = 23.48$, df = 12, p < 0.02), contact by letter/phone with grandparents (N = 570, $\chi^2 = 30.51$, df = 12, p < 0.002), and both types of contact with siblings (visits: N = 1131, $\chi^2 = 37.11$, df = 12, p < 0.0002; letter/phone: N = 1131, $\chi^2 = 39.35$, df = 12, p < 0.00009). There was no significant difference between income groups in the likelihood of maintaining at least some contact in any of these four analyses. In all cases, however, the trend was for respondents in the low-income group to be less likely to maintain contact. For three of the four analyses, face-to-face contact with parents and both types of contact with siblings, respondents in the low-income group were more likely to be in daily contact with their relatives (parents: $\chi^2 = 9.11$, df = 1, p < 0.05; visits with siblings: $\chi^2 = 14.00$, df = 1, p < 0.05; letter/phone with siblings: $\chi^2 = 8.60$, df = 1, p < 0.05). The grandparental contact analysis, while failing to reach significance, showed the same trend.

Analyses of frequency of contact data for females ages 25–34 showed a pattern similar to the male results; the analyses of frequency of contact with grandparents failed to reach significance. The relationship between income and frequency of contact was significant for parents and siblings for both types of contact (visits with parents: N = 1236, $\chi^2 = 32.85$, df = 12, p < 0.001; letter/phone with parents: N = 1234, $\chi^2 = 30.24$, df = 12, p < 0.003; visits with siblings: N = 1344, $\chi^2 = 44.51$, df = 12, p < 0.00001; letter/phone with siblings: N = 1343, $\chi^2 = 35.95$, df = 12, p < 0.0003). Respondents in the high-income group were significantly more likely to maintain at least some contact with parents by letter/phone than low-income respondents ($\chi^2 = 8.46$, df = 1, p < 0.05), and results for sibling and grandparental contact were directionally similar, but nonsignificant. All four analyses showed that respondents in the low-income group were significantly more likely to be in daily contact with their relatives than high-income respondents (visits with parents: $\chi^2 = 10.17$, df = 1, p < 0.05; letter/phone with parents: $\chi^2 = 5.82$, df = 1, p < 0.05; visits with siblings: $\chi^2 = 6.13$, df = 1, p < 0.05; letter/phone with siblings: $\chi^2 = 10.31$, df = 1, p < 0.05).

For male respondents ages 35–44, there was a significant relationship between income and frequency of face-to-face contact with parents and siblings (parents: N = 708, $\chi^2 = 38.03$, df = 12, p < 0.0002; siblings: N = 850, $\chi^2 = 25.80$, df = 12, p < 0.001), for female respondents, there was a significant relationship between income and frequency of contact with parents by letter/phone and face-to-face contact with siblings (parents: N = 677, $\chi^2 = 27.80$, df = 12, p < 0.006; siblings: N = 812, $\chi^2 = 51.56$, df = 12, p < 0.00001). Analyses of frequency of contact with grandparents were not run on male or female respondents ages 35–44 because of the small sample sizes that led to expected values of less than 5 in some cells, a situation that violates the requirements for performance of this test. Once again, for two of these significant analyses, higher income respondents were more likely to keep in at least some contact with family than lower income respondents (parents for males: $\chi^2 = 4.92$, df = 1, p < 0.05; siblings for females: $\chi^2 = 10.11$, df = 1, p < 0.05); the remaining two showed the same trend. Once again, all four also showed that lower income respondents were significantly more likely than higher income respondents to be in daily contact with family (parents for males: $\chi^2 = 9.60$, df = 1, p < 0.05; siblings for males: $\chi^2 = 6.49$, df = 1, p < 0.05; parents for females: $\chi^2 = 3.78$, df = 1, p < 0.05).
p < 0.05; siblings for females: $\chi^2 = 21.71$, df = 1, p < 0.05).

What does this mean for the prediction that high-income families should be more stable? Certainly, the available evidence indicates that high-income families are more likely to maintain social ties at some level and to engage in exchange, but the present analyses also suggest that the strength of those ties may be weaker. Prediction 2 did not make an explicit distinction between these two outcomes, but it seems reasonable to interpret family stability as variable in strength rather than as a binary variable. So what could account for the observed relationship between income and frequency of contact?

One factor overlooked in the present analyses is the availability of support from family members. Individuals with low incomes may require more support, hence the greater frequency of contact among those who maintain contact. Since they are lower income families, however, they may not always have relatives with the capacity to provide support, hence the greater likelihood of not maintaining any contact. Individuals with high incomes, on the other hand, may be more likely to have family members capable of providing support, hence the greater likelihood of maintaining at least some contact. Those who need support do not need as much of it and so may maintain a lower frequency of contact. There may also be some correlation between communicative capability and income. For example, high-income people may be better able to pay the expense of long distance calls. This brings us back to the notion that family contact is modulated by economic and social considerations: the wealthier one’s relatives, the more able they are to help in times of need, and the more one would be expected to keep in touch with them.

**Prediction 3: Kinship and Cooperation**

*Prediction 3. Assistance in rearing offspring (cooperative breeding) will be more prevalent in family groups than in otherwise comparable groups composed of nonrelatives (Emlen 1995:8094).*

*Prediction 4. Assistance in rearing offspring (cooperative breeding) will be expressed to the greatest extent between those family members that are the closest genetic relatives (Emlen 1995:8095).*

These predictions will be considered together, since both are derived from Hamilton’s (1964) inclusive fitness theory. Hamilton pointed out that individuals can contribute genetically to future generations by producing offspring of their own (direct fitness), and by assisting their relatives to do so (indirect fitness). Thus, because the fitness return is greater per unit of assistance, helpers are expected to help relatives in preference to nonrelatives, and close relatives in preference to distant ones. The prevalence of reciprocal exchange among humans challenges this expectation, however. Friendly reciprocal alliances between unrelated individuals could reduce or abolish the expected association between relatedness and assistance rearing offspring. In a study of infant care among the Efe hunter-gatherers of Zaire, for example, Ivey (1993) found evidence for nepotistic caregiving, but she also observed significant amounts of infant care performed by unrelated individuals. Ivey also notes that there are other possible reasons for allomaternal care in humans or other animals in addition to nepotism and reciprocity.

If assistance with childcare has, in fact, been shaped by inclusive fitness considerations, then these considerations should be reflected in the psychological adaptations affecting the propensity to provide such assistance. Once again we return to the idea of love as an investment-promoting mechanism. If Predictions 3 and 4 are correct, and if love does indeed function to create a desire for self-sacrificing benevolence, then we would expect the degree of love of a particular child to be influenced by an individual’s relatedness to that child. In other words, cues that a child is a relative should influence the amount of love felt for it. This, in turn, presumably would lead to more assistance in rearing it. Factors affecting paternal love of children are considered under Prediction 6, which deals specifically with this issue.

The evidence we present here once again comes from modern Western society. Although this culture is in many ways removed from the one in which the human psyche evolved, there is no reason to suspect that these changes have interfered with cues of relatedness and the evolved psychology of familial attachment. One potential effect of modern environments, however, is that greater distances between family members may decrease their ability to provide
childcare assistance; this should be considered when evaluating the results.

We used the Canadian GSS data to test the prediction that assistance in rearing offspring will be more prominent in family groups, against an alternative hypothesis that assistance in rearing offspring will be dependent on the opportunity for reciprocal exchange. One of the questions in the survey was specifically concerned with the allocation of childcare. We performed a $\chi^2$ test that compared respondents living with children 12 and under versus respondents with no coresident children, with respect to the following question: When respondents provide childcare, to whom are they more likely to provide it, family or friends? Because the GSS only gathered data on childcare assistance to relatives of degree $r = 0.5$ (parents, children and siblings), it is not possible to test Prediction 4's implication of a finer gradation of assistance in relation to degrees of relatedness.

Analysis revealed that respondents without children in their home are significantly more likely to provide childcare to family, while respondents with children 12 and under in their home are more likely to provide it to friends ($\chi^2 = 339.57, df = 1, n = 3085, p < 0.00001$). This result supports the notion that those with children invest in other's children mainly in reciprocal contexts, while those without children allocate any childcare that they provide nepotistically. This effect, however, could be a result of age differences between respondents and their relatives: older respondents are less likely to have children of their own and less likely to have friends (who are presumably in the same age group) with children, so when they help they may have little option but to help relatives. In an attempt to correct for this, we also analysed the likelihood of respondents, who were 40 years old or younger, providing childcare to siblings (who are more likely to be close to the respondent in age) versus friends versus other relatives. Although the overall number of respondents who helped friends versus relatives was almost evenly split (49.2% helped friends, 50.8% helped relatives), respondents without children were more likely to help siblings and other relatives than expected, and respondents with children were more likely to help friends ($\chi^2 = 61.82, df = 2, n = 2193, p < 0.00001$; see Figure 4). This supports the notion of childcare as a form of reciprocal exchange between friends, and as a form of unreciprocated nepotism between relatives.

Predictions 3 and 4 seem reasonably robust with respect to human family systems, but given the intricate nature of exchange relationships between humans, they would be even more accurate if they specified that assistance be non-reciprocal—in other words, that the amount of aid given without expecting compensation will be higher when the recipient is a relative, and higher still with a more closely related relative (Burmstein et al. 1994). Given the complexity of reciprocity in human social systems (Trivers 1971), it may prove difficult to test whether help to kin is really unreciprocated. One approach might be patterned after Hames's (1987) demonstration that Ye’kwana men will permit unpaid labor reciprocity debts to build up more with close kin than with unrelated friends. But the best tests of these predictions are likely to come from studies elucidating the adaptive structure and function of the motivational and emotional mechanisms that produce alloparental and other “altruistic” acts.

Prediction 5. Sexually related aggression will be less prevalent in family groups than in otherwise comparable groups composed of nonrelatives. This is because opposite-sex close genetic relatives will avoid incestuously mating with one another (Emlen 1995: 8095).
It appears from Emlen’s discussion that he intends the term “sexually related aggression” to refer primarily to competitive interactions between same-sex rivals and less to violent or coercive heterosexual transactions. Although incest avoidance is not an absolute, in many species there exists a lack of sexual interest in opposite-sex close relatives. This incest avoidance is thought to have evolved owing to an increased likelihood of rare deleterious recessive alleles becoming homozygous and hence being expressed when close relatives pair in normally outbreeding populations.

If we consider, again, the level of the relevant psychological adaptations, this prediction can imply that close genetic relatives will not be perceived as potential mates, and thus will not inspire intrasexual competitive conflict with those who do react to them as potential mates. This is not to say that there are no grounds for conflicts with the mates and potential mates of one’s close relatives, but only that the conflicts are not a result of sexual rivalry. And of course, if the helper in such a system is not capable of reproduction, then there should be no such “sexually related aggression,” regardless of the degree of relatedness between family members.

Emlen (1995) argues that inbreeding avoidance will result in “a reduced incidence of mate guarding and other forms of sexually related harassment and aggression within family groups” (p 8095). While we agree that rivalrous aggression over sexual access to relatives should be and apparently is rare in humans, it should be noted that parental attempts to control the sexual behavior of children are not rare. In a cross-cultural analysis of adolescence, Schlegel and Barry (1991) found that the expected degree of subordination (obedience and deference) of both girls and boys to their parents was significantly related to both the ability of children to choose their own mates and the existence of economic marriage transactions (e.g., bridewealth, dowry). In societies where parents chose mates for their children and where goods were exchanged at the time of marriage, more subordination was expected from adolescents. This exercise of control is not sexual competition, but it is a sort of “sexually related aggression.”

Prediction 6. Breeding males will invest less in offspring as their certainty of paternity decreases (Emlen 1995:8095).

The terms certainty of paternity and confidence of paternity have been used interchangeably in the sociobiological literature, with both terms encompassing two closely related concepts whose distinct meanings are obscured. One referent of these terms is a population parameter, which might better be called the “probability of paternity” (i.e., 1.0 minus the proportionate incidence of extrapair paternity). This parameter is invoked in modeling the evolution of species-typical male reproductive effort allocations, and in particular in addressing the evolutionary stability or instability of paternal care. The appropriate tests of Prediction 6 under this interpretation are comparative, with paternal investment expected to be present or substantial in those species or populations where paternal probability is high, and absent or relatively slight where it is lower. The second meaning of certainty of paternity is more literal: a psychological parameter varying among individuals within populations according to available cues of the paternity of particular young.

Evolution-minded students of human behavior have long been cognizant of the grounds for Prediction 6, and it has inspired a number of cross-cultural analyses. The main issue of interest has been whether avuncular inheritance—the practice of passing a man’s resources to his sister’s sons or other matrilineal relatives rather than to his putative offspring—is associated with and motivated by paternity doubt. The idea antedates Darwin (Hartung 1985), but Alexander (1974) revived it in a modern context, and subsequent studies have both strongly confirmed the association between avuncular inheritance and threats to paternity, and lent some support to the proposed mediation through male reluctance to invest in unrelated children (Kurland 1979; Gaulin and Schlegel 1980; Flinn 1981). It is unlikely that the level of paternity probability is so low in any human society that a man’s sister’s son is a closer relative, on average, than his wife’s son, and this consideration has been invoked as a refutation of Alexander’s hypothesis. Flinn (1981) and Hartung (1985) argue, however, that bequests are not individual deci-
sions but are rather outcomes of social influence and conflict; moreover, a man’s parents, siblings and other relatives will prefer that he bestow resources on his sister’s child, rather than his own, at any level of paternity probability that is less than 1.0 (see also Euler and Weitzel 1996). Thus, it is hardly surprising that avuncular inheritance should prevail at levels of paternity probability higher than the man’s own threshold for such a preference.

At the level of modulated parental investment within a society, Prediction 6 remains largely untested. A putative father has two principle sources of information about his likelihood of paternity: the phenotype of his putative offspring plus whatever sort of information he may have that bears on the probable fidelity of his mate at the time of conception. There is evidence that males of various species use mate fidelity cues as paternity cues, but there is no evidence as of yet that any non-human vertebrate uses offspring phenotype in this context. People, however, are capable of this feat, and although systematic studies remain to be done, there is an abundance of anecdotal, ethnographic and folkloric evidence of phenotypic resemblance affecting human male investment decisions (Daly and Wilson 1987; Wilson 1987). Moreover, people exhibit strong patrilineal bias in their interest and claims about the familial resemblances of newborn babies, and the details of this bias are readily interpreted as indicating that people are concerned both to improve their own estimates of the likelihood that a putative father is correctly identified and to manipulate the beliefs of the father and other interested persons (Daly and Wilson 1982; Regalski and Gaulin 1993). Presumably this implies that paternity confidence or doubt is consequential.

Daly and Wilson (1987) suggested that paternal affection or love may have evolved to be more strongly influenced by resemblance to self than maternal affection because of paternal “uncertainty”; this influence may still be manifest in adoptive parenthood despite the social father’s knowing full well that he is not the child’s genitor. Essentially, this hypothesis remains to be tested. Similarly, it is at least plausible that cues of paternity affect paternal love in men who sincerely profess complete certainty that the children in question are their own. There is a venerable anthropological controversy about whether any recent human society had yet to discover the link between sex and reproduction, but there is no question that there are societies in which ideology and professed belief deny paternal descent. Interestingly, one of these societies, the Trobriand Islanders, provides one of the most intriguing suggestions of modulated patrilineal investment in relation to paternity cues. Although the Trobriand people explicitly denied patrilineal descent and ostensibly practiced strictly matrilineal inheritance, material goods were also bestowed on patrilateral relatives in ways apparently contingent on phenotypic resemblance (Daly and Wilson 1987).

Although paternity certainty is not necessarily synonymous with consciously accessible beliefs, it is also not necessarily independent thereof either. A sudden revelation of nonpaternity, provided by the evolutionarily novel information source of genetic testing, can at least occasionally demolish paternal affection in one fell swoop (Daly and Wilson 1987). A challenging question for the future is how verbally transmitted and other sorts of more direct information are integrated with motives and emotions in this sphere. Nevertheless, the currently available evidence strongly supports the relevance of Prediction 6 for humans.

**Family Dynamics: Disruption after Breeder Loss or Replacement**

**Prediction 7.** The loss of a breeder will result in family conflict over the filling of the resulting reproductive vacancy. In the specific case of simple conjugal families, the surviving parent and its mature opposite-sex offspring will now compete for breeder status. The conflict will be especially severe when offspring are of the dominant sex and when resources controlled by the family are of high quality (Emlen 1995:8095).

**Prediction 8.** Sexually related aggression will increase after the re-pairing of a parent. In the specific case of simple conjugal families, the surviving parent and its mature same-sex offspring will now compete for sexual access to the replacement mate (step-parent). This conflict will be especially severe when the asymmetry in dominance between the surviving breeder and its same-sex offspring is small (Emlen 1995:8095).
In some polygynous societies, sons indeed compete with fathers for sexual access to the fathers’ junior wives, but this has nothing in particular to do with mate replacement. A father’s decision to take a young wife can enforce postponement of his son’s marital prospects, especially in polygynous bride-price societies (e.g., LeVine 1961), and such conflicts can indeed be severe, even lethal (Daly and Wilson 1988). In contradiction to the situation envisaged above, however, such competitive conflict is likely to be exacerbated by scarce familial resources rather than by their high quality, and more importantly, the “loss of a breeder” is not the precipitating circumstance. Once again we are reminded that the potential to use resources to finance offspring dispersal or reproduction may be an additional and important parameter beyond sheer resource availability.

Neither is such competition sexually symmetrical, as Emlen’s formulation in Prediction 8 may be taken to imply. According to the widely accepted theory developed by Bateman (1948), Williams (1966) and Trivers (1972), sexual access to females is indeed a scarce resource limiting male fitness in animals where females make greater parental investment (or at least greater obligate parental investment) than males, but female reproduction is not importantly constrained by sexual access to males. In light of this generalization, we interpret sexual access in Emlen’s statement of Prediction 8 as another way of again alluding to scarce reproductive vacancies, and insofar as such vacancies are inapplicable to human family dynamics (as we argued with reference to Predictions 1 and 2), so too are Predictions 7 and 8 inapplicable. In any event, the available evidence does not support these predictions. Mother-daughter competition for sexual access to the latter’s stepfather is apparently rare and aberrant. A far more frequent scenario is the stepfather’s imposition of unwanted sexual attention on the stepdaughter (e.g., Russell 1984; Gordon 1989).

In the human animal, one’s entire reproductive career is affected to an unusual degree by mating decisions and reproduction in early adulthood, especially for women, and that may be one reason why Predictions 7 and 8 do not hold. A woman’s early sexual and reproductive behavior can have crucial consequences for her capacity to make and maintain a good marriage; in part, it may seldom be advantageous for a young women to “compete” for reproductive status while residing with a still fertile mother. The degree to which such reputational and marital career constraints are evolutionary novelties versus long-time elements of human sociality will require further consideration in order to construct a fuller cost-benefit model of optimal sexual and reproductive decision-making at different lifestages.

Prediction 9. Replacement breeders (stepparents) will invest less in existing offspring than will biological parents. They may infanticidally kill current young when such action speeds the occurrence, or otherwise increases the success, of their own reproduction. This will be more likely when the replacement mate is of the dominant sex (Emlen 1995: 8096).

The first part of this prediction seems clearly applicable to the human case. Stepparental investment is indeed bestowed more reluctantly and in lesser amount than genetic parental investment, according to a wide range of direct and indirect evidence, and this difference is apparently cross-culturally universal (see Daly and Wilson 1996).

It is also true that people murder step-children at very much higher rates than their genetic children (Daly and Wilson 1988, 1994). Such homicide is nowhere typical, however, and it cannot reasonably be interpreted as evidence of a specifically infanticidal adaptation, since it fails the tests of functional “design” proposed by Williams (1966) and others. It is carried out too inefficiently to meet conventional criteria of an adaptation, for example, as it is often the culmination of a prolonged period of nonlethal abuse that actually raises the investment costs for the abuser. It has too high a cost in potential retribution (although it is admittedly difficult to assess what this cost might be in premodern, nonstate societies), and, contrary to the predominant adaptationist explanation for infanticide in other species as a sexually selected adaptation (e.g., Hausfater and Hrdy 1984), it is far more likely to bring an end to the homicidal stepfather’s relationship with the mother than to hasten the next birth. Daly and Wilson (1995a,b) argue that such ho-
micides are rare, nonadaptive byproducts of discriminative motivational mechanisms that, for the most part, function adaptively to keep stepparental affection and investment restrained.

Prediction 10. Nonreproductive family members will reduce their investment in future offspring after the replacement of a closely related breeder by a more distantly or unrelated individual (Emlen 1995: 8096).

Prediction 11. Replacement (step-) families will be inherently less stable than biologically intact families. This will be especially true when offspring from the originally intact family are of the same sex as the stepparent (Emlen 1995: 8096).

Prediction 10 seems to be a special case of Prediction 4 in that it is the reduced relatedness that presumably drives the decreased helping behavior. Thus a further prediction that can be derived here is that individuals may experience reduced love for children born into their family after one of their parents has been replaced. In this case, replacement of a parent should function as the cue of reduced relatedness. This psychological mechanism apparently has not been tested, but again we can still consider evidence at the level of the behavioral outcome, i.e., the stability of stepfamilies. This evidence is also derived from modern Canada, but as with determination of relatedness in general, there is no reason to suspect that modern culture would have interfered with an individual’s ability to determine if a parent has been replaced.

The proposition that human stepfamilies will be relatively unstable appears to be true. Human stepchildren indeed leave the parental home at earlier ages than genetic children (White 1994); our analysis of the age at which Canadian stepchildren and genetic children leave home, again using GSS data, produces the same result. We also agree that the conflicts leading to departure are ultimately founded in genetic self-interests and the various parties’ opportunities for nepotism (Daly and Wilson 1996). However, our analyses did not support Prediction 11’s claim that boys with stepfathers will leave earlier than girls, and girls with stepmothers earlier than boys; in fact, stepsons leave earlier than stepdaughters regardless of the sex of the stepparent (Figure 5).

Analysis was carried out on the age at which children left the respondent’s home for those who had either stepchildren or genetic children, but not both. Only the oldest child from each family was included in the analysis, and the independent variables included were sex of the child, sex of the respondent and parental status of the respondent. Results of a three-way analysis of variance (ANOVA) showed significant main effects for all three variables (N = 4287; parental status: F = 34.203, p < 0.001; sex of the child: F = 17.864, p < 0.001; sex of the parent: F = 68.843, p < 0.001), and a significant interaction effect between parental status and sex of the child (F = 4.619, p < 0.032). None of the other interaction effects were significant. Overall, the following pattern was the same regardless of sex of the responding parent: stepchildren left earlier than genetic children, but stepsons left earlier than stepdaughters, while genetic sons left later than genetic daughters.

This difference in the age of dispersal for stepchildren versus genetic children could reflect the child’s own decreased inclination to be a helper, as Emlen seems to suggest, but it could also be the result of anticipated or actual diminution of received investment from stepparents. An additional GSS analysis showed no difference in the age at which stepchildren left home as a function of whether their younger siblings were half or full siblings. This analysis

![FIG. 5. RELATIONSHIP OF CHILD TO RESPONDENT AND THE AGE AT WHICH THE CHILD LEFT HOME](image-url)
was run for stepchildren who were the oldest children in the family, and who had either half or full siblings, but not both. Results of a two-way ANOVA, on the age at which they left, by the sex of the stepchild and type of sibling, showed no significant effects (N = 261; sex of child: F = 1.934, p < 0.166; type of sibling: F = 0.938, p < 0.334; interaction: F = 1.218, p < 0.271).

Human stepfamilies are also unstable in that the marriage partners themselves (the “established breeders,” using Emlen’s terminology) are relatively likely to separate. Moreover, whereas for marriages of similar duration, the likelihood of American divorce has been found to decrease with each additional child of the union (at least for the first few), it increases with each child of former unions (Becker et al. 1977; White and Booth 1985). Thus a more general notion that steprelationship engenders conflict of interests and discord regardless of the sex of stepchildren and stepparents, as argued by Daly and Wilson (1987), is certainly upheld.

FAMILY STRUCTURE: REPRODUCTIVE SHARING LEADS TO EXTENDED FAMILIES

Whereas the previous predictions focus on families in which only one pair bred, the final four deal with situations where there may be more than one pair of breeders. Of course, the line between what is relevant for simple versus extended families can be unclear, since the preceding predictions are still consistent with situations in which more than one pair within a family breeds. The following predictions, however, are meant to deal explicitly with that situation. They are derived from reproductive skew theory, which Emlen (1995) summarizes as follows:

All models assume that dominant individuals control the reproduction of subordinates. All further assume that, all else being equal, dominant individuals will maximize their own fitness by monopolizing breeding themselves.

The central idea of skew theory is that when dominants in the group benefit from the continued presence of subordinates, dominants may, under certain circumstances, share reproduction in order to induce the subordinates to remain.

Skew models identify four parameters that specify the conditions under which reproductive sharing should occur and the amount of sharing expected. These are (i) the magnitude of any benefit realized by the dominant if the subordinate should stay, (ii) the expected success of the subordinate if it should leave, (iii) the relative asymmetry in dominance between the potential cobreeders (the dominant and subordinate), and (iv) the genetic relatedness between them [Emlen 1982b; Keller and Reeve 1994]. Each parameter influences the relative payoffs of staying vs. leaving for the different participants. Collectively, they determine the leverage that the dominant has in “withholding,” and the subordinate has in “demanding,” (anthropomorphically speaking) a share of reproduction (pp 8096–8097).

It is in considering the application to human family groups of these predictions, which are based on this reproductive skew theory, that the issues of helper dominance and the helper’s capacity to reproduce become most important. If it is assumed that parents remain dominant to their children at least through late-middle age, then the potential exists for postmenopausal women to act as nonreproductive, dominant helpers to their children. While this situation should have little if any impact on reproductive skew theory, it has a significant effect on Emlen’s predictions as they are currently worded, since it is assumed that dominants are reproductive.

Discussion of the remaining predictions is primarily theoretical, since we were unable to find enough studies that bear on these predictions, and the GSS data are insufficient for conducting further novel analyses of them.

Prediction 12. Reproduction within a family will become increasingly shared as the severity of ecological constraints decreases, that is, as the expected profitability of the subordinate’s option of dispersal and independent reproduction increases (Emlen 1995: 8097).

Of course if dominants are incapable of independent reproduction, then it would be impossible for them to share their reproduction with anyone. Instead, dominant nonreproductive helpers should function as helpers. Reproduction will not be shared, and dispersal is unlikely to occur, regardless of ecological conditions, as we have argued earlier. Dominant nonbreeders could, however, still exert control over the reproductive decisions of subordinates. As previously discussed, available evidence indi-
cates that this is widespread in human societies. The extent to which dominants are able to exert such control may very well be determined by the subordinates’ dispersal options. Especially if there is the potential for multiple breeding pairs (e.g., if the dominant has several potentially reproductive offspring), the fitness interests of the dominant and subordinate may diverge, thus engendering conflict. Too much pressure from dominant helpers does have the potential to make dispersal a preferred option. We suggest that a cross-cultural analysis of the relationship between the potential for successful “dispersal” (i.e., survival outside the family sphere) and who controls marriages would be one way to test this hypothesis. The expected psychological adaptation should make attempts to control relatives according to cues indicative of dispersal options available to those relatives.

**Prediction 13.** Reproduction within a family will become increasingly shared as the asymmetry in social dominance between potential cobreeders decreases (Emlen 1995:8097).

Assume again that the “family” in question is composed of parents and young adult offspring. Even allowing for the possibility that asymmetry in dominance decreases as children age, it is improbable that reproduction could become increasingly shared, since the mother must be of steeply declining reproductive value. However, maternal control over the reproductive decisions of children may indeed decline as their dominance increases relative to their mother’s.

We are aware of one case, which involves an apparent effect of dominance on the sharing of reproduction by siblings, that fits Prediction 13 better. In fraternally polyandrous Tibetan marriages, the oldest brother reportedly shares sexual access to the family’s lone wife more equitably when the younger brothers, who are his cohusbands, are closer to him in age (Crook and Crook 1988).

**Prediction 14.** Reproduction within a family will be shared more equitably when the potential cobreeders consist of siblings than when they consist of parent(s) and grown offspring (Emlen 1995:8097).

This prediction is based on the idea that because siblings are symmetrically related to each other’s children (r = 0.25), whereas parents and offspring are not, parents have more to gain by refusing to share reproduction than their offspring do in demanding it be shared (parents are related by r = 0.25 to children’s children, while children are related by r = 0.5 to their parents’ children).

In the human case, reproduction is probably more equitably shared between siblings than between parents and offspring; lesser sharing with parents is more likely to be a result of the cessation of parental reproduction and not the suppression of offspring reproduction. That is, to the degree that there is parent-offspring reproductive competition in humans, children, not parents, should garner a disproportionate share of reproduction, since by the time the children begin reproducing, parental ability to reproduce is reduced or exhausted. Of course, in some societies, where fathers continue to marry new wives and reproduce well into old age, this sort of reproductive competition could take place between them and their grown offspring; some ethnographic evidence exists that supports this idea (LeVine 1961; see also the discussion of Predictions 7 and 8).

**Prediction 15.** Reproduction will be shared most with those family members to whom the dominant breeders are least closely related. In species in which dominants actively suppress reproduction by subordinates, such suppression will be greatest in those subordinates to whom the dominant is most closely related (Emlen 1995:8097).

This counterintuitive prediction is based on the idea that the inclusive fitness benefits obtained by helpers will vary with the degree of relatedness to the breeder. If a breeder benefits from having help, then the breeder may be selected to offer incentives to potential helpers in the form of direct reproduction to entice them to stay. Since the indirect fitness benefits of helping are lower for more distantly related helpers, they will require greater “staying incentives.”

Nonreproductive helpers, especially postreproductive helpers, should not help unless they gain at least some inclusive fitness benefits, and then they should pattern their assistance so as to maximize those benefits. Thus, the peculiar human reproductive lifespan again undermines the prediction with respect to parent-offspring relations, in which the “dominants” at least sometimes yield all repro-
duction to the “subordinates” and are physiologically constrained to do so. Reproduction should not be shared, and the provision of help should be greatest to those breeders to whom the helper is most closely related. Assistance with childcare and other forms of aid should then be patterned, as discussed with respect to Prediction 4, with helping responsive to cues of genetic relatedness.

A human case of the mutual influences of cowives in polygynous families would be interesting for testing the applicability of this counterintuitive prediction. There is considerable (although not cross-culturally universal) evidence that women married to polygynists do indeed incur some loss of fertility, and that this is especially or solely true for junior, subordinate wives (Anderton and Emigh 1989). Prediction 15 suggests that this suppressive effect should be greater in sororal than in nonsororal polygyny. We could locate no such comparisons in the literature, but we predict that there will be no such effect and perhaps even an opposite one, if cowives who are sisters are more cooperative than unrelated cowives (as seems to be the case; Daly and Wilson 1983), and if they therefore waste less energy in cowife conflict. As noted earlier, human cooperation may often be such that all parties can gain relative to loners.

**GENERAL DISCUSSION**

Extensions of Emlen’s analysis to the human case may either be intended to predict current choices between reproductive and nepotistic investments, or to explain why the human animal has evolved its particular life history in which, for example, nepotistic investment becomes an option before personal reproduction. The questions of why a behavior occurs now and why it evolved require different, separable levels of analysis (Emlen et al. 1990). Read literally, the 15 predictions seem clearly to refer to expectations about socially and environmentally contingent behavioral responses, and that is how we have interpreted them. Insofar as Emlen’s intention was only to reconstruct aspects of the evolution of family systems, much of our critique is admittedly less relevant. Assumptions that the potential for successful dispersal exists and that reproductive opportunity decreases as group size increases could be appropriate in a theoretical analysis of possible origins of helping in humans, for example, even if they are invalid in a discussion of the current nature of family systems and contingent behavioral decision-making.

Available evidence and additional theoretical considerations render aspects of some of these predictions inaccurate with respect to human family systems. They could be rendered more applicable were they reformulated to take into account certain peculiar aspects of the human animal. We have reviewed these aspects and their effects on each prediction and from that discussion we draw several conclusions of our own about the nature of human family interactions. Humans are more or less obligately familial (cf. Emlen’s Predictions 1 and 2). We have evolved to be reciprocal altruists (cf. Emlen’s Predictions 3 and 4), and nepotists who provide unreciprocated assistance commensurate with genetic relatedness (cf. Emlen’s Predictions 3, 4, 6, 9, 10, 11). The human psyche contains mechanisms that make it keenly aware of social standing and of the means by which such standing can be improved or maintained; relatives are not immune to this manipulation (cf. Emlen’s Predictions 2, 5, 7, 12).

A careful consideration of the unique features of the human animal, which justify these additional propositions, is much more useful than a simple cautionary tale about the relevance of studies of nonhuman animal sociality to the analysis of the human case. We have no quarrel with Emlen’s pursuit of general theory at a level applicable to people and other creatures alike. Understanding why Emlen’s predictions so often fail for Homo sapiens can help refine the theories from which they are derived, as well as improve their predictive accuracy with respect to animal family systems, generally. We will therefore discuss them at greater length below.

Some of the lack of fit between the available data and predictions is likely to be a result of the complexity of reciprocal exchanges in human society. Certainly, predictions that specify greater assistance between relatives than nonrelatives (Predictions 3 and 4) would be rendered more accurate if nonreciprocated assistance were distinguished from reciprocal altruism. The existence of menopause, so that
mothers who are no longer capable of reproduction act as helpers, has obvious effects on the predictions about reproductive sharing (Predictions 12 through 15), since dominant family members incapable of independent reproduction cannot share it with others. This issue also has a more subtle effect on the predictions pertaining to family formation and stability (Predictions 1 and 2). If helpers are dominant and incapable of reproduction, they are unlikely to be tempted to disperse, regardless of ecological conditions, as long as they can gain inclusive fitness benefits by helping. Subordinate breeders should remain as well, as long as the actions of the helper provide a net benefit to them.

Of course dominant helpers, by virtue of being dominant, will have more latitude in the degree of help they provide than would subordinate helpers. The breeder may not be satisfied with the amount of help provided by the helper, but as long as it is better than nothing, the family grouping should have been selected to remain stable, regardless of whether there are acceptable reproductive opportunities elsewhere and regardless of the resource situation of the family. An increase in acceptable independent breeding opportunities may change the degree of influence the dominant helper has over the breeder, but it should have little effect on the stability of the family. In other words, the existence of postreproductive family members as helpers should provide an unusually strong incentive for both the helped and the helpers to not disperse.

A detailed study of parent-adolescent conflict would be an interesting avenue for further exploration of intrafamilial dominance relationships; it is one that could shed more light on the nature of the mechanisms by which adult dominance rank is achieved. When parents and adolescents argue, their conflict typically revolves around the adolescent's resistance to parental attempts to control his or her life (Montemayor 1983; Ellis-Schwabe and Thornburg 1986). This is not as true for younger children. According to Turiel (1975, 1977), early adolescents consider certain social conventions to be largely arbitrary, deferring to them when convenient, while still denying their legitimacy. While younger children agree that parents have the right to establish rules, by the age of 12 or 13 they begin to question the legitimacy of parental rule-making. Furthermore, the temporal pattern of this conflict has been shown to follow an inverted U-shaped pattern (Montemayor 1983; Steinberg 1989). Conflict increases with the onset of puberty and reaches a zenith at the apex of pubertal growth before declining, at least in modern Western society (such adolescent conflict with parents does not appear to be cross-culturally universal, according to Schlegel and Barry 1991). Together these findings suggest that the onset of adolescence is a trigger for changes in dominance relations with parents, and perhaps also the community at large. An increased understanding of the factors leading to differences in cross-cultural expression of parent-adolescent conflict could be enlightening.

So far the discussion has taken it for granted that mothers of adult offspring are postreproductive. Why don't mothers share reproduction? Why do they undergo such early menopause? There is no definitive answer yet, although there are a few theories. One of the most common explanations is that by ceasing reproduction early and spending her remaining years assisting her existing offspring, a woman gains greater overall fitness benefits than she would if she were to keep reproducing. However, Hill and Hurtado (1991) have tried to test this hypothesis with data gathered from Ache hunter-gatherers, and found negligible support for it; support for any of the competing hypotheses they outline is really no better, and they suggest in conclusion that the correct answer may invoke a combination of factors.

Recall that parents are related to all their children equally ($r = 0.5$), while each child is more closely related to itself ($r = 1.0$) than to any nonidentical full sibling ($r = 0.5$) or half-sibling ($r = 0.25$). Parents can thus promote their fitness by influencing offspring to allocate their nepotistic and reproductive efforts a little differently (Trivers 1974), as we noted with respect to intrafamilial influence on avuncular versus patrilineal flows of resources. Postmenopausal women are apparently specialists in the exertion of such influence (Brown 1982). The existence of menopause also affects the costs and benefits of offspring dispersal decisions. Although a postreproductive mother...
may not have the best interest of a particular child in mind, she still has only one available means of promoting her fitness: helping children and other relatives reproduce successfully. Assuming that she has the ability to do this, those relatives that stand to benefit, e.g., her children, ought to maintain ties with her throughout their lives. Thus, while Predictions 12 through 15 can merely be slightly reworded, Predictions 1 and 2, which deal with family stability, need to be reconsidered; they are likely to be inapplicable to the human case as far as parent-offspring relations are concerned.

There is an additional pattern that emerges from the analyses presented in this review that Emlen did not consider in his list of predictions, but which is relevant to an understanding of human familial interactions. Deviations from Emlen’s predicted results by and large seem to be related to efforts to gain or maintain status. The idea that status striving is an evolved mechanism that helps to maximize the genetic success of individuals in social species is not new. In general, the correlation between status and genetic success in nonhuman animals is good, although not perfect: high ranking individuals tend to achieve greater mating success and to leave more offspring (for reviews see Dewsbury 1982; Fedigan 1983). The problem, and a source of much debate among those who study the evolution of human behavior, is that this relationship does not always hold for humans (see Ethology and Sociobiology 1990).

It is unlikely that a conscious striving for genetic success is a normal or necessary mechanism for its achievement in any human or other populations. Instead such ends are achieved through the development of adaptations that track more easily determined things that have been reliably correlated with high genetic success. Status seeking is a good candidate for such an adaptation. Both nonhuman and some human evidence suggest that status seeking is likely to have been a good proximate mechanism for achieving high genetic success in the past (Dewsbury 1982; Fedigan 1983; Betzig 1986; Péruse 1993). The universality with which high status is assumed to be a good thing, to such a degree that the existence of a desire for increasing it is often taken for granted, is perhaps the most convincing argument that it is an adaptation for something.

The benefits of high status may have remained through much of recorded history, at least for men. Betzig (1986, 1994) has reviewed historical and cross-cultural evidence from Roman times until the present and has found a pattern: wealthy and powerful men obtain sexual access to the greatest number of women, access that is usually but not always converted to reproduction, often in the form of large numbers of illegitimate children. The tendency for high status to impart polygynous mating opportunity was evidently much reduced with the advent of modern democracy, but it did not disappear. It has been shown in modern Quebec that men’s sexual opportunities (and hence presumably their fertility, were it not for contraception) are positively correlated with social status (Péruse 1993), and we expect that this association is widespread.

The relationship between status and reproductive behavior in women is less clear. It appears that in societies where women gain prestige through motherhood the expected correlation between high status and high fertility exists, but it seems to break down when women can gain status by other means, such as by employment or education, or when high fertility can lead to a reduction of status for offspring (Kasarda et al. 1986). Similarly, the number of legitimate offspring sired by wealthy or powerful men also seems to decline when large numbers lead to overpartitioning of resources and decreased familial status. Obviously more work needs to be completed on this topic, as pioneered by Betzig (1986).

Status seeking seems to be governed by such a strong drive that it interferes with rather than increases genetic success in certain environments. It is fine to claim that status, therefore, would be correlated with genetic success but for the effects of technical and social novelties, yet the real question is why has it broken down this way. The most frequently blamed culprit for this dissociation is birth control (Péruse 1993). However, the common notion that effective birth control did not exist until recent decades is at best a serious oversimplification.

In fact, partially effective attempts to limit fertility through contraceptive techniques, abortion or infanticide are so ubiquitous as to be considered a human universal (Himes 1936; McLaren 1990). The ancient Greeks and Ro-
mans, for example, possessed remarkably effective contraceptives and abortifacients. These were derived from various plants, which recent research has shown do, in fact, serve their desired purpose. The demand for effective birth control in the ancient world was so great that the most popular remedy, a plant called sylphium (Ferula sp.) was rendered extinct by the 4th century AD (Riddle 1992). Nor is classical civilization unique in this knowledge. Plants with contraceptive utility are harvested today by women in places as diverse as India, Latin America and the Appalachian Mountains of the United States (Riddle 1992).

The availability of modern birth control methods, and knowledge of how to use them properly, are not enough to guarantee their use, however. Such knowledge and availability have been ineffective in reducing fertility in overpopulated third world countries (McLaren 1990; Kasarda et al. 1986), where women tend to use modern methods in place of their traditional birth control techniques to regulate birth intervals, but not to limit family size (McLaren 1990). The interesting questions, then, are what are the contingent controls of efforts to limit fertility, and what psychological adaptations, with what ancestral functions, influence these reproductive ambitions and decisions (Kaplan 1996)?

We hypothesize that inclinations to limit family size are somehow linked to attempts to gain or maintain status. When having children drains resources and can thereby lower status, women may seek to have fewer children. In an attempt to find a means to reduce birth rates in developing countries, Kasarda et al. (1986) argue, in a review of the available literature on the relationship between social mobility and fertility, that the status of women is critical to the shaping of reproductive behavior. Their fundamental conclusion is that in order to limit fertility, it is necessary to shift the determination of a woman’s status from predominantly male-dependent to a female-oriented, self-determined focus. They discuss three variables that have been shown to be the most successful in limiting family size: increasing the amount of education women receive, increasing women’s participation in the labor force (but only if the job held provides the opportunity for advancement and cannot be combined with childcare), and decreasing the value of children as net wage or labor producers in the household.

Certainly all of these conditions are met in modern industrial society, which also exhibits remarkably low fertility. Just as effective contraception is not as novel as widely believed, the modern world is not the only one to experience decreased fertility. The Roman Empire is known to have suffered population decline between AD 1 and 500 (Riddle 1992). Writers of the time decried the phenomenon, and laws were passed to encourage increased family size (McLaren 1990). Women are also known to have held an unusual amount of power in Roman society: they could inherit, own and bequeath property. A Roman woman could obtain a divorce from her husband, and upon separation her dowry was returned to her, not her natal family (Leftowitz and Fant 1992).

In answer to the puzzle of the relationship between status and reproductive success in humans, given the available evidence, we think it a reasonable hypothesis that when people are forced to make a trade-off between having an additional child and increasing or maintaining their social status, they opt for status maintenance (for a similar argument see Donaldson 1991). Perhaps this choice was the more judicious way to ensure lineage survival and long-term fitness in ancestral societies, an idea that we think plausible but hard to test. (Evidence concerning the long-term fitness consequences of reproductive and contraceptive decision-making in the modern context has little if any relevance, a point that has often been misunderstood, e.g., by Vining 1986.)

The data on marriage transactions reviewed by Schlegel and Barry (1991) imply that when parents are in control, the timing of marriage is based on status concerns. The idea that such concerns affect reproductive decisions is implicit in some of Emlen’s predictions, but it needs elaboration. Parents sometimes try to influence children to further their own personal interests. If a given behavior can lead to increased status, then humans are likely to engage in it, regardless of its fitness payoff. Since Emlen’s predictions are predicated on maximization of this distal payoff, rather than on the proximal currencies that evolved psychological mechanisms can actually monitor, they may not always hold.
One final issue worth considering is the appropriate level at which to define a human group or family. Humans are highly social and can live in extremely large groups composed of many different families, who may or may not interact extensively with each other. Much of the theory behind these predictions may also be appropriately applied to analyses of human behavior in these larger social units. Research has already been carried out in this area by Betzig (1994), who successfully applied skew theory to understand the existence of despotism versus democracy in human societies through history.

In conclusion, a solid base from which to explore the detailed nature of human family systems will be created if the predictions can be refined to take into account (1) the importance of intragroup solidarity in the context of intergroup competition, (2) the complex nature of exchange and reciprocity in human society, and (3) the implications of menopause and the existence of potentially dominant, postreproductive helpers. Of course, further exploration of the evolved psychology of human family relations should not be limited to the scope of these predictions. Inclusive fitness theory, ecological constraints theory and skew theory provide a wealth of ideas about the expected outcomes of family dynamics. Their basic logic or insights will have to be part of any truly comprehensive theory of human familial affiliation and stability.

Rather than focusing effort exclusively on the determination of universal organizing principles, we suggest that an additional strategy for examining the tremendous variability that can exist within one species, such as humans, is the degree to which this variability can be usefully interpreted in light of these theories. Finally, an understanding of the psychological adaptations that govern family relations will prove just as valuable in the search to understand our families and ourselves.

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