

Biological Basics and the Economics of the Family

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Many economic models of the family are based on a generic “person one/person two” household or “parent–child” family, rather than their anatomically correct counterparts: sons and daughters, fathers and mothers, and grandfathers and grandmothers. These economic models can offer powerful insights into family behavior, but also can leave certain patterns unexplained and neglect potentially important crosscurrents. Melding biological insights with family economics can cast new light on existing knowledge and open up novel paths for research.

For example, study after study has found that putting family income in the hands of mothers, rather than fathers, tends to increase the consumption of children, as noted in this journal in Lundberg and Pollak (1996). Yet the way such results are usually described might strike a noneconomist as exceedingly circumspect. Economists point out that these findings reject the “common preference” model of household decision making in favor of one with “independent decision-making spouses”—but usually make little mention of motherhood or fatherhood *per se*. Or consider the dramatic expansion of South African government pension programs in the early 1990s, which put lots of extra money in the hands of grandparents, many of whom lived with their grandchildren. In a compelling and oft-cited study, Duflo (2003) found evidence of pension spillovers to grandchildren. But the most intriguing patterns were demographic: pensions to *maternal grandmothers* redounded to the benefit of *granddaughters*. Economic analysis uncovers the income effects but turns out to be of little help for explaining why these particular gender effects predominated.

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Or think of economic studies of “matching”—that is, dating, mating, marriage, and divorce—which often derive their primary insights from models invented for analyzing worker–job matches in the labor market (for example, Mortensen, 1988; Brien, Lillard, and Stern, 2006). This otherwise compelling analogy can become strained when considering issues such as the establishment of paternity, the biological clock, or sexual infidelity. Infidelity, for example, is a high-ranking correlate of marital disruption and a leading indicator of divorce (Kitson, Babri, and Roach, 1985; Amato and Rogers, 1997). Further, overwhelming evidence shows that men and women differ in their preferences for short-term sexual liaisons (Clark and Hatfield, 1989). A full description of sex differences in mating preferences, marital stability, and economic well-being is likely to require going beyond economics and into the realm of biology.

Of course, the economics of the family has not ignored biology altogether. Gary Becker’s (1991) pioneering *Treatise on the Family* incorporates biological considerations into household behavior and acknowledges intellectual debts to several eminent biologists. Biology plays a key role in a number of economic studies: for example, Siow (1998) on the biological clock and labor market behavior of women versus men; Edlund (1999) on parental preferences for girls versus boys; Willis (1999) on the different consequences out-of-wedlock child-bearing poses for mothers versus fathers; and Case, Lin, and McLanahan (2000) on the treatment of biological versus nonbiological children. Hirshleifer’s (1977) paper on the insights biology offers to economics was far ahead of its time. Evolutionary theory is a cornerstone of Bergstrom’s (1996) landmark survey of economics of the family, and the recent work of Robson (2001, 2002) shows how biological thinking can be applied to time preference, risk aversion, rationality, and more.

Despite these inroads, evolutionary biology still tends to be peripheral to economic studies of the family, and a closer look is clearly warranted. “Bio-founded” approaches that explicitly consider sex differences in reproductive capabilities and constraints can illuminate corresponding differences in the goals and interests of men versus women regarding preferences for a mate, decisions to marry or to terminate a marriage, how much to invest in a relationship, how much to invest in children, and how much to value the quality relative to the quantity of children.

This paper explicates the oft-used “hub-and-spoke” format for generating biologically based hypotheses about family behavior. The *hub* is Hamilton’s rule, which holds that the costs and benefits of altruistic acts are weighted by the closeness of the genetic relationship. The *spokes* emanate from various fundamentals of human reproductive biology. (For instance, a father might be uncertain of his genetic relationship to offspring, but a mother almost never is.) This arrangement generates a unified approach for modeling diverse aspects of family behavior. My discussion of these biological fundamentals will include applications, empirical illustrations, and suggestions for how to merge these basics with current economic thinking.

Hamilton's Rule

The biological basis for why one relative might make sacrifices on behalf of another has its origins in a puzzle that took over 100 years to solve. Charles Darwin argued that the living world is a select set of progeny whose ancestors managed to *survive and reproduce*. However, some phenomena, such as a honeybee's suicidal defense of its hive, seemed to contradict the Darwinian dictum. Hamilton's rule, proposed by biologist William D. Hamilton (1964), is a straightforward but far-reaching argument about the biological foundations for familial altruism. Hamilton focused on the *gene* rather than the *individual*. The honeybee's heroism could be optimal from the "gene's-eye view": though the altruist's genetic code is lost, even more of that same code can prevail within rescued relatives.

Imagine that my brother and I are soldiers and a sniper is aiming a grenade launcher at him. I can cry out, drawing deadly fire toward myself but saving him. The stakes? For any particular gene I have, there is a 50 percent chance that it came from my father and a 50 percent chance that it came from my mother. Since my brother has the same parents, there is a 50–50 chance that he will share any particular gene; to put it differently, my brother would be expected on average to match half of my genes.¹ Thus the expected benefit from calling out is that only 50 percent of my genes survive—best to keep silent! But if *three* brothers were imperiled, the benefits of saving them—150 percent of my genes in expected value—would outweigh the costs of sacrificing myself. Thus, from a gene's-eye view, an organism will issue a risky, even suicidal, warning cry if it rescues *sufficient numbers* of relatives of *sufficient genetic closeness*.

In more general terms, denote the *cost* of the altruistic act to the donor by C , and *benefits* of the act to the recipients by B . Let r denote the *coefficient of relatedness*, that is, the extent to which the donor and recipient share genes. Hamilton's rule stipulates that the donor provides help if

$$rB > C.$$

In this example, B and C are counted in terms of lives saved. More generally, evolutionary biologists characterize benefits and costs not only in terms of a person's own genes, but the sum of any expected future progeny. They use the term *extended fitness* to encompass the reproductive value of one's relatives (appropriately weighted by r) in addition to one's own.² Return to the example and imagine that

¹ More technically, relatedness is can be thought of as the proportion of my genes that are identical *by descent* to those of my brother. The "by descent" qualifier distinguishes genes that are inherited from either the mother or father from those shared simply because they are common in the population (including, for instance, genes we might share with, say, chimpanzees).

² Just as economists use the term "utility" to denote *well-being*, but allow its exact arguments to (possibly) differ from one application to the next, so too biologists use the term "fitness" to denote *reproductive success*, but the specifics can likewise vary (de Jong, 1994). In some applications, fitness might be designated by number of surviving offspring, for example, while in others the term captures, say, one's contribution to the gene pool of the next generation relative to competitors. In the soldier example, I

I am sterile but that my brother is expected to have three children. (For simplicity, stop at the second generation.) Now my cost–benefit analysis factors in my brother’s fecundity. He still embodies 50 percent of my genes, but now each of his children confers an additional 25 percent in expected value. Thus, rescuing my brother (and his three future children) will now save 125 percent of my genes, so Hamilton’s rule predicts that I would sacrifice myself.³ This example illustrates how Hamilton solved Darwin’s dilemma of altruistic behavior among often sterile but related insects. In fact, Hamilton’s rule does a remarkably good job of explaining the complex social life of social insects as a function of their Byzantine mode of reproduction and relatedness (Trivers and Hare, 1976).

Lest you think kinship among sterile insects a bit esoteric, consider that postmenopausal women are sterile too. Indeed, behavioral ecologists have suggested that menopause might be an adaptation that encourages investment in children (Hawkes, O’Connell, and Blurton Jones, 1997).

Biology and Behavior

Before considering implications of Hamilton’s rule for family behavior, note that biology and genetics do not obviate choice. True, some behaviors—yanking one’s hand from a hot stove, say—might aptly be construed as “hardwired,” but surely this is not the most useful way to think about spending for a child’s education. Genes matter through the cascade they set into motion—the building of proteins, thus building bodies, which in turn cope with their habitat and the outside world. (What good is being hormonally primed for parental bonding if one is somehow prevented from holding one’s newborn?) Biological causality ranges from distal to proximate, a parade of forces increasingly interactive with, and contingent upon, environmental conditions.

Indeed, evolutionary thinkers have argued that intelligence and the capacity to choose are adaptations for coping with an ever-changing environment. Though evolutionary thinkers may be divided on certain details—for example, an evolutionary psychologist might envision that humans are saddled with outmoded “Stone Age brains,” while a behavioral ecologist might highlight nimble strategies for optimal food foraging—they nonetheless would agree on the centrality of biolog-

implicitly define my fitness as the value of my own genes (normalized to 100 percent) plus the expected value of those genes that would be passed along to my progeny. My *extended* fitness equals my own fitness, plus 0.5 times the fitness of my brother(s). To keep the exposition simple and brief, I concentrate mostly on the biologists’ maximand of extended fitness, rather than the economists’ maximand of utility. For an excellent, nuanced discussion of how to bridge the two, see Bergstrom (1996).

³ Were my brother expected, in this two-period world, to have just one child rather than three, Hamilton’s rule predicts refraining from heroism, since I could only save 75 percent of my genes. But now extend the horizon to three periods, and suppose also that my brother’s one child is expected to produce four more of his own. In this instance, Hamilton’s rule again predicts that my sacrifice can save 125 percent of my genes: 50 percent from my brother, 25 percent from his son, and 4 times 12.5 percent from his children. Note that, without some sort of discounting (say, by the probability of a child’s surviving to reproduce) infinite dynasties can pose convergence problems for the biological maximand of extended fitness. Again, see Bergstrom (1996) for discussion of how to introduce economic realism, tractability, and generality to the extended fitness idea.

ical forces such as sex, reproduction, and kinship for understanding families. Accordingly, economists could regard biological basics as a backdrop for thinking about gender or age-related inclinations, interests, and constraints, as illustrated by the applications below.

Age Asymmetries in Altruism

The earlier allusion to menopause is one illustration of the evolutionary insight that altruistic sentiments can have built-in generational asymmetries. All else equal, a post-menopausal grandmother is expected to be more altruistic toward her fertile granddaughter than vice versa. Kaplan (1994) and his collaborators have found in traditional societies that, consistent with Hamilton's rule, transfers from old to young predominate—even the very oldest women produced more food than they consumed. The traditional context matters in light of the (controversial) idea that preferences may have evolved during the so-called “Era of Evolutionary Adaptedness” that began two million years ago, when humans lived as hunter-gatherers. Lee (1997) summarizes related evidence for industrial economies (where resources likewise tend to flow from old to young) and agricultural economies (where they sometimes flow in reverse). Lee conjectures that a preponderance of old-age support in agricultural economies might nonetheless make evolutionary sense if it helps maintain stocks of farm-related knowledge (like rainfall history) that benefit younger generations. The possible connection between transfer flows and the value of elder human capital is a worthwhile and feasible topic for future research.

Of course, studies of intergenerational transfers must grapple with a myriad of crosscurrents. Cultural forces might counter or complement biological ones (for example, Bergstrom, 1996; Cox and Stark, 2005). Realized transfers could be driven largely by relative incomes, liquidity constraints, and the like, thus revealing little about altruistic preferences.

Using evidence of a different sort, such as measures of grief following the death of a relative, allows a sharper focus on preferences. Observed grief patterns are consistent with the age asymmetries inherent in Hamilton's rule. For instance, Sanders (1979) used a psychological survey instrument, the Grief Experience Inventory, to assess experiences of 102 newly bereaved persons, and found significantly higher intensities of grief on the part of parents surviving a child's death than vice versa. Age-specific values of mortuary remains for a Native American burial site in the American Southwest analyzed in MacDonald (2001) are consistent with more intense grief at the loss of kin whose reproductive value is high. He found that the estimated value of artifacts such as pots, necklaces, and rare stones were higher for graves of sub-adults (aged 10–20) than for infants, young children, or adults.⁴

⁴ Of course, age-specific reproductive value has changed enormously in recent history. An infant's chances of surviving to reproduce are much higher nowadays than in ancestral times. Evolutionary psychologists would argue that ancestral conditions are most pertinent to altruistic preferences. Evidence from Crawford, Salter, and Lang (1989) supports this idea: they found that experimental subjects' subjective assessments of intensity of parental grief by age of deceased child tracked the age profiles of

Nepotism

Hamilton's rule predicts that, all else equal, the closer the genetic relatedness, the stronger is familial altruism. Evidence consistent with this appears in many forms—including the aforementioned experience of grief, which has been found to be more intensely felt at the loss of an identical twin, for whom $r = 1.0$, compared to a fraternal twin, whose $r = 0.5$ (Segal and Bouchard, 1993). More broadly: most nonspousal bequests go to children, with relatively little going to more distant relatives or nonrelatives (Smith, Kish, and Crawford, 1987). Likewise, kin-based favoritism has been found in migrant remittances (Bowles and Posel, 2005), the allocation of food to children (Case, Lin, and McLanahan, 2000), and the succession of chief executive officers in publicly traded firms (Pérez-González, 2006).

The last example could be construed as maximization of a firm's value if, for example, family ties facilitate cooperation, transmission of knowledge, or a healthily long, dynastic horizon—except that nepotistic succession was found detrimental to firm value (Pérez-González, 2006). Still, one might counter that the various nepotistic patterns above could instead be the workings of culture, law, or norms, rather than biology. Yet it need not be a case of “either/or.” In the late 1950s, in what is now Tanzania, land was plentiful and cheap, and commonly bequeathed to distant relatives (Gulliver, 1961). But cash crops made land expensive, and fathers then wanted to leave it to their sons. These preferences were immediately codified into law, suggesting that biology and culture could work in tandem (Cox and Fafchamps, forthcoming; Cox, forthcoming).

Parent–Offspring Conflict

The flip side of Hamilton's inequality concerns instances where nepotistic transfers are *not* forthcoming or are smaller than the recipient would like—a state of affairs analyzed in Trivers's (1974) model of parent–child conflict. Trivers's idea is that the value of r I would assign my own greedy self is 1.0, which trumps the values I attribute to my parents or siblings (except an identical twin). Accordingly, upon withdrawal of parental resources, I might throw a tantrum, not merely to communicate need (since a quieter signal could do that), but to blackmail my parent into giving more. In humans, the fallout from such blackmail might be public embarrassment; in other species, perhaps heightened risk of being preyed upon (Zahari and Zahari, 1997).

Becker's (1974) famous “Rotten Kid” theorem points to a quite different scenario in which even the most selfish “rotten kid” will act altruistically toward siblings and parents if their financial incentives are aligned through the prospect of future intergenerational transfers. If my adolescent renditions of Led Zeppelin wreak havoc on my mother's earning potential, the resulting prospects of sharply downsized living quarters might be incentive enough for playing my guitar through

reproductive value calculated for a *traditional* society (the !Kung San) better than they tracked profiles calculated from *modern* data.

headphones without having to be reminded! Despite ensuing arguments that circumscribed the theorem's generality (for example, Bergstrom 1989), its "don't-bite-the-hand-that-feeds-you" logic remains appealingly straightforward. It is therefore surprising that little empirical work has been done to test the implications of Becker's theorem against alternatives like that of Trivers (1974).

A compelling testament to the power of Becker's (1974) theorem is human pregnancy itself, whose exacting tolerances (owing to the large-headedness of humans) threaten the viability of any "misbehaving" fetus that consumes too much and risks getting stuck in its mother's birth canal. That childbirth can happen at all is surely due in no small part to the fetuses' "behaving as if" they must respect the mother's interests. And yet there is recent evidence that the *in utero* application of the theorem does not always hold! Evolutionary biologist David Haig (1993) found that the fetus sometimes diverts more glucose to itself than its mother wants by secreting a hormone (via the placenta) that weakens the mother's insulin. Though the mother counters the secretions by upping her insulin production, the child sometimes gains extra fat at the expense of his mother, who then risks pregnancy complications as well as gestational diabetes.⁵

Sorting out when and why intergenerational relationships would go the way predicted by Becker (1974), versus the way of Trivers (1974), is to my mind a central priority for future research.

Uncertainty over Paternity and Investments in Children

Some economic studies of intergenerational transfers distinguish between maternal and paternal grandparents; others do not. The addition of the "spoke" of paternity uncertainty to the "hub" of Hamilton's rule provides a biological argument for doing so. Barring something like a mishap in the maternity ward, a mother can be certain her newborn is a genetic relative. But barring something equally extreme like the full-time sequestration of his mate, a husband might harbor a flicker of doubt.⁶

⁵ There's more to the drama. In light of the risks noted above, it is puzzling that a fetus would "want" to risk growing overly large. Hrdy (1999) suggests that the fetus's demand for fat is derived from a desire to demonstrate viability, and Mann's (1992) study of maternal favoritism toward the heavier of pre-term fraternal twins lends support to this idea. Further, the complete story suggests another conflict—between the father and the mother. The fetal "sugar grab" has been found to be an expression of *paternal*, not maternal, genes (Haig, 1993). This is in line with expected costs of such a gambit, which presumably are lower for the father than the mother, since he doesn't have to directly incur the hazards and costs of pregnancy.

⁶ Attempts to gauge the extent of misattributed paternity are bound to be difficult (Birkhead, 2000), and estimates in the literature vary widely from 1 to over 20 percent (Geary, 2005). Such difficulties would only be compounded if, as evolutionary psychologists contend, paternity concerns that count most are those that prevailed in ancestral times. There is also no shortage of myth and legend surrounding cuckoldry (Cox, 2003), which could prove important for behavior, since perceptions could matter more than population parameters. For example, ethnographies of the urban underclass reveal explicit concerns about paternity confidence among female relatives of putative fathers of babies born out of wedlock (for example, Anderson, 1993).

At the level of grandparents, the maternal grandmother is the *only* grandparent with complete certainty that she is related to the grandchildren. All else equal—and one can think of countervailing economic and cultural factors—“biological basics” imply a greater degree of altruism from the maternal grandmother than from the paternal one. This consideration accords with Duflo’s (2003) South African evidence of maternal grandmotherly largesse mentioned earlier. Likewise, Sear, Steele, McGregor, and Mace (2002), who examined kin and child mortality in rural Gambia, found that, among grandparents, only the availability of the maternal grandmother significantly affected child mortality. Indeed, her death was more deleterious for child survival than that of even the child’s father, even though the villages were patrilocal (meaning that after marriage families usually lived near the husband’s side of the family). In a different setting, Euler and Weitzel (1996) found that maternal grandmothers outscored their paternal counterparts in retrospective ratings of grandparental solicitude among German adults. Using the U.S. National Survey of Families and Households (NSFH), I found similar maternal/paternal grandmotherly differentials in involvement with grandchildren across a variety of measures: visits, calls, letters, “sleepovers,” even grandmothers’ reported feelings of closeness toward grandchildren (Cox, 2003).

Of course, such raw differences could spring from many possible causes. Maternal grandmothers, for instance, tend to be younger and healthier than their paternal counterparts and thus better able to interact with and care for grandchildren. In Cox (forthcoming) I extend the NSFH descriptive analysis to a multivariate context, and find that the maternal/paternal differentials are indeed narrower after adjusting for these and other characteristics. I also consider partial correlations ostensibly implicated in paternity uncertainty, such as attitudes toward permanent monogamy (as reported privately, in self-enumerated questionnaires, by individual spouses). Intriguingly, such attitudes emerge statistically significant in but a single instance: the *paternal* grandmother’s propensity to provide childcare was positively related to the *wife’s* reported proclivity toward marital permanence. While such partial correlation is doubtless interpretable in several ways, it is, on the face of it, consistent with a biologically-based slant on marriage—namely, that marriage is an arrangement whereby potentially suspicious spouses monitor one another’s fidelity. In this context, the link that would matter is the one between the paternal grandmother’s childcare and her daughter-in-law’s marital fidelity.

I hasten to add a *caveat emptor* to this interpretation: some other estimated partial correlations, such as those related to reports of attitudes toward a spouse’s (hypothetical) infidelity, appeared to contradict the paternity-uncertainty hypothesis. Nonetheless, one advantage of the paternity-uncertainty approach, even at a descriptive level, is that it implicates variables that might not be otherwise singled out for consideration.

For instance, consider the Fragile Families data set, a survey of single mothers (and, in 75 percent of the cases, also the fathers) taken soon after the birth of the child. Both fathers and mothers were asked about the newborn’s resemblance to parents and other relatives. In the second wave, conducted a year or more later, mothers were asked how many days during the previous month the non-co-resident

father had spent with the child. There were large positive and significant differences by reported resemblance—but intriguingly, only for fathers of boys (Cox, forthcoming). Again, daunting problems can arise in inferring causality. Nonetheless, biological thinking helps to illuminate potentially pertinent, non-obvious behavioral pathways.⁷

Key “Biological Basics”—Sex and Reproduction

Consider another reproductive “spoke” to append to Hamilton’s rule: males and females differ vastly in the size and number of sex cells (gametes) they produce. Males produce abundant, cheap sperm at the rate of about 3,000 per *second*; women produce only about 400 viable eggs in an entire *lifetime*. More important, female mammals invest biologically more in creating new offspring than do males, and this is especially true for humans. Our extraordinarily large brains make childbirth far more dangerous and painful for humans than for other primates. Moreover, even full-term human newborns enter the world essentially 12 months premature, helpless, and needing much parental support, and women are biologically equipped to provide sustenance during that time.

Trivers (1972) was the first to argue that this sexual dimorphism in investment costs can create conflict over quality/quantity tradeoffs in fertility: mothers favor quality; fathers, quantity. This sex difference has potentially large implications for differing concerns and capabilities of men versus women in mating and childcare. Women can advance their genetic legacy by securing resources from their mate, friends, and family for supporting their offspring. While men also have an interest in investing in their children, they can also advance their extended fitness by securing additional mates.

Sex Differences in Mate Selection

Trivers (1972) emphasized the implications of sex-specific investment costs for patterns of sexual selection by gender. In humans, women are the intensive investors in offspring, and hence they are the scarce resource and the binding constraint. Thus, in Trivers’s model, men compete for women. By dint of their minimal required investment, men can be prone to wanderlust and fecklessness. Further, polygyny (multiple female mates, either socially sanctioned or *de facto*) can sometimes emerge as an equilibrium mating system.

There is both biological and survey evidence that proclivity toward polygyny lurks within the male psyche. Biological evidence comes from sex differences in size, with men weighing about 10 percent more on average. Biologists have found that, across species, the bigger this so-called sex dimorphism in size is, the more polygynous the species tends to be. They interpret the enormous size of, say, male elephant seals relative to their female counterparts as an adaptation that enables the males in this hyperpolygynous species to fight for and guard their enormous

⁷ For instance, another channel through which paternity uncertainty could conceivably be expressed is via differential solicitude of maternal versus paternal aunts and uncles (Gaulin, McBurney, and Brakeman-Wartell, 1997).

harems. Likewise (though to a lesser degree), the larger size and upper body strength of men is indicative of the male-on-male competition for mates in our evolutionary history. The 10 percent difference in human size by gender is modest compared to the 80 percent male–female weight advantage of our markedly polygynous primate cousins, the gorillas, but larger than another of our species cousins, the non-dimorphic gibbons, which are thought to be paragons of monogamy.

Survey evidence gathered by psychologists indicates that by a variety of measures—self-reported numbers of desired sex partners (Buss and Schmitt, 1993), descriptions of sexual fantasies (Ellis and Symons, 1990), and numbers of extramarital affairs (Laumann, Gagnon, Michael, and Michaels, 1994)—men desire more sexual partners than do women. Such findings are exceedingly robust across cultural contexts (for example, Schmitt et al., 2003).

Though only a fraction of socially sanctioned unions are indeed polygynous, biological basics can still imply marked female–male differences in searching for a long-term mate. Because females bear the biological burden of investment in a child, they risk abandonment by a ne'er-do-well who deposits his seed and then distances himself. Their challenge is to discover (possibly hidden) qualities of loyalty, commitment, responsibility, earning potential, and other traits in a mate that will help to assure that their genetic legacy receives long-term support. Biologically, males face a less difficult inference problem because correlates of reproductive potential in women are relatively straightforward to assess; the primary problem for men lies in *attracting* such mates.⁸

Of course, infidelity is not strictly a preoccupation of males, and there are biological incentives for—and physical evidence supportive of—certain kinds of human female infidelity too. The biologically based sex differences in quality/quantity tradeoffs in reproduction suggest that female infidelity would be motivated by concerns for the provisioning of offspring (for example, Hrdy, 1999). For instance, the wife of “Steady Eddie” copulates with handsome “Fast Freddie,” conceiving a son who inherits both Freddie’s chiseled features and Eddie’s financial support.⁹

⁸ A favorite classroom exercise of mine is to give undergraduates what I bill as the “easiest quiz in the world”: guess the source of a list of titles from either *Cosmopolitan*, a women’s magazine heavily devoted to issues of mating, or its male analog, *Maxim*. *Cosmo* articles like “Nine Weird Ways to Know This is the One,” coach single women to keep an eye out for signals of commitment and competence (how he interacts with his nephews, pets, houseplants; evidence he’s drawing a steady paycheck) whereas *Maxim* articles tout the joys of intrasex competition (“Beating People Up: An Awesome Fitness Regimen”). Could this be a social construction that in truth has nothing to do with biology? Perhaps, but I would want to see a cultural counterexample where the tenor of the articles is reversed. In a telling *biological* reversal, which accords with Trivers (1972), the heavily investing male seahorse—which gestates the young in a special brood pouch—is the one that chooses among competing females.

⁹ Biological traits thought to be indicative of female infidelity are related to so-called “sperm competition,” the idea that ejaculate volume evolves to compete with that of other males who might also have inseminated a desirable female (for example, Short and Balaban, 1994). The weight of human testes relative to body weight is larger than that of the gorilla (who instead protects his genetic interests by using physical strength to guard his harem), but much smaller than that of the chimpanzee (whose hyper-promiscuous mating style features rampant sperm competition).

Single women and men differ significantly in their valuations of certain traits possessed by a prospective mate: women tend to place earning capacity ahead of physical attractiveness; men rank them the other way around (Buss, 1989). Not that men and women are expected to differ on all concerns: not many of either sex are likely to find misanthropy, stupidity, or visible evidence of infection wildly attractive. Indeed, Buss found that both males and females ranked kindness and intelligence at the top of desired characteristics in a long-term mate or marriage partner. But sex differences that *did* occur tended to accord with the Trivers (1972) model. Moreover, these were found to be consistent across a variety of cultures and locales (Buss, 1989). Recent economic evidence from both a speed dating experiment (Fisman, Iyengar, Kamenica, and Simonson, 2006) and a study of on-line dating (Hitsch, Hortaçsu, and Ariely, 2006) confirms these patterns. In the latter study, women cared more about a prospective mate's income, whereas men were more responsive to whether a posting had included a photo. Further, the evidence of Hitsch, Hortaçsu, and Ariely (2006) is consistent with the idea of males competing for choosy females: women received five times more first-time email contacts than men on average; men were more likely to never be contacted or to have their approaches ignored.¹⁰

While such patterns could in principle originate just from culture, to cast culture and biology as *presumed* alternatives (thereby ruling out that they might work together) risks an incomplete and perhaps over-simplified approach to sex-based differences in mating preferences.

Biology and the Economics of Marriage and Divorce

Sex-linked mating preferences and other exigencies of reproductive biology can readily be incorporated into models of matching, marriage, and divorce. For example, biological basics suggest that women might encounter more difficulty than men in *predicting* the long-term viability of a match—as well as have a stronger incentive for quickly *ending* one discovered to be nonviable. Recall that because of their larger parental investment, women are concerned with assessing difficult-to-measure qualities such as loyalty, commitment, dependability, and future propensity to invest in offspring. Social conventions like gifts can help (Camerer, 1988); and they are also further evidence of sex differences in mating, since men, not women, typically use gifts like engagement rings to signal loyalty (Brinig, 1990).

Considerations of the biological clock add time pressure to the inference problems women face. Women might prefer to initiate a seemingly viable match

¹⁰ Evolutionary psychologist Geoffrey Miller (1999) has conjectured that displays inherent in, say, artistic and athletic pursuits might be interpreted as advertisements of one's desirability as a mate. Such considerations, though clearly speculative, nonetheless suggest sex differences and age patterns in incentives to show off one's intelligence, fertility, physical prowess, wealth, or generosity. For instance, consider this *Cosmo/Maxim* question: Which magazine would be more likely to feature "How To Be Funny in Three Easy Steps"? How about: "What Someone's Sense of Humor Reveals"?

despite lingering uncertainties, but likewise quickly terminate one that shows signs of not living up to its initial promise. The idea that reproductive concerns might figure into a wife's decision to end a marriage is supported by a study of 1.8 million divorces granted in England and Wales during the 1970s and 1980s (Buckle, Gallup Jr., and Rodd, 1996). Among spouses in their early 20s who petitioned for divorce, wives outnumbered husbands more than four to one, a disparity that steadily narrowed with the age of the party seeking divorce. (Among those 60 and older, for whom reproductive considerations are likely absent or negligible, there was parity between numbers of petitioning wives and husbands.)

Despite these large male–female differences, it is nonetheless conceivable that *both* spouses wanted the marriage to end, but that (in a last gasp of household division of labor!) the lower-earning spouse made the trip to the courthouse. However, in a sample of separations and divorces from the NSFH, Sweeney (2002) found that only one-quarter of the breakups were initiated mutually, with each spouse equally desirous of ending the union. Moreover, among spouses for whom one or another had the stronger desire to end the marriage, wives outnumbered husbands by more than two to one.

Biological considerations can also potentially illuminate the *causes* of divorce. In a cross-cultural study based upon ethnographic evidence from 186 societies, Betzig (1989) cited 54 in which wives'—but not husbands'—adultery was considered grounds for divorce, and only two societies where the reverse was true. (This, despite the male bias in adulterous leanings cited earlier.) One evolutionary-based explanation is the infamous double standard thought to emanate from differential severity of the consequences of a spouses' adultery for betrayed husbands (cuckoldry) versus consequences for betrayed wives (diversion of resources from own children). In contrast to the results for adultery, nearly all of the societies that cited “lack of economic support” as grounds for divorce stipulated that these grounds applied just to husbands.

Biological Basics and Women's Time Allocation

Surely one of the most impressive achievements in economics is the literature on labor supply, which even 25 years ago had already taken an exacting empirical approach to such conceptual subtleties as the distinction between the decision to work versus how much to work (Heckman, 1993). Yet even this sophisticated framework could not have anticipated the trends in women's allocation of non-market time: the studies reviewed in Cox (forthcoming) indicate that, as market opportunities for women rose, time spent in household chores fell much faster than time spent caring for children. Though time-saving technology is no doubt a factor, such an outcome emerges naturally from considerations of Hamilton's rule, which might be expected, with ever-tightening time budgets, to trump concerns about, say, clean floors or tidy lawns.

Men, Money, and Mating

Are wealth and status positively correlated with male reproductive success? For most traditional and early agricultural societies, the answer seems to be “yes”

(Hopcroft, 2006). Male wealth, hunting ability, political status, religious rank, landownership, and the like have been found to be positively related to the number of surviving offspring in hunter-gatherer societies such as the Aché of Paraguay and the !Kung of the Kalahari, as well as agriculturalists like nineteenth-century Swedish farmers. But how about for contemporary industrialized societies, which are past their demographic transition and have convenient contraception? Bergstrom (1996) cites evidence that maximization of extended fitness does *not* appear to characterize modern life.

Yet Hopcroft (2006) argues that many survey instruments are not well-suited to measure possible “reproductive skew,” that is, the (perhaps larger) variance of male relative to female reproductive success from polygynous mating, whereby high status males spread their genes disproportionately. A survey that measures number of children at the household level, that fails to distinguish between a parent’s biological and nonbiological children, or that canvasses only female respondents for information on family structure, might not be well-suited for measuring reproductive skew. Even a survey that sets out to measure individual fecundity could miss pertinent outliers such as institutionalized or homeless men disproportionately prone to bachelorhood; super-rich men; and men who might have left descendents difficult to track.

Even if the *ultimate* connection between male status and reproductive success might have weakened or reversed itself in advanced modern societies, *proximate* connections could well persist. For instance, in contemporary data, male status has been found to be positively associated with frequency of copulation (for example, Perusse, 1993; Kanazawa, 2003; Hopcroft, 2006).

Sons, Daughters, and the Trivers–Willard Hypothesis

Sex differences in reproductive potential could spill over into parental preferences for sons versus daughters. A number of economic studies of the family consider differential treatment of children by sex, but they commonly ignore what could be a key explanatory factor: the family’s socioeconomic rank within the marriage market. The rationale for rank emanates from the Trivers–Willard (1973) hypothesis: imagine you are the poorest parent in your community and can have just one child (but can choose its sex), and that the marriage market is polygynous. Which would offer better prospects for your extended fitness, a girl or a boy? Against wealthier, polygynous competitors, a son would likely fare poorly in the mating sweeps. But a daughter could stand a good chance of reproducing, and might better her socioeconomic status via marriage. Conversely, were you the richest parent, a son would be a better choice since the family wealth puts him in good stead to provide several high-quality grandchildren, perhaps by many wives and/or concubines.

Though Trivers and Willard (1973) sought to explain sex ratios at birth, their theory can also be applied to investments in children (Edlund, 1999). Among the poor, for instance, Cronk (1989) found pro-daughter bias among low-status East African pastoralists—the Mukugodo of Kenya—who intermarried with richer neighbors in a semi-polygynous marriage market. The Mukugodo produced more

daughters than sons (at a ratio of 3:2). Fertility was higher for daughters, and many sons (but not many daughters) failed to reproduce at all. Daughters were also overrepresented among young Mukugodo children taken to a nearby health clinic; among the non-Mukugodo children, in contrast, sons were overrepresented.

Recall as well Duflo's (2003) finding of grandmotherly favoritism towards granddaughters in the aftermath of South African pension expansion. Trivers–Willard considerations could point the way to gaining traction on an otherwise unexplained gender effect in intergenerational transfers. Poor granddaughters, for instance, might stand a better chance of reproducing and marrying “up” the socioeconomic ladder (so-called “hypergamy”) compared to grandsons.

An example from the wealthy extreme is Boone's (1986) genealogical study of fifteenth- and sixteenth-century Portuguese nobility. In a mirror opposite of the Mukugodo, sex ratios among Portuguese elites favored males, and among high-ranked nobles, males produced more offspring than females. Among upper nobility, males were more likely to receive inheritances to finance their marriages while their lower-nobility counterparts were often left to join the military. With females, it was the reverse: *lower*-nobility females were more likely to receive dowries to finance their marriages, while their *upper*-nobility counterparts were often left to join the convent.

The above cases are extremes, reflecting the Trivers–Willard logic concerning the poles of the distribution; what about intermediate cases? As might be expected, the little work that has been done for the contemporary United States is mixed: Cox (2003), Norberg (2004), and Almond and Edlund (2006) find evidence consistent with Trivers–Willard effects; Freese and Powell (1999) and Keller, Nesse, and Hofferth (2001) do not. Of course, there is a lot more to family life. Undoubtedly, the more standard concerns (sex differences in returns to human capital investment, the desire for sons to provide old-age support in poor agricultural households) add strong crosscurrents to favoritism of sons versus daughters.¹¹

One lesson from the Trivers–Willard approach is that misogyny might not be an “inferior good,” with its prevalence falling as incomes rise. Sen (2001, p. 40) found marked variation in sex ratios and sex-specific child mortality across individual Indian states, and remarked in puzzlement: “The pattern of contrast does not have any obvious economic explanation. The states with antifemale bias include rich states . . . as well as poor states . . .” A combination of economics and biology could offer a useful framework for tackling such nuances.

Conclusion

Steven Jay Gould (1978) memorably critiqued evolutionary-based explanations of behavior as little more than a collection of “just so” stories, as in Rudyard

¹¹ Another biological factor that may lead to a lower percentage of females is hepatitis B, which has been implicated in larger ratios of male to female births (Oster, 2005). See also Das Gupta (2005), who challenges this hypothesis.

Kipling's fanciful tales about how the elephant got its trunk, the leopard got its spots, and the giraffe got its long neck. Gould's underlying assertion is that plausible biological explanations could be invented to support any set of facts, and thus the overall approach was not testable. That critique is far too sweeping. The voluminous empirical literatures of evolutionary biology and its behavioral offshoots like human behavioral ecology and evolutionary psychology display a discipline that is heavily empirically based. Counter to the "just-so" criticism, hypotheses like Trivers–Willard are clearly falsifiable, and in some cases *have* been demonstrably falsified (for example, Freese and Powell, 1999).

Further, and also counter to the "just-so" allegation, the evolutionary perspective clearly delineates phenomena that are puzzling—adoption of nonrelatives, for example, or care of indigent, frail elderly—versus those that can be explained. (*Ad hoc* patches can be concocted for those anomalies, but cogent explanations await.) Such delineation is precisely the task of any theory that aspires to progress; anomalies are what move us forward. Another hallmark of good theory is that it stimulates researchers to engage in creative new pursuits, something that biological basics, I believe, is bound to continue to do.

There are vast possibilities for bringing preferences to life in family economics by applying Hamilton's rule and its various offshoots. Moreover, recent findings in evolutionary biology offer a source of new hypotheses. For instance, one of the most exciting ideas in evolutionary biology these days is "genomic imprinting"—instances where a gene is expressed differently depending on whether it is contributed by the father versus the mother. Family conflict is a perennial mainstay of the "biological basics" approach, and genomic imprinting thickens the plot considerably.

The vistas for a "bio-founded" approach to family economics are wide open. (When I typed "Hamilton's rule" into JSTOR's search engine for economics journals, I got only four hits!) Biology holds the potential to propel the study of family economics in creative and fruitful directions.

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