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Human Sex Differences in Behavioral Ecological Perspective

Abstract: Behavioral ecology, based in the theory of natural selection, predicts that certain behaviors are likely to differ consistently between the sexes in humans as well as other species: aggression, resource striving, information content of sexual signalling. These differences, though of course open to modification by cultural practice, arise because male and female humans, like males and females of other mammal species, typically optimize their reproductive lifetimes through different behaviors: males specializing in mating effort (which has a high fixed cost, and is not offspring-specific), and females in parental effort (which has more linear reproductive returns, and is offspring-specific). The resulting patterns are reviewed.

1. Introduction

We are all intensely interested in differences between the sexes, from "vive la difference" to Freud's plaintive "what do women want?" to current debates over what, if any, sex differences are real, and which, if any, should be counted in social decisions. Here I want to introduce a somewhat different perspective, that of behavioral ecology.

Why add a behavioral ecological perspective, with its evolutionary context, to the question of sex differences, which seems to be such a current, and cultural, matter? I will argue that such a perspective gives us new insight on phenomena that are older and broader than we usually imagine. Evolutionary approaches to explaining why we behave as we do, including behavioral and evolutionary ecology, have their roots in Charles Darwin's work (1859; 1871). In the 19th century, he worried (among other things) about why populations grow and are limited in the ways we see, why and how species arise, what might cause individuals to sacrifice themselves, and how emotions are expressed in humans and other animals. Despite the fact that, in Darwin's time, much was unknown about both inheritance or ecology, his insight provided the foundation for exciting work today. Modern work integrating Darwin's insight with advances in genetics and behavior can be called by a variety of names: sociobiology, behavioral ecology, evolutionary ecology. The term "*sociobiology*", coined by E. O. Wilson (1975) in a pioneering synthesis by that title, generated considerable debate (with perhaps more heat than light, in many cases) during the 1970s and 1980s. Perhaps for that

reason, many workers today use the terms "behavioral ecology" and "evolutionary ecology".

Both behavioral and evolutionary ecology, when applied to humans for the purposes of generating hypotheses, utilize the central paradigm in biology: *humans, like other living organisms, have evolved to maximize their genetic contribution to future generations through producing offspring and assisting non-descendant relatives; that the particular strategies accomplishing such maximization will differ in specifiable ways in different environments; and, just as for other mammals, these strategies will typically differ between the sexes.* The principal difference between them is that of time frame: behavioral ecology is likely to focus on behavior in a shorter (1 generation) period (cf. Cronk 1991a; Smith/Winterhalter [eds.] 1992). Both assume that behavior is the product of genes and environment interacting, though the balance may differ, and though we have little idea of the genetic components of most behaviors, in humans or in other species (e.g., Grafen 1984). Both ask whether, if we know about environmental conditions (including social conditions), and about how those conditions change actors' (genetic) costs and benefits, we can predict the kinds of behavior we are likely to see.

Several new perspectives mark behavioral and evolutionary ecological approaches. First is the importance of using repeatable observations in ways similar to other sciences, primarily in one of two ways: optimality modelling (seeking to model and test optimality of behavior) and comparative method (using existing variation as a 'natural experiment' to test hypotheses) (Smith/Winterhalter [eds.] 1992; Alexander 1979). Which approach is used depends partly on what kind of data are available. Most novel for social scientists, perhaps, is the idea that genes themselves are a currency to be maximized, and thus that individuals might be predicted to act in certain ways in particular situations. This generates new concepts of individual interests leading to group-wide patterns – and begins to make sense of some previously puzzling patterns. Behavioral and evolutionary ecology straddle traditional subfields in the social sciences: they look at behavior, like cultural anthropology, they ask about the behavior of individuals, like sociology; but they do so using principles derived from biology, like biological anthropology. They also bridge fields as diverse as animal behavior, and various branches of sociology, like the rational-actor approach in economics.

Incorporating quantitative methods and techniques from many fields has given us new tools for analyzing complex social behavior. Behavioral and evolutionary ecology have a strong tradition of scientific method, phrasing questions as testable hypotheses, in order to examine them with repeatable observations. Yet there need be no conflict between these new approaches, and more traditional sociological analyses: they represent different levels of focus, on the 'proximate' triggers versus the ultimate (evolutionary) driving forces in behavior. Perhaps most exciting, these approaches lead us to ask new questions that might never have been interesting before.

Although we tend to think of humans as special in many ways, for many questions, we really can profitably ask questions in the same way about humans as

about other species. Other species' behavior, though we expect it to be simpler, can often be more complex than we at first suspect, and can show us how genes and environment interact. For example, optimal foraging theory postulates that foraging efficiency increases relative reproductive fitness. In ground squirrels, optimal foragers survive better and have more offspring than non-optimal foragers (Ritchie 1990). Optimality in foraging is heritable: babies are more like their parents than like others in the population. However, learning is important. Heritability is about 60 per cent genetic; the other 40 per cent of the parent-offspring correlation in optimality comes from babies foraging near their mother and learning what to eat (Ritchie 1991). The functionally important facts are that heritable variation exists; that one can predict, in a specific environment, which strategies (learned as well as genetically transmitted) ought to result in an increased reproductive fitness for their possessors, and an increased proportion of the possessors in the population; and that one can test and falsify these predictions.

Thus, behavioral and evolutionary ecology add a new sort of support to work done in many sub-fields of sociology. We discover, as we look, that many human behaviors have precise homologues (similar function, similar evolutionary history) in other species. Sometimes, because the behaviors are simpler in other species, we can decipher the important environmental correlates in the simpler cases, returning to the complex human variation with new insight.

Proximate and Ultimate 'Why' Questions

A behavioral ecological approach is a supplement to, not a replacement for, studies in sociology; it questions why we see the patterns we do at a different, and complementary, level. 'Why' questions are posed at two different levels in biology: It is useful to ask questions about both 'proximate' triggers and 'ultimate' selective causes, and it is important to understand that these two approaches are not alternatives, but complements. The ultimate cause of a behavior's existence, in evolutionary terms, is always its impact on lineage persistence through survival and reproduction. Proximate triggers, sometimes also called 'causes', of a behavior tell us what kinds of environmental cues are reliable.

Take a simple non-human example: Why does a bird migrate? One might answer "changing daylength causes hormonal changes, triggering migration". If birds could be interviewed about their preferences, we might have another set of proximate causes. Elucidating the proximate cue, daylength, does not, however, explain why individuals in this species migrate (as opposed to others who do not), why not all individuals migrate, and why daylength (as opposed to temperature, some other cue, or a combination of cues) has become the trigger. The ultimate cause of migration is a seasonal better-versus-worse geographic shift in foraging and nesting areas; individuals who seek the better areas, shifting seasonally, leave more descendants than those who remain in one area. When daylength is a reliable predictor of these seasonal shifts, individuals who use it as a cue will fare

better than those who use some other proximate cue or who fail to migrate. The benefits and costs of migration in terms of survival and reproduction may differ substantially for older, prime-age birds, compared with yearlings; in such cases, different categories of individuals are more or less likely to migrate.

Most sociological analyses involve what behavioral ecologists call proximate triggers, forces like changing daylength and hormonal shifts, and these are important. Important, too, I would argue, are the ultimate, selective forces. Proximate cues and ultimate (selective) causes tell us very different things. Warfare and homicides, for example, have a plethora of proximate causes – insufficient or incorrect information, insults, territory acquisition – so many triggers that we might despair of finding a pattern. Interestingly, both homicide and warfare tend to be male endeavors, and buried in the lists of 'causes' are many that relate to reproductive matters! I will argue below that this is in fact no accident, and that if we explore the patterns further, we'll find that there are good ecological reasons for the sex differences we find in aggression, over and above the social possibilities.

Similarly, for many reasons, we are very interested in human fertility and its decline, and demographic transition theory has not proved to be as robust as we had hoped (Coleman/Schofield 1986). Taking a behavioral ecological perspective may provide us with new insight. Lowered fertility could have a proximate 'cause' of later marriage age, and an ultimate selective cause of greater lineage success through fewer, better-invested children (Low et al. 1992; also Low/Clarke 1991; Voland 1984; 1989; 1990). We may discover that, in a particular society, men who marry younger women have more children in their lifetimes than men who marry older women (e.g., Low 1989a; 1990a); we would not then be surprised to find a proximate expressed social preference for youth in wives. Answers to both kinds of 'why' questions are informative; however, no proximate 'cause' will be maintained if it does not serve an ultimate selective cause. That is, nothing prevents the emergence of a group like the Shakers, dedicated to community work and celibacy; but we predict that any pattern requiring complete celibacy by all members will not persist for many generations. Indeed, fewer than a dozen Shakers remain alive today.

A behavioral ecological approach, then, begins with the argument that *behaviors which become common and remain so are those that produce reproductive profit for their performers*: those who use a strategy that is effective in a given environment will leave a more successful lineage. At first glance, this would suggest that optimal fertility would be maximum fertility – yet, even for non-human species the world is often far more complex than one might at first imagine. In fact, 'most successful reproduction' does not necessarily mean producing the most offspring, or even the most surviving offspring (e.g., Dawkins 1982; 1989; Williams 1966; Daly/Wilson 1983; Low et al. 1992, Low 1993); effective investment in surviving offspring is also important. The characteristics of the environment (e.g., resource richness, predictability) will influence the optimality of any particular strategy, apparently even for humans (Cronk 1991a; Low 1989b).

These arguments are based on the relative reproductive costs and benefits of individuals and do not require that a specific gene be postulated as underlying any behavior. Rather, behavioral ecologists ask: Under what environmental conditions does a behavior arise and persist? Who does it? Whom does it profit? What is its impact on each individual's lineage success? Even in the case of many simple behaviors, selection has apparently operated on complexes of loci, many of which affect other behaviors. External environment and genes interact during development in a complex way. For many important behaviors, behavioral ecologists cannot specify the genetic loci involved (e.g., Grafen 1984); they study the correlations between the trait and environmental conditions. Often one can make powerful and unexpected predictions from these correlations, using selection theory (e.g., see Krebs/Davies [eds.] 1991; Daly/Wilson 1983).

Levels of Selection

Clearly, only behaviors that enhance the success of a genetic lineage (such as behaviors which are selfish, parental, reciprocal, or help relatives and therefore enhance inclusive fitness), can evolve by natural selection. 'Genetic altruists' (those who, to their cost and others' benefit, restrict or cease reproduction, like the Shakers) decline in the population, being replaced by individuals that behave to their own reproductive benefit, as Darwin himself recognized (Darwin 1859, 260). Nothing prohibits the occurrence of a Mother Teresa or the Shakers with their rules of celibacy, but we predict that they are unlikely to become, or remain, a majority of any population.

Genetic selfishness still produces both apparently altruistic behavior, and apparent population responses to resource levels. For example, open competition both appears selfish, and is genetically selfish. When I nurse my child, is it clearly expensive, and in common parlance we call it 'altruistic' – but in fact, it is genetically selfish (see Alexander 1979; 1987). The apparent 'regulation' of human populations is an emergent phenomenon (Low 1993a; Low et al. 1992), because: [1] many families, differing in their resources, attempt to optimize their own fertility in varying conditions, or [2] subgroups impose legal or religious coercion. These two fertility responses are functionally quite different. The extent to which restrictions impose costly constraints on individual optimization may predict the extent to which individuals will resist them. It would be rewarding to explore empirically when fertility shifts arise from 'ordinary' selection – when, for example, having fewer children results in more living descendants, for individuals, versus coalition-imposed fertility shifts. Recently Hawkes and Charnov (1988; see also Botkin 1990) have summarized the arguments cogently in anthropology.

Learning, Novelty, and Complexity

Although any behavior that enhances fitness deserves a closer look, a caveat is important, particularly in examining the complex social behavior of humans.

Because a 'trait' or characteristic exists, even if it has a current positive impact on fitness, does not necessarily mean that it is an adaptation (Williams 1966; also Reeve/Sherman 1993). It is an onerous task to demonstrate that any trait is an evolved adaptation: we must show that the trait not only correlates with some environmental condition, but is effectively 'designed' *in response to* that condition. We may see, particularly in highly developed social systems (even in other species), non-evolved effects of behavior that had originally an entirely different function. In such cases, we are often asking not "what is the evolutionary history?" of the trait, but rather "what, if any, is its current utility?" in terms of fitness. In the case of resource/reproduction relationships, we ask: Does resource garnering confer a reproductive advantage? If not, why does it exist?

But there are cases, particularly in humans, in which previously adaptive behaviors continue to exist after any adaptive advantage is gone. If for a long time there has been a reproductive advantage to some behavior, and then conditions change, the behavior can continue to be driven by proximate cues (which previously correlated with reproductive advantage), even though the proximate cues are now unhinged from the (past) functional advantage. This situation is most common in cases of environmental changes that represent evolutionarily novel events; human technological changes are an important source of such shifts.

This complexity can cloud our study of behavior unless we are aware of it. Consider a simple example. For omnivores, food sampling represents a risk. It is common in many species both to sample new foods at a low level, and to use correlates in establishing preferences. If there are toxic effects, they will likely be minimal and simply unpleasant rather than lethal. Sweet foods are seldom harmful, and sour and bitter tastes are often correlated with the presence of harmful alkaloids; thus a preference for sweet tastes has become widespread in species with a generalist diet – including many primates, and probably our ancestors. In natural situations, it is difficult to obtain sufficient sugar, without other nutrients and fiber, to create obesity. Once humans invented technologies for refining and concentrating sugar, we created foods that had enormous levels of sugar, breaking the link between sweet taste (the proximate cue) and good food source (resulting in enhanced nutritional status and better survival).

But no organism evolves to have any awareness of ultimate selective relationships; proximate cues drive the system, and natural selection, as a passive sieve, operates through differential survival and reproduction. What we perceive has always been some proximate cue like pleasure or pride, although the reason the behavior persists or dies out is its effect on inclusive fitness. So, we retain a preference for sweet taste that is often currently counter-adaptive (because of health risks, and perhaps one's diminished chances of being chosen as a mate). It is not only possible, but likely, that we will be able to identify numerous behaviors in humans, particularly in modern societies, that do not have current reproductive utility. Thus, I do see behavioral ecology as an important complement to sociological analyses, not a replacement.

The behavior patterns I discuss here are clearly influenced by social transmission and learning, whatever genetic components might exist. Thus we learn, for

example, that in particular societies high or low, early or late, legitimate or total, fertility is valued; this tells us something of the proximate causes of the observed fertility behaviors, analogous to elucidating the role of daylength or hormone shifts in migration. We can also ask whether individual choices among possible patterns have any impact on the relative success of the genetic lineages of different strategists – the 'current utility'. The question is: Does it matter to a behavioral ecological approach whether strategies are learned? Learning is a form of intergenerational transmission elevated to a high art in humans, but it is not unique to us. Organisms with different environmental problems to 'solve' have very different predilections for learning quite different skills, and at different times in the life cycle; thus the existence of learning does not obviate the impact of natural selection. Knowing the extent to which learning contributes to heritability tells us, however, something about environmental variance (what aspects of the environment are sufficiently unpredictable to make learning advantageous), and about what is selectively crucial (i.e. what is important to be able to learn), rather than about how much impact selection has.

2. Our Mammalian Heritage: The Ecology of Two Sexes

The theory of natural selection is the basis of behavioral and evolutionary ecology. Two propositions are the foundation of this theory: (1) heritable variation exists – offspring are more like their parents than like strangers; and (2) in any environment, not all variants survive and reproduce equally well. Over time, certain variants come to comprise a greater proportion of the population. Behavioral and evolutionary ecology share this underlying paradigm, but in different time frames. Behavioral ecology focuses on predicting behaviors that succeed in a particular environment, while evolutionary theory predicts and assesses genetic and population changes over time. The allocation of somatic and reproductive effort relates to the problems of surviving and reproducing relatively better than one's competitors. This was the original meaning of 'fitness' as used by Darwin (Dawkins 1982, ch. 10).

To analyze the fitness of particular strategies (e.g., age at maturity, clutch or litter size) in particular environments, behavioral ecologists make specific predictions about what behaviors should succeed best in which (highly specified) environments. Another insight from behavioral ecology is that fertility should be an ecological phenomenon. Over time, the families of optimal strategists come to control more of the available resources and to comprise a greater proportion of the population. Yet unalloyed fertility is seldom the winning strategy. The relative success of opposing strategies (producing many offspring versus investment in each offspring) imposes a real constraint (Darwin 1871; Trivers 1972; cf. e.g., Tilly 1978; Easterlin 1978; Becker/Lewis 1974). Reproductive strategies and ecological factors such as resources (richness, controllability, and predictability) and the sources of juvenile mortality (i.e., whether parental effort can enhance survivorship) are clearly correlated.

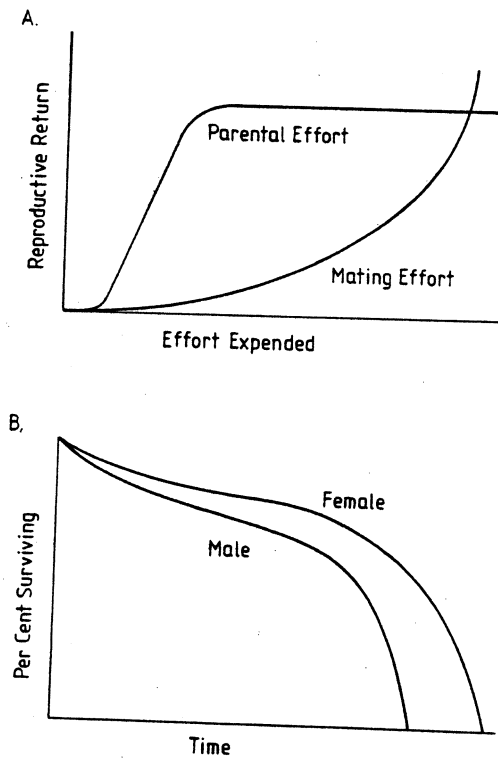
Behavioral ecologists view organisms as 'packages' of calories to be spent and risks to be taken. Because natural selection favors individuals who expend their effort in ways that increase survival and reproduction, some predictions emerge. At any moment, an organism might spend its effort on maintaining its soma, or body (*somatic effort*: thermoregulation, eating, metabolizing, etc); or it might spend *reproductive effort*, either in attracting a mate (*mating effort*) or in caring for offspring (*parental effort*). Behavioral ecology begins from the premise that, in any described environment, some patterns of expenditure will be more optimal than others in their effect on survival and reproduction. Further, it appears that in most species, it pays individuals to specialize in either mating or parental effort – the behaviors that make one successful in mating are often mutually exclusive of the behaviors that promote parental success (reviewed by Low 1993a; also Daly/Wilson 1983). In most, but not all, species, mating specialists are likely to be male, and parental specialists are likely to be female.

This specialization has profound (and not immediately obvious) implications. If one sex specializes in getting mates, and the other in investing in offspring, we predict very different sorts of behaviors between the sexes, for mating and parental effort show very different 'return curves' (reproductive success gained per unit of resources or status acquired; Figure 1, adapted from Low 1993a). Mating effort has a very high 'fixed cost' – typically, a male must establish himself as successful (in other species this might involve growing antlers, fighting for dominance or a territory) before he can get even his first mate. Parental effort shows a more linear return curve: each additional offspring is likely to cost about as much as the first. This simple observation has profound impact on male, versus female, behavior. Far fewer males than females in most species actually reproduce, but the most successful male has perhaps an order of magnitude more offspring than the most reproductively successful female (e.g. among elephant seals, over 80% of males fail to reproduce; the most reproductive female had 11 offspring in her lifetime, while the most successful male had over 90; LeBoeuf/Reiter 1988).

Since males typically experience more variance in reproductive performance than females, the stakes are higher for males. Great expenditure and risk may be profitable, so risky behavior and conflict are, in polygynous species, male endeavors. Thus sexual conflicts (more frequently by males in mammals) are more likely to escalate to lethal proportions than conflicts arising from other sorts of individual selection. In humans, too, male reproductive variance typically exceeds female variance (see Low 1990b). This leads us to make a series of predictions about sex differences in risk-taking, promiscuity, and aggressiveness. Several of these are problems for which sociology has no guidance, while behavioral and evolutionary approaches offer clear and testable theory: sex-preferential infanticide (Dicke-mann 1975); sex ratio and resources (Volland 1990); sex differences in reproduction and striving (Low 1988; 1990b), including the difference in remarriage rates between widows and widowers (Low 1991), and how wealth affects the lifetime reproduction of men versus women (Low/Clarke 1992); birth order and parental investment (Boone 1988); how Fisher's concept of reproductive value influences

men's as opposed to women's reproductive choices (Low 1991); how interbirth interval and sex of child might be related (Low 1991).

Figure 1



(a) Mating and parental effort have very different return curves. Getting a mate frequently requires great initial effort and expenditure (a high fixed cost), even to get a single mate; thus a red deer male may need to grow for an extra few year (to get big enough to compete with territorial males), grow antlers, and fight for territory, just to get a single mate. Investing in offspring (parental effort), however, typically shows a very different pattern: there is some investment below which the offspring cannot survive and reproduce; above that amount, the offspring's chances improve, and there is some limit above which increased investment will not improve the offspring's chances (Low 1978). Thus, in any species, or human society, in which males specialize in mating effort and females in parental effort, very different behaviors will typify the two sexes. (b) As a result of these return curves, males will tend to be risk-takers, females will tend to be risk-averse. Reproductive failure will be higher, and survivorship lower, among males.

3. Human Sex Differences

These return curve differences for male and female mammals have profound impact in two ways: males and females will find quite different payoffs for their accumulation of resources, and for their acceptance of risk. For men and women, too, despite all cultural variation, this underlying difference sets the scene for widespread, predictable sex differences.

Male Cultural and Reproductive Success: The Importance of Resource Value

When resource-controlling men can have higher fertility than others (e.g., through polygyny in bride-price societies), fertility will tend to be high but variable. Such conditions obtain in many traditional societies and some pre- and proto-industrial societies (e.g. Pfister 1989a; b). In quite varied societies, wealth or status and reproductive success are positively correlated for men [e.g. Hill 1984]. Richer Turkmen had more wives and more children than poorer men (Irons 1979). In the pastoral Mukogodo of Kenya, wealth enhances men's reproductive success (Cronk 1991b). Similarly, the Meru use livestock for bride-wealth, and richer men can marry more wives (Fadiman 1982). In societies as diverse as the Hausa (Barkow 1977), Trinidadians (Flinn 1986), and Micronesian islanders (Turke/Betzig 1985), status and wealth correlate with male reproductive success.

In some societies, such as the Ache (Hill/Kaplan 1988; Kaplan/Hill 1988) and the Yanomamö (Chagnon 1979; 1982; 1988), few physical resources are owned; even here, status represents a resource. Among the Ache, men who are good hunters not only get more matings than other men, but their children survive better (Hill/Kaplan 1988). In the Yanomamö, male kin available for coalitions also represent a resource, and men manipulate kinship terms in ways that make more women available for mates, and render powerful men available as coalition partners (Chagnon 1982; 1988), so that reproductive success is uneven. In Yanomamö, the most successful methods of gaining wives are being a member of a powerful kin group, and gaining recognition as a revenge-killer (Chagnon 1988; also see below *Sex Differences in Homicide and Warfare*). Among the polyandrous Toda, a man's centrality in the kinship network is related to his reproductive success (Hughes 1988).

These patterns are consistent with the behavioral ecological hypothesis that resources contribute to reproductive success (Low 1989a; 1990a; Low/Clarke 1992), but not consistent with the demographic children-as-resources/producers hypothesis (e.g., Hammel et al. 1983). If children were perceived by parents as producers in agricultural work, not only land owners but land *workers* should have higher fertility. Yet this is not true; only land *owners* typically have higher fertility and larger resulting families no matter what the economic times; and landowners' family size shows less variance than that of non-landowners (Low/Clarke 1992; Pfister 1989a; b; Cain 1985; McInnis 1977; Hayami 1980; Hughes

1986; Voland 1990). Land ownership apparently provides a more reliable resource control, a buffer against hard times.

The positive correlation between resources and lifetime reproductive success holds through the demographic transition. Results from contemporary societies are mixed (Low et al. 1992). However, studies using proxy measures rather than actual resource control often find negative results (reviewed by Low/Clarke 1992). Studies which examine lineages (e.g. Mueller 1991), individual patterns (Rank 1989), and some census data (Daly/Wilson 1983, 334) find positive results. Today, contraception technology complicates the issue; when sexual access, rather than fertility, are measured, richer men clearly have more sexual access than poorer men (Pérusse 1992).

Bride Age: The Importance of Reproductive Value

Fisher's (1958) concept of *reproductive value* was used by Keyfitz (1985, 142-161) to make predictions about migration, contraception, and population growth; it is also useful in understanding trends in marriage age and remarriage rates. Reproductive value, derived from age-specific fertility and mortality rates, is defined as the probable number of daughters a female will have in the rest of her life – thus encompassing age-specific fertility and survivorship functions. Thus, in societies with bride price or some other exchange of goods at marriage (74 %; Murdock 1981), younger women might be expected to command a higher bride price. If high reproductive value is seen as desirable, men with greater economic resources may be able to command women with higher reproductive value in the marriage market. One can also put it that women with high reproductive value are free to choose men with greater resources, although direct female choice is difficult to demonstrate in many societies. Among the agricultural and pastoral Kipsigis, the brideprice required for a woman was directly related to her reproductive value (Borgerhoff Mulder 1988a; 1988b). With the introduction of western technology and medicine, differentials were reduced.

An interesting social dilemma follows. Poor men might choose to marry older women with greater resources when they can, explicitly trading reproductive value for resource value. Thus in 18th and 19th century Scandinavia, daughters of upper-middle class men (who would marry richer men) were considered women (marriageable) at eighteen years, while daughters of poorer men, who would marry poorer men, were not considered marriageable until years later, in their mid-to-late twenties (Drake 1969; Low 1991). Richer men, in marrying younger women, gained high reproductive value, but provided resources themselves. Hughes (1986) found similar patterns with men's wealth and women's reproductive value in England.

Remarriage for Widows and Widowers

In most societies, widows commonly remarry far less frequently than widowers, with no obvious sociological or economic explanation. Further, women remarry at younger ages (higher reproductive value) than men, and women's probability of remarriage declines with age (as reproductive value declines). Classical demographers (e.g. Knodel 1981; Knodel/Lynch 1985) have found such patterns puzzling, for women's economic value, like men's, does not decline with age – however, women's reproductive value (RV) does decline, and the decline after peak RV is a certainty (declining fecundability), rather than the risk of death which causes lower-than-peak RV at early ages.

Not surprisingly, when men remarry, they tend to marry younger women, of higher reproductive value. This undoubtedly contributes to the greater fertility of men's second marriages, compared to women's, even in societies with late ages at first marriage and socially-imposed monogamy. In many societies, though the pattern can be slightly modified by the operant sex ratio (Imhof 1981), the patterns are quite strong: widows remarry far less frequently than widowers (e.g., Imhof 1981; Bideau 1980; Wolfe 1981; Åkerman 1981; Cabourdin 1981; Corsini 1982; Bideau/Perrenoud 1981); widows with dependent children remarry at an even lower rate (e.g., Bideau 1980; Corsini 1982; Bideau/Perrenoud 1981; Griffith 1980); and widows commonly do not remarry at all when they are older (e.g., Cabourdin 1981). In contemporary society, too, these patterns persist (Glick/Lin 1986; Hill/Low 1991).

Training Children

The conditions described above represent a selective background favoring specific differences in the behavior of men and women when presented by a conflict of interest: we expect men to exert overt efforts to change rules, to manipulate rules, to change coalitions; if women have seldom or never been able to profit reproductively from such actions, we expect them to behave in ways which will maximize the probability of continuance of the current coalition, although not to eschew subtle attempts at manipulation.

It is an obvious prediction that parents should bring up children of the two sexes differently, and that these differences should be exaggerated or minimized, depending on the nature of the society, and thus the likely reproductive consequences. Males more frequently than females have succeeded by openly and aggressively competing, often co-operating in coalitions, for power and the control of resources in the community sphere. If this is true, sons should be more strongly trained than daughters in behaviors useful in open competition, while daughters should be more strongly trained in such values as sexual restraint, obedience, and responsibility – traits sought by men in wives. Re-examination of Barry et al.'s (1976) cross-cultural data on how boys and girls are trained (Low 1989c) suggest that both these things are true. Further, inculcation of sons in attributes like

aggression and fortitude is strongest in those societies in which the reproductive stakes are highest (polygynous societies), and lowest in rigidly stratified societies, in which individual striving is least likely to reap reproductive rewards.

Patterns of child rearing in different cultures can differ strikingly (e.g., Barry et al. 1957; 1976; Whiting/Edwards 1973). As Konner (1981) noted, cross-cultural research based on children's behavior in natural circumstances has suggested that sex or gender differences we observe in American and English children are not limited to Anglo-Saxon cultures (e.g., Whiting/Whiting 1975; Whiting/Edwards 1973; Blurton-Jones/Konner 1973), and that there are both differences and similarities cross-culturally in how boys versus girls are treated. However, previous analyses of sex differences in child rearing (Ember 1981; Rosenblatt/Cunningham 1976) have not found any clear logical patterns in the existing variation. In part, this may have arisen from a failure to use the extraordinary advances in evolutionary theory of the past decade, something Konner (1981) has urged.

The ecology of mating returns (above), makes different predictions about the functional significance of raising boys and girls differently across cultures. In other species, patterns of parental care, offspring development, and play are related to the mating system, trophic level, and degree of sociality and group-living of the species (Krebs/Davies 1981; 1991; Daly/Wilson 1983; Trivers 1985). Sex differences are more pronounced in polygynous than in monogamous species, with exaggerated male traits related to competition for resources and/or mates. Our human evolutionary background also appears to be polygynous, and 1078 out of 1158 (93%) societies for which data exist are polygynous (Murdock 1967; 1981).

What do the patterns show across cultures? Boys' and girls' training tends to co-vary across societies (Barry et al. 1976; Low 1989c). Societies in which boys are trained to show considerable fortitude, for example, are also the societies in which girls are trained to show fortitude. These trends tell us only that some societies train their children more intensely than others. These broad, non-sex specific differences in intensity of training are reflected in the different parenting styles reported by Whiting and Edwards (1988), who found three broad different inculcation styles: 'training' mothering styles (e.g., in sub-Saharan Africa), who used prosocial commands, and recruited their children to help them work at an early age; 'controlling' mothers (e.g., in the Philippines and Mexico) who used reprimands and threats in child training rather than task assignment; and 'sociable' mothers (e.g., in their U.S. sample) who had more opportunity for play and information transfer.

More interesting are the significant differences in the training of boys and girls *within* societies, independent of broad differences in training intensity. Across all societies, boys are taught, in early and late childhood, to show more fortitude and be more self-reliant than girls (Low 1989c). Girls are taught, in early and late childhood, to be more industrious, responsible, obedient, and sexually restrained than boys. Strength of inculcation is more striking in later childhood, when children begin to assume responsibility, than in early childhood for most

traits, and the probable impact of training is greater in later childhood than in infancy. The greater the degree of polygyny, measured as per cent of men and per cent of women polygynously married (cf. Low 1988), the more older boys are taught to show fortitude, aggression, and industriousness (Low 1989c). Marginally significant trends exist for self-reliance and obedience. As the maximum harem size allowed increases (cf. Betzig 1986), so does intensity of training for boys to show fortitude, industriousness, responsibility, and obedience.

The more women actually control important resources or exercise power, the less daughters are taught to be submissive. For example, the more women are able to inherit property, the less daughters are taught to be obedient. The more formal power women have within the kin group, the more daughters are taught to be aggressive, and the less they are trained to be industrious. In societies in which women can hold political office, daughters are more strongly inculcated in achievement and striving than in societies in which women cannot hold office, although the difference is only marginally significant. The more authority women have over children older than four, the less daughters are taught to be obedient (Low 1989c).

Barry et al. (1976) noted that intercorrelations among traits were stronger for boys than girls; that is, boys are trained more intensely and consistently than girls. Indeed, if male reproductive success varies more than female reproductive success in polygynous systems, the reproductive payoffs for parents are higher for successful training of sons than of daughters. In this context, it is interesting that in our society children themselves quickly show sex differences in perceptions of dominance and aggression. By age three, boys play in groups and play more aggressive games than girls (Freedman 1974; Omark/Edelman 1976). By age four, boys tend to advertise themselves as toughest (Omark/Edelman 1976); by age six, they have formed dominance hierarchies, perceive them accurately, and attempt to manipulate their position (Freedman 1980) – while girls find the entire question irrelevant!

The interplay between the effects of polygyny and stratification on possible reproductive success for males, and males' training, are particularly interesting. The greater the possible reproductive rewards, the more boys are taught to be industrious, obedient, aggressive, and show fortitude – but the variation is great only in non-stratified societies. In non-stratified polygynous societies, inheritance tends to be male-biased (Hartung 1982; 1983), and coalitions of related males are likely to be powerful, particularly in patrilocal societies (Chagnon 1982; 1988; Boone 1986; Flinn/Low 1986). To be successful, a boy must not only show traits useful in getting and managing resources, but also traits recommending him to his elders in the coalition whose help he will need to bargain for wives. In stratified societies, male coalitions may also be important, but in these large societies, they are likely to be among non-related men, and a man's ability to move up the hierarchy may be severely constrained (see Betzig 1986).

Thus, patterns of child training across cultures vary in ways predictable from evolutionary theory, differing in specifiable ways between the sexes, and varying with group size, marriage system, and stratification. The link to variance in

reproductive success is not firmly established, and represents a fruitful focus for research.

Abortion, Infanticide, and Abandonment

In other species, it is typically not parents, but reproductive competitors (e.g. males taking over a harem), who commit infanticide (Hrdy 1974; 1978; 1979; Packer/Pusey 1983; 1984). Typically, males are more likely than females to commit infanticide, although females may (Wasser/Barash 1983). In other species, the context is principally that of reproductive competition. Among primates, the overwhelming majority of infanticides are committed by immigrant males, or males who do not belong to the victim's social group. In humans, also, step-parents are more likely to abuse or neglect children than own parents (Daly/Wilson 1984; 1985; 1987). Even when socioeconomic factors are taken into consideration, the risk for babies of being killed is seventy times as great if the child lives with a step-parent as well as its natural parent. Among the Tikopia and the Yanomamö, a man may demand the death of his new wife's prior children. Such cases dramatically reflect the conflict of genetic interests between the parent and the non-parent who may be called upon to invest in the children.

Yet parents can commit infanticide, abortion, and abandonment. Because each infant requires great investment, investment biases, even to the extent of infanticide, can be reproductively profitable. Natural selection can favor termination of investment, depending on: mother's ability to invest, mother's access to additional resources (family, mate), child's ability to succeed, and the economic and reproductive value of other existing or future possible children. Cross-culturally, deformed or seriously ill newborns are at greater risk for infanticide. Similarly, when circumstances reduce a mother's chance of successful investment (e.g., too-close births, twins, lack of an investing male), infanticide or neglect is more likely (Daly/Wilson 1988; Bugos/McCarthy 1984). Abortion, too, appears more common in circumstances in which the birth of an additional child is likely to reduce the mother's lifetime reproductive success. As women age, and their reproductive value declines, termination of investment is less likely (Hill/Low 1992). Even attitudes toward abortion in our society are related to the proportion of women in any group who are 'at risk' of unwanted pregnancy (Betzig/Lombardo 1991).

In many societies, a sex preference in infanticide exists; this represents a conundrum if it becomes widespread and persistent, for the rare sex comes to be more valuable in any marriage market (Fisher 1958, 159). In hypergynous societies, in which women may marry 'up' and men 'down', but the reverse is not allowed, daughters are valuable to lower-class families, but costly to upper-class families. There is no single within-society sex bias, but infanticide tends to be female-biased in high-status families, and son preference less strong in low-status families (e.g. Dickemann 1979). These patterns, Dickemann argued, probably also represent a Trivers-Willard effect (see below). It is possible, too, that (otherwise rare) male-biased infanticide occurred in high-status families (Parry 1979).

Voland (1984) examined the effect of father's status on children's survival in a 19th century German parish. The overall sex ratio of children born was almost exactly even; the effect of mother's age was not analyzed. Deaths during the first year of life due to parental neglect were status-related: for farmers, daughters were likely to be considered less desirable than sons; for other classes, the reverse appeared to be true. Voland thus has evidence of uneven parental investment tied to the perceived value of each sex for parents in different classes. In a similar sample from 19th-century Sweden, I found (Low in press) no bias in the birth sex ratios of children born to richer versus poorer men, but a very strong sex bias in investment by rich versus poor men; both kinds of fathers produced more rich sons than rich daughters – but poor men dramatically funnelled their (more limited) resources into sons.

Historical studies of child abandonment also reflect such selective considerations as a mother's ability to invest in the child (including own health, familial resources, economic conditions), and the child's health, legitimacy, and sex. Child abandonment in historical France (Fuchs 1984), Spain (Sherwood 1988), and Russia (Ransel 1988) was related to economic factors, child's condition, and mother's abilities. Similarly, Boswell's (1990) well-known historical overview of child abandonment reveals that 77% (49/63) of cases were, despite great variation in time, country, and other circumstances, related to maternal ability to invest and offspring quality. Perhaps the other side of the coin is represented by adoption – taking care of someone else's child. Cross-culturally, when someone adopts a non-related child, most often it is a poorer, or lower-status family offering to care for the child of a richer, more powerful lineage!

Physiological Sex Biases: Trivers-Willard Effects

In many polygynous species, including humans, male offspring are more expensive to raise than female offspring (Trivers/Willard 1973; Daly/Wilson 1983): they are carried longer *in utero*, they are larger at birth, they nurse more and more frequently, and they are weaned later. Trivers and Willard (1973) argued that in polygynous species under such conditions, females in good nutritional condition should be likelier to bear sons than daughters. A more broadly applicable statement might be: when variance in reproductive success of one sex exceeds that of the other sex (as in elephant seals), or when parental investment can influence the reproductive success of one sex but not the other (as in baboons), there should be a correlation between parental condition and investment in that sex (cf. Clutton-Brock 1991). Frank (1990) reviews the complexities.

Trivers and Willard assumed that mother's physiological condition (resources available to rear a successful offspring) would decline with age. In non-human species, and in many non-technological societies and developing countries, this is appropriate. Whenever the nutritional condition of mothers does not decline with age, a male bias in sex ratio might be found in older mothers (Low 1991). In polygynous iteroparous species, if a female's condition is good, a male bias is

predicted to be profitable as a female nears the end of her reproduction – to invest more heavily, with a greater potential reproductive profit if successful (e.g., male-biased sex ratios for older female gorillas [Mace 1990] and 19th-century Swedish mothers over 35 [Low 1991]). Such patterns underlie social phenomena like parental sex-preference (Knodel 1988).

Among polygynous Mormons, sex-ratio and parental status are correlated as predicted by Trivers and Willard (1973). Gaulin and Robbins (1991) have found a series of other Trivers-Willard effects in contemporary US society. They examined interbirth interval, birth weight, and proportion of children nursed as they related to income and the presence of an adult male in the household. They found that as income increased, so did interbirth interval and per cent breast-fed – for sons, but not daughters. For all seven of their measures, patterns differed for sons versus daughters – daughters received relatively more from low-investment mothers, and sons got more from high-investment mothers.

Sex-Biased Inheritance

Because resource control is an effective and widespread strategy for men in acquiring mates (above, also Betzig 1986; Flinn/Low 1986; Low 1990b), sex biases in resource inheritance are important; they can influence survivorship and likelihood of reproduction. Perhaps no other species exhibits the degree of resource transfer that can take place through inheritance within human families. Inheritance is frequently biased by sex, legitimacy, and birth order.

In societies with heritable goods, the size of a family and the sex of siblings may influence men's and women's ability to marry at appropriate times somewhat differently. Within polygynous marital systems, inheritance is strikingly male-biased (Hartung 1982), precisely the pattern predictable if male reproductive success varies more than female reproductive success, and male success is influenced by resource control. In many societies, earlier-born sons tend to inherit the greatest proportion of the resources, even where more equal distribution is stipulated by law (e.g., 19th-century Sweden). Women's lifetime reproduction decreased as their number of siblings increased (Low 1991). For men, only the number of brothers mattered, suggesting that brothers represent resource competitors for men, and that as total sibship size increases for women in many societies, they are more likely to be drawn into caring for their siblings (regardless of sex), at some cost to their own reproduction. Among 15th- and 16th-century Portuguese nobles the proportion of ever-married men and women decreased with birth order, as did fertility for married individuals (Boone 1986, 1988). And in contemporary Tennessee, sons in higher-status families fare better than others (Abernethy/Yip 1990).

Lethal Conflict: Homicide and Warfare

Behavioral ecology predicts that potentially lethal conflict will occur when the possible reproductive (usually mating, not parental) rewards (mates, status, resources for mates) are high; and that, within mammals, males will more often be in a position to gain than females (below; also Manson/Wrangham 1991; Alexander 1987; Low 1992). Sexual selection (in competition over mates) and kin selection (in infanticide and inter-group conflicts) will be the driving forces. Inter-group, rather than inter-individual, conflict will occur only in long-lived, social species. Several recent analyses reflect these predictions. Shaw (1985) and Shaw and Wong (1989) have argued that evolutionary explanations may be useful in analyzing warfare in complex nation-states. They focused primarily on kin selection arguments as the background for xenophobia and ethnocentrism, major factors in promoting war (see also Johnson 1986 on the use of kinship terms by political leaders). Kin selection leads to the development of cohesive groups that are predisposed to intergroup conflict (though it does not predict the sex differences we see in most mammals). Ethnicity is the remnant of this process in modern societies, and kinship ties change the costs and benefits for individuals taking risks in potentially lethal combat (Low 1993b).

Arising from the return curve differences discussed above, mammalian striving and aggression are sexually dimorphic. Coalitions of males in non-human mammals are riskier, more aggressive, and more often among non-relatives than coalitions among females (Low 1990a; 1992). Females' conflicts center on food or parental resources, while males' conflicts are likely to center on the acquisition of mates. Because of these patterns, the reproductive impact of conflict for male mammals may be many times greater than that for females (Low 1990a). Thus it is not surprising that aggression is one of the most consistent sex differences across cultures (Ember 1981; Barry et al. 1976; Low 1989a), and homicides are principally a male endeavor (Daly/Wilson 1988). This difference in risks and returns, of course, is what prompted Darwin (1872) to treat sexual selection differently from 'ordinary' natural selection, even though functionally it is identical. Ross's (1983) observation that women's politics and conflict over resources tend to be at the familial and neighborhood level, while men's conflicts tend to have broader scope, is therefore hardly surprising (Low 1990a; 1992); similarly, women warriors are predicted to be rare.

Cross-culturally, men can make enormous direct reproductive gains with access to power, status, and great amounts of resources, but it is not clear to what extent women can do so (above); this parallels the reproductive ecology of resource control and status in other polygynous species. In the few societies in which women wield substantial public power, as opposed to informal influence, they evidence no clear reproductive gain. In fact, in some of the examples, it is apparent that there is a conflict between political and direct reproductive gain for women. In matrilineal and double descent systems, women's power appears to accrue to their sons, who may reap reproductive benefit (Trivers 1985; Clutton-Brock et al. 1986; Low 1993a). Through evolutionary history, then, men have

been able to gain reproductively by warring behavior; women almost never have been able to do so.

Women warriors, however, are not unknown. During the seventeenth, eighteenth, and nineteenth centuries women occasionally passed themselves off as men and fought in the ranks of infantry and cavalry regiments (Holmes 1875, 102). From at least the time of Alexander (Keegan 1987), women travelled and sometimes fought with their men; children were legitimized in Alexander's time after the soldier completed his duties.

It is important to distinguish this argument from others that might seem similar. This argument does not hinge on sexual size dimorphism in humans – the fact that men are generally bigger and stronger than women. Even in ungulate species like red deer, in which status and resource control are mediated through physical combat, and there is no evidence of reciprocal 'political' alliances, size is not the only determinant of status (e.g. Clutton-Brock et al. 1982). In primate species, and in human societies, the social complexities so far outweigh the impact of physical size that size alone is a poor predictor of success. Similarly, this argument does not reduce to an assertion that women are bound by the constraints of pregnancy, nursing and child care. If that were true, sterile women and post-menopausal women might broadly be expected to engage in intergroup conflict, as do some other primate females (Low 1993a).

Sexual dimorphism in use of resources and power in reproduction is the critical factor. Men appear to seek direct reproductive gain (e.g. stealing wives) in intergroup conflict, while women, when they are (rarely) involved, seek resources for themselves and their offspring. Sometimes this is accomplished through indirect or informal influence and nepotistic gain. Most commonly, the amount of resources controlled by women is sufficient to support their family, although sometimes, particularly in matrilineal and duolineal societies (Low 1992), women may gain for their families. These societies, like the Cherokee and perhaps the Ashanti, are also those in which there is an occasional woman warrior.

Because women have evolved to use resources differently from men in reproductive matters, their involvement in war seems likely to be very different. Women, like other female mammals, have seldom if ever been able to gain reproductively from the extraordinary risks of warfare. Further, patriliney with exogamy fosters men's, but not women's confluences of reproductive interests in war, because related men – but not women – live together. Adams (1983) pointed out that under these conditions, women face a conflict of interest with their husbands (their husbands may be making war upon their fathers and brothers), and argued that the formal exclusion of women from warfare in so many societies may have its roots here.

Sex Differences in Ornaments and Signals

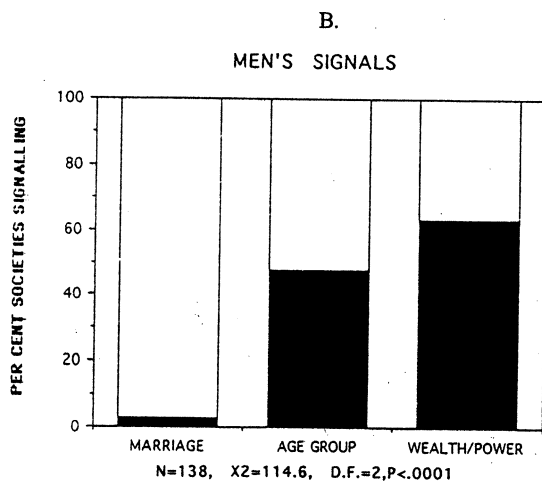
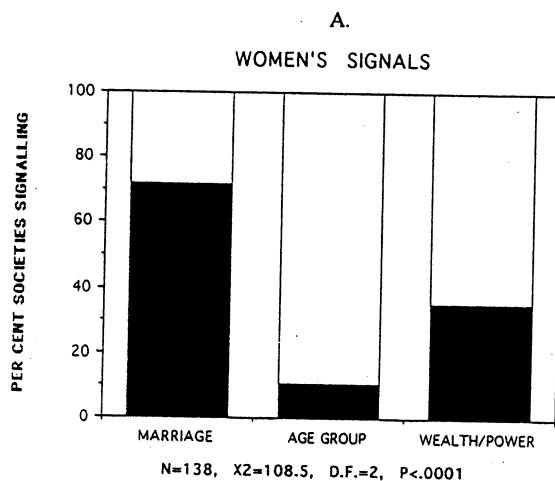
In non-human species, signals of status benefit the bearer: some signals make actual confrontation less likely, saving calories and avoiding risk; other signals

serve as sexual attractants – a phenomenon Darwin (1872) noted over a century ago. In non-humans, the sex competing for mates is the sex likely to give such signals: males in polygynous species, females in polyandrous species (e.g., Alexander et al. 1979 and others).

Humans are paradoxical with regard to sexual selection and sexual displays: most scholars agree that their evolutionary history is polygynous (like most other primates), and 83% of societies for which we have information are polygynous. Such an evolutionary history would immediately bring to the fore a prediction that males should be 'ornamented', yet the concepts of ornamentation and sexual signalling are most likely to be associated with women. Humans are also unusual (though not unique) in augmenting their or their possessions' appearances behaviorally ('culturally'), and they do this to a sometimes extraordinary degree. And, finally, humans have within a single species, a variety of mating systems, facilitating comparative tests of any hypotheses about sexual selection and ornamentation.

Human societies vary (Low 1979): asymmetries in information in ornaments worn by both sexes are related to the marriage system (Low 1979). Further, there was a general trend related to the polygynous background of humans and the asymmetry in resource control between the sexes. Of 138 societies, 87 distinguished male status by ornaments, 39 of them without distinguishing marital or pubertal status. Only four societies, two of them monogamous, distinguished female marital status. In contrast, 102 societies distinguished female marital or pubertal status, and only three of these failed to signal marital status. Forty-nine societies signaled wealth or status by female ornament or attire, but I was at that time unable to distinguish whether the status was the woman's own, or a reflection of her husband's status. In fact, across societies, men are likely to signal access to wealth and power, while women's marital status is typically signalled – suggesting a potential conflict of interest for men and women (Low 1979; Figure 2). Further, men do not signal marital status (perhaps we infer that they are, as males in other species, always available for matings, if not for parental investment). Although there is a general asymmetry in resource control, there are societies in which women control significant resources, or wield considerable influence over others (Low 1990b). Women's ornaments or dress reflecting wealth or power status (Figure 2) showed no relationship with measures reflecting women's actual resource control: property inheritance, control of dwellings, kin leadership positions, control of the fruits of men's, joint or women's labor, participation in community decisions (Low 1990b). Thus, in general, women's ornaments of status and power reflect their husband's, or other male relative's, status rather than their own. This is consistent with the observation that males seek resources as a form of mating effort, competing against other males to whom they are variously and

Figure 2



Across societies, men and women signal different attributes. (a) Women's marital status in most societies is obvious from their dress and ornamentation; because this is a signal of 'unavailability', it may represent a conflict of interest between the sexes. Women's signals of wealth and power are not related to their own wealth and power, but that of their male kin (see text). (b) Men signal wealth and power status, as well as age-group status, but not marital status.

often not related, and interacting with individuals they know less well; while females seek resources as a form of parental effort, working at home with sisters or co-wives.

Evolved Sex Differences and Our Society

In other species, and across human cultures, there is a sexual dimorphism in resource acquisition, control, and use, and the pattern is that predicted by behavioral ecology. Men compete to control resources in order to get wives, and form coalitions with both relatives and non-relatives; women compete to acquire resources to feed dependents, and form coalitions mainly with other members of the household.

This is an obvious oversimplification – humans have elaborated the art of coalitions to a degree unknown in any other species; nepotism and coalitions can persist after the death of major participants; in many societies men can control the reproductive destinies of not only their mates, but other female relatives, and so on. Nonetheless, the general pattern is clear, and ecological correlates exist. In our society, many ecological constraints are removed; nonetheless, certain major patterns – clusters of female power measures – are also apparent in our own society. Women in societies in which they could inherit property were also likeliest to be able to control the fruits of male and joint labor, and to participate in community-wide non-religious activities; and control of the fruits of male labor was highest when female contribution to subsistence was high. Women's ability to hold political leadership posts is high in bilocal and neolocal societies (Low 1990b).

Today, in Western industrialized nations, women have great actual resource control. Women spend money earned jointly and by men, as well as money they themselves earn; women can inherit property. Although 'marital residence' is a concept foreign to an analysis of our own society, we are certainly principally neolocal, with the couple typically settling in an area independently of the location of either natal family; and, while women may be neither as numerous or as powerful as men, they can hold political posts. There are differences in our society from the general pattern, many of them recent. Because our society is so large and technologically advanced, what can the existence of patterns predicted by behavioral ecology tell us? Several general points are important.

Because women have, in the past, and in traditional societies, held little power in the community sphere, this *does not* mean that women are 'biologically' or 'ecologically' unfit to do so. It means that under past conditions, and in preindustrial societies, women did not profit reproductively from risky competition for great gains in resources and status, while men did (also above). In our own society, the link between power/resources and reproductive success may well be weakened (see review by Low 1993a). Today, investment in fewer offspring, rather than production of many, may be the strongest reproductive strategy (see also Rogers 1992). In our society, having children does not, as it may have in

some pre-industrial societies, help accrue resources. Infant and child mortality are low, and resources are typically divided through wills among children. Thus, the strategy of resource accumulation and family limitation is liable to remain strong. Under such circumstances, women's access to resources and power may enhance family resources without a serious cost to net reproductive fitness – though women's accrual of resources in market economies clearly has net fertility costs (e.g., Kasarda et al. 1986).

If women and men have been most successful by pursuing very different strategies, and if parents reinforce such differences by training, as I have suggested, women may be successful by confronting this history of differences, rather than ignoring it. It may be useful to work directly with young pre-professional women, studying male and female 'styles' of assertion and competition, particularly in situations (such as many advanced academic and professional areas) in which criteria and deadlines are not clearly specified, and in which a very self-directed competitiveness appears successful. Some successful attempts are already underway. Data from studies of signalling (see review by Low 1990b) suggest that it will be generally true that 'styles' which are simply mimics of male strategies will tend to be unsuccessful, yet the data from non-technological societies are of little help, because the context of resource competition in our society is so broad, and most competitors and coalition members are not kin.

With regard to specifics of particular strategies that are effective for women, we face an entirely new challenge. We can predict that certain strategies (submissiveness, giving up the game rather than disagreeing) will be unsuccessful, that other strategies (signalling power) may help. Yet exactly how this is accomplished (e.g., which power signals are effective) awaits further study within our own society. Miles (1985) found that a majority of top women executives were first-born, born in cities, had strong and non-traditional (non-domestic) women in their family, admired fathers who encouraged them, but who disappeared from the family during the woman's dependent years. In arenas such as this, we seek the proximate correlates of success – the most useful work will come not from behavioral ecology, but from sociology and psychology.

4. Conclusions

My purpose here has been to suggest that theory and information from behavioral and evolutionary ecology can help us set into context some important problems we wish to solve about human behavior; my focus here has been sex differences in behavior and life histories. Behavioral and evolutionary ecology suggest that the lives of men and women, like the lives of males and females in other species, have evolved as a result of the interaction of ecological constraints, historical constraints (e.g. being mammals), and both genetic and cultural inheritance. Knowing about these constraints allows us to make testable predictions about male-female differences in behavior: when these differences will increase or decrease, and how. It does not sentence us to the patterns of the past. I suspect evolutionary

and behavioral ecology can tell us useful things about our past, and trends that exist (many of these are things we wish to change, rather than perpetuate); sociology and psychology will tell us more about how to accomplish these changes.

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