

Adaptations for social living: relationship-specific social psychological adaptations, by Margo Wilson & Martin Daly. In G. Bock & G. Cardew, Eds. *CIBA Foundation symposium on Characterizing Psychological Adaptations*: Chichester: Wiley.

Relationship-specific social psychological adaptations

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Abstract. Mainstream social psychology has sought parsimonious explanations of broad general applicability, and has in practice focused on stranger interactions. An evolutionary perspective, however, justifies predicting a rich diversity of relationship-specific social psychological adaptations. The demands of motherhood, fatherhood, mateship, sibship and other relationships are qualitatively distinct, and so, it appears, are the psychophysiological mechanisms that have evolved to deal with them. One window on what distinguishes social relationships is provided by the substance and epidemiology of interpersonal conflicts. Homicides exhibit victim-killer relationship-specific patterns in context, motive and demography, which we discovered only because we adopted an evolutionary psychological perspective. We offer a number of specific hypotheses about possible human psychological adaptations that have yet to be assessed, but are readily derived from consideration of the particular qualities of specific relationship types.

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Psychologists have paid surprisingly little attention to social relationships. For decades, experimental social psychologists studied interactions with strangers, often imaginary strangers minimally described, on the presumption that basic processes -- such as liking, conforming, etc. -- are best illuminated in controlled, decontextualized studies. Recently, this restrictive focus has been somewhat alleviated as the study of 'close relationships' has become a significant subfield, but research under this rubric remains unduly narrow. Berscheid's (1994) extensive review, for example, is concerned primarily with dating and marital relationships and secondarily with same-sex friendships, making no reference to rivalries, patron-client relationships or any sort of familial relationship whatsoever.

With backgrounds in non-human animal behaviour, our bias has been to seek ecologically valid windows on real world behaviour. Homicides have provided us with an especially interesting 'assay' of interpersonal conflict, permitting tests of various hypotheses about the substantive issues of central importance in different relationship types (Daly & Wilson 1988, Wilson & Daly 1996). This window proves cloudy, however, when one wishes to characterize putative psychological adaptations in detail.

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An evolutionary adaptationist perspective suggests that several distinct types of interpersonal relationships are sufficiently ancient and important to have affected the functional organization of our evolved social psyche. Sexual partnership, friendship, parenthood and so forth are qualitatively distinct kinds of close relationship differing in many specific ways. The attributes of an ideal mate, say, are quite different from those of an ideal sibling or friend, and it is clear that the mind processes information about these different sorts of intimates in different, specialized ways (Symons 1995). The things that require attention differ between relationship types, and so do affect and phenomenology. What constitutes a betrayal of one type of relationship might be irrelevant to another. Even the several fundamental sorts of close genetic relationship require distinct analyses.

Kinship psychology

Inclusive fitness theory suggests that evolved social psyches will respond discriminatively to cues indicative of degrees of genetic relatedness. Although there is intriguing cross-cultural diversity in human kinship systems, diversity of evolutionary psychological interest in itself, there are also some telling universals (Daly et al 1997). Parent-offspring relationships are the fundamental building blocks of ego-centred kindred terminologies in all societies, such that terminology implies genealogy, and people everywhere conceive of kin relations as arrayed along a 'close-distant' dimension. This closeness is always positively (albeit imperfectly) correlated with both genetic relatedness and actual co-operativeness. Diverse homicide analyses, for example, indicate that relatedness reduces risk, *ceteris paribus* (Daly & Wilson 1988). Some recent studies have belatedly introduced relatedness into the social psychological literature on the determinants of altruism, and the results have been highly supportive of selection-minded models (Burnstein et al 1994, Petrinovich et al 1993, Wang 1996; see Fig. 1). Whether the human mind contains procedures for computing something like relatedness coefficients and whether the same estimates are used in distinct domains demand investigation. For example, Wedekind et al (1995) have provided evidence that olfactorily mediated detection of shared major histocompatibility complex alleles dampens human sexual attraction and thereby facilitates outbreeding, but whether the same cue affects discriminative nepotism is unknown.

There is an a priori reason to suspect that kin classification might employ specialized mental processes. Unlike most other categorizations, kinship cannot be represented as a nested hierarchy because of sexual reproduction. Our ancestors double at each generation, making 'family' an altogether different computational problem. Nevertheless, people often seem determined to bend their conceptualization of family links to fit the inappropriate nested hierarchy model, placing themselves and others in named families (usually patrilineages). Why do people resort to this inappropriate mental model? D. Jones (unpublished work 1996) has argued that selection can favour a relatively undifferentiated kin group identity if mutually enforced

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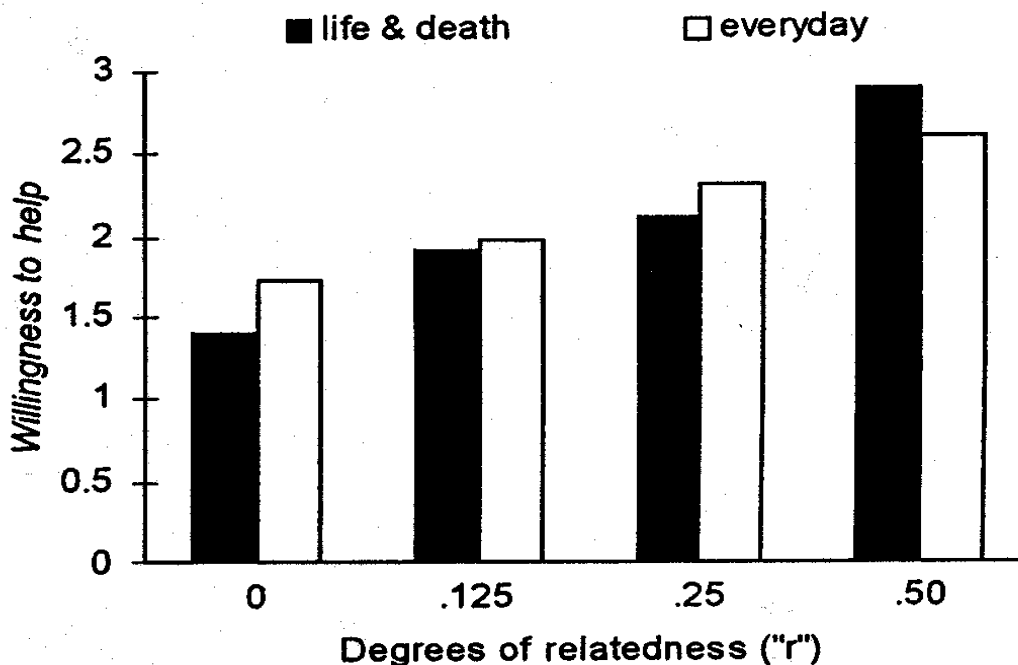


FIG. 1. Effect of relatedness on undergraduates' professed inclination to help a same-sex person, depicted as sibling, parent, nephew/niece, cousin or acquaintance, in two hypothetical situations (Burnstein et al 1994). Relatedness was significantly more predictive of choice of beneficiary in the 'life-or-death' situation; sex and nationality (US vs. Japan) of subjects had no effects.

group norms are incorporated into a variant of Hamilton's theory. Perhaps so, but even the most extreme systems of unilineal descent reckoning do not suppress bilateral affiliation and sympathy (Fortes 1969), so one may question whether clan memberships and patrinyms are really such powerful elicitors of familial feeling as they sometimes appear. Another issue for psychological research.

Genealogical kinship is not simply unidimensional. It encompasses several qualitatively distinct categories of relationship. The business of being a mother is quite different from that of being a father or an offspring or a sibling. There is no question that *Homo sapiens* possesses specific psychophysiological adaptations for dealing with the peculiar demands of motherhood and offspringhood, and we probably have others for dealing with the challenges of being fathers and siblings. Psychological adaptations for grandparenthood and perhaps for other distal kin relationships remain plausible, too.

Motherhood

The most intimate of mammalian social relationships and the one with the largest inventory of special-purpose anatomical, physiological and psychological machinery is that between mother and young. But the task demands of motherhood are a good deal more complex than even a consideration of the component demands of conceiving, gestating and raising a baby would imply. Because offspring are not equally capable of converting parental nurture into parental

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fitness gains, selection for subtle discrimination in allocating maternal effort is intense, and the evolved motivational mechanisms regulating maternal investment decisions are complexly contingent on variable attributes of the young, of the material and social situation, and of the mother herself, including life span developmental changes from youth to menopause.

Adaptive allocation of maternal investments is an especially subtle problem because of the active intervention of other parties with conflicting interests, particularly the offspring themselves. Parent-offspring conflict (Trivers 1974) is endemic to sexually reproducing species because of a certain asymmetry of relationship. Mother is equally related to her offspring, but each offspring is more closely related to self than to sib, so each offspring is selected to covet a little more from mother than would be optimal for her own fitness. This conflict accounts for the otherwise puzzling existence of seemingly maladaptive aspects of mother-young interaction, including weaning conflict, tantrums and the dangerously high levels of allocrine substances of fetal origin, such as human chorionic gonadotrophin and human placental lactogen, in the blood of pregnant women (Haig 1993).

Social psychologists and motivation theorists have largely ignored maternal inclinations, but paediatricians have done a lot of research on the immediate postpartum period. This literature implicitly treats maternal attachment as unidimensional, but an evolutionary perspective suggests instead that it is likely to involve at least three separable processes proceeding over different time courses: (1) assessment of the quality of the child and the situation; (2) rapid discriminative attachment to the baby as an individual; and (3) more gradual deepening of individualized love (Wilson & Daly 1994).

The first hypothesized process functions as an immediate postpartum assessment of the reproductive episode's prospects. Adaptationist thinking suggests that present material and social circumstances, the baby's phenotypic quality and the mother's residual reproductive value will all be determinants of a 'decision' whether to follow through or opt out. The hypothesized effect of a mother's reproductive value is supported by age-specific infanticide rates (Fig. 2) and by the finding of Jones et al (1980) that responsiveness to one's infant increased with maternal age, independent of any effects of marital status, socioeconomic status or postpartum contact. As for infant phenotype, deformities and signs of low viability raise the risk of maternal abandonment in non-state societies and elicit shocked rejection even in modern hospital settings. Postpartum maternal responsiveness also varies with more subtle cues of infantile quality and health. In this context, it is noteworthy that healthy human neonates exhibit a precocious social responsiveness that superficially mimics that of an older infant, including eye contact and selective attention to maternal speech, behaviours readily interpreted as infantile tactics for advertising quality and eliciting maternal commitment during this risky assessment phase.

Many new mothers experience a brief period of the 'blues', and some a more debilitating postpartum depression associated with concerns about their ability to cope with the baby. Such

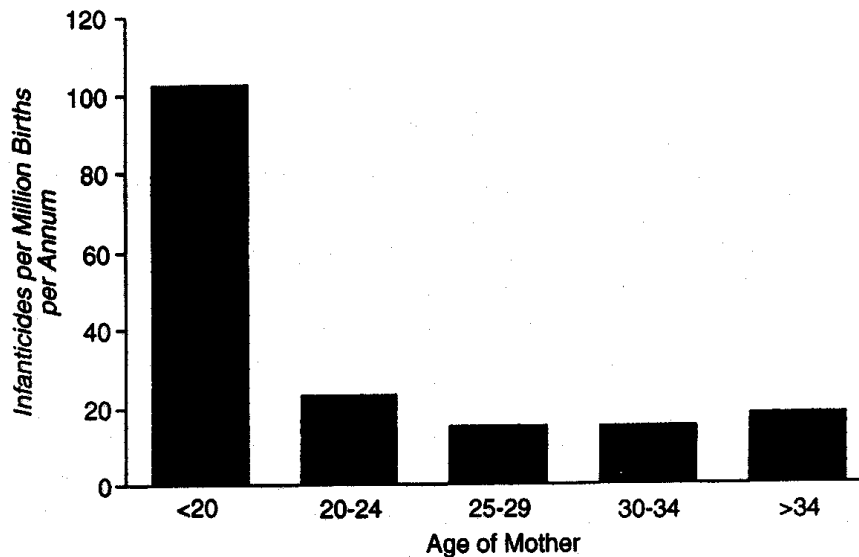


FIG. 2. Rates of infanticide ($N = 227$) perpetrated by mothers in England and Wales in 1977–1990 as a function of maternal age. Homicide data provided by the Home Office; age-specific births from the Office of Population Censuses and Surveys.

depression is apparently especially likely when the mother is young, single or otherwise lacking social support, and when the infant is unhealthy. Postpartum depression is typically discussed as pathology, and in extreme cases it surely is, but these correlates suggest that it must be understood as an extreme form of an adaptively modulated emotional response.

If postpartum evaluation justifies further investment, the mother must then develop an individualized commitment such that she is emotionally prepared to invest heavily in her baby's welfare without being vulnerable to parasitism by unrelated children. This is the adaptive rationale for our second proposed maternal-bonding process. In social mammals with precociously mobile young and synchronous births, this discriminative attachment is urgent, and special-purpose neurochemical mechanisms for attaining it within a few hours of birth have been discovered in sheep (Kendrick et al 1992). In the human case, this individuation occurs at a more leisurely pace: mothers commonly report developing a feeling that their baby is uniquely wonderful over several days.

Mothers are highly sensitive to their newborns' distinctive features, recognizing them by voice, smell or touch after scant exposure, and these abilities are often portrayed as specific adaptations for discriminative bonding. This argument is weak. Evidence that discriminative abilities are actually heightened in new mothers is lacking, nor is it likely that postpartum infant recognition errors were an important selective force in human evolution. (And our more general ability to discriminate faces visually would solve the problem if they were.) Special offspring recognition adaptations exist where they are needed; for example, such abilities vary among

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closely related species of swallows according to whether the breeding ecology is such as to expose parents to the risk of misdirected parental investment (Beecher 1990).

The third predictable process of maternal attachment is much more gradual. A mother's love may be expected to grow with the child's increasing reproductive value, especially over the first few years as the probability that the child will survive to reproduce rises steeply. The relentless decline in filicide rates even into the teens (Daly & Wilson 1988) supports this expectation, as does the longitudinal study of Fleming et al (1990) in which positive maternal affect towards baby grew monotonically over months, while the same measures held relatively steady with respect to self and husband.

Information that mothers garner from monitoring offspring quality should affect the depth and time-course of their love and commitment, especially while mortality risk remains high. In many societies newborns are not immediately named or officially acknowledged by the community, a practice more or less explicitly linked to their uncertain future; naming bestows personhood and facilitates the individuation of affection. The delay in recognizing infants' personhood facilitates difficult divestment decisions, lessening emotional pain should the infant die. Since maternal effort is not to be squandered, chronic changes in infantile responsiveness and robustness due to malnutrition, dehydration and pathogens may be expected to diminish maternal inclinations, despite the sickly infant's greater need. In an observational study of low birthweight twins, Mann (1992) found that the healthier twin was indeed more effective in eliciting maternal responsiveness; factors such as duration of postpartum separation and infant smiling could not account for the mother's differential treatment.

Fatherhood

Much of the above theorizing applies to fathers as well, but there are crucial differences. Both parents are selected to assess offspring quality and need, but the father lacks the special avenues of communication (and manipulation) between mother and fetus or nursling. Both parents are also likely to respond to cues of the fitness value of available alternatives to present parental investment, but here it is even clearer that the specifics are different: the chronic chance that extra-pair mating effort might enhance male fitness is a selection pressure against intensive commitment to fatherhood. Finally, both parents are selected to discriminate with respect to available cues that the offspring is indeed one's own, but the relevant information sources are again distinct. Paternity can be misattributed, so putative fathers must rely on information about possible infidelity and/or familial resemblances. One implication is that fathers' affection may be influenced by their children's resemblance to themselves, whereas little or no such effect would be expected in mothers. This hypothesis awaits a good test, but there is evidence that all interested parties pay much more attention to babies' resemblances on the paternal than on the maternal side, and that mothers and their kin actively promote perceptions of paternal resemblance (Daly & Wilson 1982, Regalski & Gaulin 1993).

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Some male songbirds adjust paternal investment adaptively in response to cues of paternity probability (e.g. Davies 1992). Male mice time the interval since they last ejaculated into a female, and become non-infanticidal weeks later when resultant offspring might be born (Perrigo & vom Saal 1994). Behavioural ecologists call these 'paternity (un)certainty' (or 'paternity confidence') adaptations with little risk of being misunderstood as implying awareness, but that implication is often drawn when *H. sapiens* is under consideration. It should not be. In principle, human paternity confidence adaptations may function in isolation from articulatable beliefs. The affection of adoptive fathers may be more strongly affected by the adoptee's resemblance to self than the affection of adoptive mothers, for example, simply because such resemblance is a cue to which the paternal psyche has evolved sensitivity.

Sibship

Sibling relations also warrant scrutiny from a selectionist perspective. Sisterhood is, of course, at the heart of the analysis of Hamilton (1964) of the evolution of altruism in social insects, but sibling relations are prominent in the sociality of diploid creatures too, especially in studies of 'helpers at the nest' (Stacey & Koenig 1990). Siblings are natural allies by virtue of relatedness, but they are also competitors for parental resources. Little wonder, then, that sibling relationships are often 'ambivalent'.

The costs that a toddler is willing to impose on its infant sibling in competition for maternal investment may vary adaptively in relation to nutritional status, the birth interval, the social situation and perhaps even the phenotypic quality of each youngster. This could be a profitable area in which to seek hitherto unsuspected psychological adaptations. It is also plausible that siblings are sensitive to paternity cues indicating full vs. half sibship. In Belding's ground squirrels, Holmes & Sherman (1982) found that full sisters are more co-operative neighbours than half sisters, even when both sister types are littermates so that familiarity is controlled. Could there be analogous discrimination in humans? Data on women's reproductive careers in contemporary foraging peoples (e.g. Hill & Hurtado 1996) imply that the distinction between full and half sibship may have been selectively significant in our ancestors, so toddlers may possess psychological adaptations for adjusting the intensity of competitive tactics towards newborn siblings in relation to either phenotypic cues or direct evidence of male turnover,

Such modulated sib competition adaptations could even be operative *in utero*. Live cells of fetal origin persist in maternal circulation for years after a birth, and may be active agents in genetic conflicts, and Haig (1993) has convincingly interpreted pregnancy pre-eclampsia as a by-product of maternal-fetal conflict over resource transfer. In light of these considerations, it is interesting that the incidence of pre-eclampsia in second and later pregnancies is elevated after a change of paternity (Trupin et al 1996). This may reflect escalated fetal conflict tactics, perhaps because the fetus can somehow assess its relatedness to its predecessor or, more plausibly, because the vestigial cells of the predecessor assess their relatedness to cells of the new fetus

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entering maternal circulation, and manipulate the mother to withhold resources more if it is only a half sib, inspiring a compensatory response from the fetus.

Birth position within a sibship is a crucial aspect of one's social ecology. The eldest child commonly enjoys a parental priority that influences life options and personality development (Sulloway 1997). Subsequent children are apt to be less familially oriented and more inclined to forge reciprocal ties with non-relatives, but a lastborn child is in some ways more like a firstborn than a middleborn (Salmon 1997). Thus, more than merely seeking psychological adaptations for sibling interactions, we may need to consider even finer intrafamilial relationship categories.

Marital and affinal relationships

People refer to 'relatives' by marriage as well as by blood, and there is a certain logic to this conflation: in both cases, relatives have a commonality of interest grounded in the fact that both gain fitness from the reproduction of their common kin. A longstanding mateship becomes increasingly like a genetic relationship because as children are produced and mature the exigencies and resource allocations that would be ideal for promoting the fitness of the two parties are increasingly consonant. Indeed, if mating partners are faithfully monogamous and their efforts are channelled predominantly into reproduction rather than collateral nepotism, their commonality of interest -- and hence of perspective -- may become near-total (Alexander 1987). This would seem to explain why established couples may become more solidary than even the closest genetic kin. Interests in their separate kindreds remain a potential source of conflict in any couple, but these 'in-law problems' may be more acutely felt when there are no children to cement the marital relationship and the broader alliance between the two parties' families of origin that the marriage represents.

An important difference between mateship and genetic kinship is that the former is more readily and irredeemably betrayed. The correlation between mates' expected fitnesses can be abolished if either engages in extrapair mating effort, and should a cuckolded husband unwittingly invest in a rival's young, the very acts that promote his wife's fitness are positively damaging to his own. These considerations apparently explain why suspected or actual infidelity is a uniquely potent source of marital conflict and violence (Daly & Wilson 1988, Wilson & Daly 1996).

Step-relationship is like cuckoldry in that the child is a potential vehicle of fitness for one marriage partner but not the other. It is different, however, in that this asymmetry is out in the open, and has ideally entered into the negotiation of entitlements and reciprocities in the remarriage. Nevertheless, the presence of stepchildren is an important risk factor for marital disruption and violence, and the stepchildren themselves incur greatly elevated risk of violence too (Daly & Wilson 1996; Fig. 3). Step-parenthood itself is evidently the relevant risk factor, rather than some correlate or 'confound', reinforcing the point that parental psychology is designed to channel affection and investment preferentially toward own offspring.

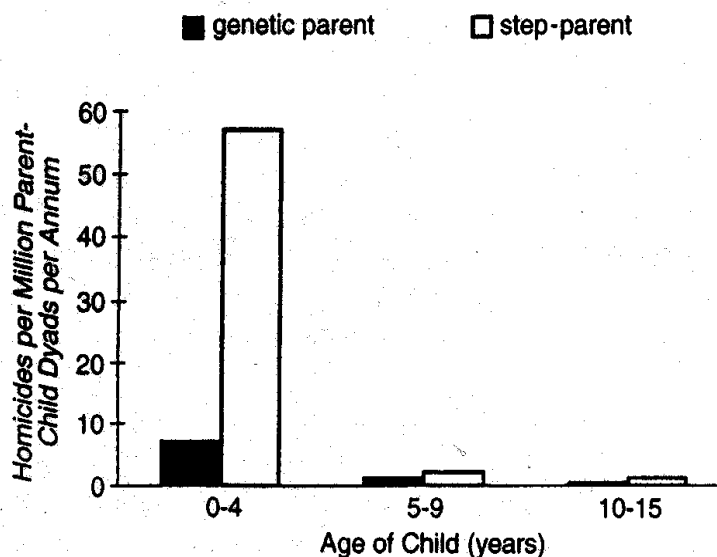


FIG. 3. Rates of filicide perpetrated by genetic parents ($N = 726$) and stepparents ($N = 141$ victims) in England and Wales in 1977–1990 as a function of victim's age. Homicide data provided by the Home Office; population-at-large estimates derived from census data and Clarke (1989).

Non-familial relationships

We have concentrated on family relationships both because of the ready applicability of selectionist ideas and because psychologists have neglected them. But non-kin relationships may have a natural taxonomy and a set of distinct social psychological competences too. One might distinguish co-operation based on individual reciprocity versus co-operation based on shared group identity versus indifference versus enmity, for example.

Fiske (1991) and Haslam (1994) maintain that relationships themselves are not discretely categorical, but that people generate them from four discrete mental models, called 'communal sharing', 'authority ranking', 'equality matching' and 'market pricing'. We suggest that these models are better described as alternative solutions to co-ordination problems than as a complete 'mental grammar' of social relationships. Whether combinations of these models can generate all qualitatively distinct non-kin relationships we cannot say, but they surely fail to encompass all the relationship-specific psychological adaptations of kin relationships as described above. Kinship is evidently the dominant mental model for helpful social interactions (Bailey 1988), and hence it provides an almost inescapable metaphor for establishing, describing or explaining co-operative relationships with non-relatives. Indeed, Alexander (1974) suggested that the cognitive abilities necessary for non-nepotistic reciprocal altruism must have evolved previously in the context of nepotistic sociality. Turning such conjectures into empirically testable propositions is a challenge for evolutionary social psychologists.

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DISCUSSION

Beecher: It would be interesting to look at olfactory signatures. Dick Porter has done quite a bit of work showing that mothers can recognize the smell of their children even when they are only one day old (Porter 1991).

Wilson: Mothers, fathers and just about anyone else can also recognize children on the basis of touch or on their voices. It's clear that the human species is good at individual recognition, but it's not clear whether mothers have a special ability at this time. It is interesting to speculate whether non-obvious cues, such as olfactory mechanisms, might impact on bonding. Martin Daly and I are interested in this issue because of the differential risks of children being killed or abused by step-parents versus genetic parents. There are mechanisms whereby individual children are identified but we know little about them.

Beecher: Is there any evidence in humans that fathers discriminate between their children on the basis of physical resemblance?

Wilson: No. We have hypothesized that physical resemblance to self or family should affect paternal attachment and not maternal attachment, but there isn't any good evidence that supports this.

Buss: Would one expect an evolved mechanism of that sort? It is possible that relatives could judge the similarity of an infant to the father, but if mirrors were not a feature of our ancestral environment

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then you wouldn't necessarily expect the self to be able to make that similarity judgement.

Wilson: It is possible that they could have had an image of their face from looking in water.

However, say for argument's sake that they never had an image of their faces, this is not a problem because there's lots of evidence in the anthropological literature that people use other cues. The question of what is the specificity of our hypothesis is interesting. It's not clear that the baby should look like the father, because from the father's point of view there should be a cue that it's his child, but that's not necessarily the case from the mother's point of view or even the child's point of view. Therefore, the actual prediction is uncertain. A study that was published in *Nature* last year by Christenfeld and Hill at San Diego claimed that when you gave people three pictures of men, one of which was the father, and three pictures of women, one of which was the mother, when the child was one year of age the people were just over 50% accurate in attributing the father to that child, but this wasn't the case for mothers or when the child was a 10-year old or a 20-year old (Christenfeld & Hill 1995).

Scheib: There have been reports on parental resemblance in the donor insemination literature. A few of these have studied what potential parents are concerned about when they're choosing a sperm donor. One of the things that I found interesting was that both the physicians and the recipient couples try to match the donor to the woman's partner, with the articulated belief that parent-offspring resemblance will help the couples keep their use of donor insemination a secret. You might also expect them to behave in the same way, even if secrecy were not a concern. In any case, they have the psychology that values father-offspring resemblance. And there are hints of sex differences too, For example, one study by Klock & Maier (1991) found that women were more concerned about the physical resemblance of the child to the father, but the women's partners were more concerned about the child's personality resemblance to themselves.

Cosmides: David Haig in his plenary address to the Seventh Annual Meeting of the Human Behaviour and Evolution Society (University of California, Santa Barbara 1995) talked of his studies on how women in short-term versus long-term relationships have different risks of various pregnancy-related disorders. It would be interesting to see whether the children of women in long-term relationships bore more resemblance to the father, and whether this was because parts of the paternal genome were being more highly expressed.

Wilson: There was a study published in *Epidemiology* last Spring that is really interesting in the light of David Haig's work on maternal-fetal conflict (Trupin et al 1996). It was an epidemiological study of pre-eclampsia in the US involving 1000s of cases and controlling for age and socioeconomic conditions. The risk of pre-eclampsia normally decreases by half from first birth to second birth or later, but they found that for the second birth or later, if there was a change of paternity pre-eclampsia rates were twice as high. Therefore, there could be some subtle factors that affect the maternal valuation and assessment phase in ways that we could never have imagined before.

Dawkins: What do you mean by change of paternity?

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Daly: The alleged father of the second child was different from the alleged father of the first.

Tooby: From looking at the animal literature one might expect there to be precise relationship-specific mechanisms at a level of detail that we're not even beginning to anticipate now. The things that you are talking about now are things that clearly ought to have been studied for the last 25 years. The recruitment of social psychologists into these kind of studies has been remarkably slow, and the number of people trying to come up with empirical results by applying these ideas is remarkably small. What do you think the prospect is for having many more scholars from the relevant fields join this research?

Wilson: The fact that we're all meeting here speaks well for the future, but Dick Nisbett is more in the field of social psychological science so I would like to hear his opinion.

Nisbett: I agree that there has been little penetration of this area into social psychology, yet the two lines of thought have so much to offer one another. Randy Nesse and I just ran an evolution seminar series at the Institute for Social Research, which was the best attended in the history of the Institute, but one of the most poorly attended by social psychologists. Social psychologists mistakenly think that evolutionary theory constitutes a conservative orientation, and the nature of the phenomena they study allows them to remain adherents of the *tabula rasa* position.

Daly: The numbers of evolution-based papers in the *Journal of Personality and Social Psychology* have been increasing over the last three years. Clearly, the 'don't know anything about it and don't want to' antipathy is waning.

Pinker: On the other hand, there are other bodies of scholarship from different disciplines which are obsessed with psychological relationships among family members: the fields of clinical psychology, counselling psychology and psychological social work. The data vary in scientific quality, but there may be relevant information in some of the better-designed studies. These fields have made no contact with scientific social psychology or with evolutionary psychology.

Wilson: We have talked to some of those clinical people. Many of them have good intuitions: they notice things that we only theorize about. However, in general, the family relations literature is dominated by social workers and practitioners, who take a systems approach to flows of information and causal influences rather than focusing on the information processing and decision making of individuals that we as psychologists or evolutionists have. Therefore, they sometimes just seem to miss the boat.

Cronin: What about your own paper 'Whom are newborn babies said to resemble?' (Daly & Wilson 1982), in which you found that the mother's family tries to persuade the father's family that the baby resembles the father?

Wilson: We (Daly & Wilson 1982) and Steve Gaulin (Regalski & Gaulin 1993) have found that mothers and their relatives push much harder in making attributions about the degree of resemblance to the father and father's relatives. It seems as though this is something that people are concerned about, but whether it has any impact is another question. Both studies also found that fathers are more sceptical. They want the truth and are not necessarily persuaded.

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Møller: In the data that were presented by Gaulin, there was a decrease in the father's parent's claims with birth order, so that the second child was less likely to be claimed to resemble the father than the first (Gaulin 1997, this volume). This is a rather puzzling result because the paternity data argue exactly the opposite. There is an increased likelihood of having extra-marital second, third or fourth children compared to the first one. Therefore, there's another factor involved in this observed pattern of behaviour. It might be the case that these claims for resemblance to the first child are due to the older generation attempting to mend the bond and once it's established it might not matter that much.

Wilson: We also found that there was more pushing of paternal resemblance for the first child, and we also thought that once the male is committed to the familial unit then it is not necessary to push so hard later. Another thing that happens is that the relatives talk about the subsequent births as looking similar to the prior one rather than to the father.

Pinker: I would like to inject a note of scepticism about the hypothesis that people rely heavily on paternal resemblance to establish paternity. In sexual reproduction there is a mixing of genes, and many children don't look like their fathers. But we do have enormous cognitive machinery for cause-and-effect reasoning, which I suspect plays a much greater role in the psychology of paternity assessment. One way to see how important the cues are is to pit them against each other, as in these thought experiments. First, imagine a man who knew that he hadn't had sex with his wife for nine months, but the offspring resembled him. Now imagine a man who had been close to his wife for the year before, so no one else could have been the father, but the offspring did not particularly resemble him. Which man would be more upset? I suspect that the cognitive calculation of whether the offspring could be his, given the physiological and physical constraints, would trump assessments of resemblance. We tend to think that low level perceptual cues such as smell and physical resemblance would out-weigh pure reasoning, but it might be the other way round--the reason we evolved cause-and-effect reasoning is to apply it to the pressing problems that we face.

Daly: There are hints in the adoption literature, and this should be analysed in more detail, that adoption failures are better predicted by non-resemblance to the father than by non-resemblance to the mother. In this case the adoptive parents have got all their cognitive equipment telling them this is a fictive relationship and still it appears that paternal affection may be facilitated by resemblance in a way that maternal affection isn't.

Sperber: It might be useful, here, to take into account the cultural dimension. There is an important variability across cultures in beliefs about the traits that a child may inherit from the mother and from the father, with extreme cases where the role of one or the other parent in shaping the child is completely denied. Similarly, there is some cross-cultural variability in beliefs regarding the duration of

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pregnancy. I have done fieldwork in Mauritania, where women seemed to be able to adjust--by several months--claims regarding the duration of a particular pregnancy so as to make it begin at a time when their nomadic husband happened to have been in their company. I have also done fieldwork among the Dorze of Southern Ethiopia, where the duration of pregnancy was claimed to be an even number of months in some clans and odd in others. It could be of course that people's judgements and practices in specific cases are somewhat at odds with their cultural beliefs.

Wilson: My understanding is that the Trobrianders, who articulate that the male plays no role in producing a child, are still concerned about being impolite by implying that a child doesn't resemble its mother's husband. Therefore, there's the whole question of articulation versus the behavioural practice. I agree that it would be interesting to look at cross-cultural variation.

Dawkins: We have talked about paternity certainty and the recognition of resemblances between fathers and offspring, and we've taken it for granted that genetic resemblance can be exploited by an adaptation strategy. However, what if genetic resemblance itself were an adaptation in some sense? One way to look at this would be to consider a strategy of a female deliberately trying to mate with an unusual male, say a male with red hair or a conspicuous character. Then, assuming that she intends to be faithful to him, her offspring are reliably labelled. In a game-theoretical sense it becomes complicated because it depends upon whose benefit we are talking about. This analysis should really be done at the gene level. Another game-theoretical question might be to consider a gene for increasing the facial resemblance between parents and offspring. What will be the fate of that gene and will it flourish or not flourish in the presence of other genes? This in itself could be regarded as a genetically manipulable variable. The result is far from obvious and it is not possible to say intuitively what the result will be because it needs to be set up as a proper model.

Daly: I agree. Some writers have assumed that selection will favour offspring who exhibit paternity cues, but it's not obvious that there wouldn't be selection against such a gene and in favour of a generic child that doesn't reveal paternal phenotypes.

Scheib: There was an article in which Frank Salter (1996) presented a similar argument. The interesting point was that the benefits or the costs of having something like that would depend on whether or not, at least for females, extra-pair copulations were a possibility and whether they would be beneficial. In a context where they were beneficial you certainly wouldn't want to be carrying around a gene that would increase paternal resemblance. However, if extra-pair copulations were not beneficial, and they occurred infrequently, then a gene for increasing paternal resemblance could be useful.

Rogers: The same dynamic would apply for any character that is both visible and heritable. Selection for increasing paternal resemblance amounts to selection for rare types.

Daly: Although males make subtle discriminations in their allocation of paternal effort in response to cues of probability of paternity in various biparental animals, and although there's evidence of various

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sorts of phenotype matching in other contexts for the allocation of nepotistic investment, there are no non-human examples of males using phenotype matching in the allocation of paternal investment context.

Wilson: In the light of that, in the arms race between cuckoos and their host species with sustained selection you can see evidence of phenotype matching. In contrast, in recently invaded species you don't see it. This suggests that there is far more subtle dynamic conflict between males and females. We don't see any non-human species that are able to use phenotypic cues as paternity cues. Bewick's swans have individual face markings that some people can identify, so the requisite information may be there (Scott 1992). Also, in Mike Beecher's work on colonial-nesting swallows (Beecher 1989, Medvin et al 1993) the information is present in the offspring, i.e. voices and face markings, to allow the parents to identify the offspring once they've been exposed to it. This suggests to me that a sexual conflict is going on.

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