

Testing Evolutionary Hypotheses with Demographic Data

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INTEREST IS GROWING in the application of evolutionary and behavioral ecological theory to problems of human lifetimes—age-specific fertility and mortality, population growth, and emerging population–environment interactions (e.g., Cronk 1991a; Borgerhoff Mulder 1991, 1992, 1998; Hrdy 1999; Low 2000a,b). An understanding of human evolution, particularly the effects of environmental constraints on age-specific fertility and mortality (e.g., Stearns 1992; Roff 1992; Kaplan 1997; Low 1998), offers insights not only into our past, but into modern problems that are both large scale and urgent. Past theories have helped little to illuminate such issues as the transition to small family size (on this see, e.g., Schofield and Coleman 1986).

Low, Clarke, and Lockridge (1992) and Low (1993) highlighted the theoretical connections between evolutionary studies of human demography and modern problems; later Wilson (1999) suggested the utility of an evolutionary approach to demographic data, especially historical data—but was apparently unaware of a wealth of existing studies. Here we review evolutionary demographic studies of traditional, historical, and modern societies. For reasons that will become clear, we emphasize historical studies.

An outstanding tradition of evolutionary approaches to the demography of traditional societies began with the work of Chagnon (1979, 1982, 1988, 1997, 2000) and Irons (1979a,b, 1980, 1983a,b, 1997) (see Table 1 for some of the more prominent examples). Empirical studies of the demography of traditional people (e.g., Howell 1979; Lee 1979; and the exemplary Hill and Hurtado 1996) are valuable in constructing hypotheses about past selective pressures: they help us understand the vital theoretical relationships between, for example, resource richness and predictability, on one hand, and age at first reproduction, fecundability, and total lifetime fertility, on the other. Such studies are always small scale and particular in

TABLE 1 Demographic research on traditional societies using an evolutionary framework; most of these have sufficient demographic data to allow further analysis

Society	Research group	Research question
Ache	Hill and Hurtado, Kaplan	Demography; resources, fertility, and mortality; status and reproductive success; infanticide
Ayoreo	Bugos and McCarthy	Social support and infanticide
Datoga	Sellen, Borgerhoff Mulder, Sieff	Fertility and offspring quality; manipulation of rules for individual and familial gain
Dogon	Strassmann	Child mortality and marriage system; sexual conflict over reproductive rules
Gabbara	Mace	Optimal fertility and inheritance for lineage
Hadza	Hawkes, O'Connell, and Blurton Jones	Optimal birth spacing; grandmothing; manipulation of rules for family benefit
Ifaluk Islanders	Betzig, Turke	Status and family success; effects of sex-specific birth order
Innuait	E. A. Smith	Optimal foraging; conflicts of interest
Kipsigis	Borgerhoff Mulder	Reproductive value and bride price; status and reproductive success
!Kung	Blurton Jones	Optimal birth spacing
Mukogodo	Cronk	Sex-biased investment; status and reproductive success
Toda	Hughes	Status and lineage success
Turkmen	Irons	Wealth, status, and reproductive success; social cues of success
Yanomamö	Chagnon	Status, aggression, and reproductive success; manipulation of rules for reproductive gain

focus, however. Optimization models of the ecological demography of traditional societies also can be informative (Mace 1996, 1998; Blurton Jones 1986, 1997; Sellen, Borgerhoff Mulder, and Sieff 2000; Luttbeg, Borgerhoff Mulder, and Mangel 2000). They help us understand our starting point, as it were, but can be difficult to relate to modern populations. In contrast, modern demographic and behavioral ecological studies, while they may have large-scale databases, focus on humans in environments that are both complex and novel;¹ further, many have only aggregate data, a shortcoming that hampers many analyses (Low 2000b). Some studies of modern populations (e.g., Daly and Wilson 1984, 1985, 1987, 1988, 1997; Kaplan and Lancaster 2000; Kaplan et al. 1995) link our evolutionary past and our ecological demographic present, but for many questions elucidating such links may be difficult.

Historical demographic data offer particular value (see especially Voland 2000). Many historical demographic datasets are large, and—importantly—based

on individual and lineage records rather than aggregate data, so that analyses can be done of variation within populations (see Low 2000b; also Voland 1995, 1998; Low 1991, 1993; Low, Clarke, and Lockridge 1992). The conditions of the population under analysis vary but are less “novel” than those of modern populations (see Table 2 for examples of historical studies). These data, as Low, Clarke, and Lockridge (1992) and Wilson (1999) suggested, act as a bridge between limited data on traditional societies living in often-remote conditions and modern populations living under novel and complex conditions. Historical data allow us to examine populations in complex and relatively modern conditions. They are typically more homogeneous than large modern datasets, and more accessible analytically; underlying relationships (still likely to function today) are more easily discerned. They are thus ideal for asking a variety of

TABLE 2 Historical demographic studies using an evolutionary framework; most of these have sufficient demographic data to allow further analysis (see Voland 2000 for a related table on family reconstruction studies)

Country/population	Time period	Research group and questions
England	1550–1900	Scott, Duncan, and Duncan, <i>Epidemiology; ecological influences on fertility</i>
	1754–72	Hughes, <i>Resources, status, and reproduction</i>
Finland		
Saami	1700–1900	Käär, Jokela, Merilä, Helle, Kojola, <i>Sex differences in remarriage patterns</i>
Finnish	1752–1850	Lummaa, Haukioja, Lemmetyinen, Pikkola, <i>Twinning; sex ratio variation</i>
France	1730s	Hrdy, <i>Infanticide</i>
Germany		
Ostfriesland	1720–1874	Voland, Siegelkow, Engel, Dunbar, Klindworth, Gabler, <i>Resources, status, and reproduction; elite status and differential investment</i>
Ireland	1800–1966	Strassmann, Clarke, <i>Resource constraints and emigration</i>
Norway	1700–1900	Røskaft, Wara, Viken, <i>Resources, status, and reproduction</i>
Portugal	1380–1580	Boone, <i>Resources, status, and reproduction; elite status and differential investment</i>
Rome	From 27 BC	Betzig, <i>Wealth, power, and polygyny</i>
Sweden	1700–1900	Clarke, Low, <i>Resources, status, landownership, and reproduction; resources, status, and emigration; evolutionary perspectives on demographic phenomena; life course analysis</i>
United States		
New England	1750–1850	Towner, <i>Resource constraints and emigration; inheritance and differential investment</i>
California	1890–1984	Judge, Hrdy, <i>Inheritance and differential investment</i>
Utah, Mormons	1800s	Josephson, <i>Resources, status, and reproduction</i>

questions of interest to demographers, anthropologists, sociologists, ecologists, and evolutionary biologists (e.g., Low, Clarke, and Lockridge 1992; Low 1993; Voland 1995, 2000). Considerable work has accumulated, and the results are instructive for inference. Although the analyses extend across traditional disciplines, they are difficult for scholars in other fields to find. A new review seems both timely and useful.

Different fields, different questions

Demographers and evolutionary scholars alike are interested in life histories, although the particular questions addressed and the methods of analysis often differ. For most demographic analyses, proximate influences on fertility, migration, and mortality are of primary interest: under what conditions (social or ecological) do these shift? Evolutionary anthropologists (Hill and Hurtado 1996; Hrdy 1999), behavioral ecologists (Alcock 1998; Low 2000a), and evolutionary psychologists (Daly and Wilson 1988; Barkow, Cosmides, and Tooby 1992) more often focus on ultimate causality: what were/are the impacts of particular behaviors on reproductive and lineage success, under particular social or ecological conditions? Thus, evolutionary scholars would never ask, as do Schoen et al. (1997), why Americans would want children; genetic and lineage success are basic currencies (see Turke 1989, 1990). Finally, demographers and evolutionary analysts aggregate and disaggregate information differently, which can make comparison difficult (Low 2000b).

There are differences in emphasis (see Smith 2000), even within fields focusing on ultimate causes: What are the fitness effects of different strategies in particular environments? One could ask about past history (or present remnants of that history in modern traditional societies), or about current reproductive utility. Both are informative about ultimate causation (Holekamp and Sherman 1989; Sherman and Reeve 1997). Finally, some scholars identify problems as within the domain of "evolutionary" demography (Kaplan et al. 1995); others as within the domain of "ecological" demography (Low, Clarke, and Lockridge 1992). The first emphasizes that all populations follow the same basic rules; the second reminds us that under the same rules we will see different outcomes for populations experiencing different conditions. Both inform us about why humans live their lives as they do, in traditional, transitional, and modern populations.

Evolutionary and ecological questions addressed with demographic data

From the pioneering work of Williams (1966, 1992), Wilson (1975, 1978), and Alexander (1979, 1987, 1988), the number of publications on evolu-

tionary ecological aspects of human lifetimes and behavior has grown exponentially. The range of topics below is striking.

Marriage and fertility

Demographers and evolutionary ecologists, working with traditional and historical societies, are well aware that marriage rates and fertility patterns tend to show correlations with resource fluctuations (e.g., Wrigley and Schofield 1981; Hill and Hurtado 1996; Low and Clarke 1993). However, evolutionary scholars also focus on within-population impacts of resource variations.

In most societies that have been studied, whether traditional or historical, men use resources—wealth or status—to gain reproductive advantage. In traditional societies, they do so typically through polygyny: additional wives. In polygynous societies men's ability to marry and to reproduce successfully varies, sometimes enormously, so great expenditure and great risk taking may be profitable (e.g., Josephson 1993). This is hardly a specifically human pattern: in all nonhuman species, striving over resources is widespread and occurs because better-endowed individuals survive better, and reproduce more, than less well-endowed individuals (e.g., Krebs and Davies 1997; Low 2000a: ch. 4). Demographic transitions are actually complex shifts in these basic behaviors.

In more than one hundred well-studied societies, clear formal reproductive rewards for men are associated with status: high-ranking men have the right to more wives. They have significantly more children than other men (e.g., Hill 1984; Low 2000a: ch. 4). Many other societies have no such formal rules (such as "men of status X may have 2 wives"), but wealthy men are nonetheless more likely to marry and to have more wives than poorer men. Among the Iranian Turkmen, richer men have more wives and more children than poorer men; among the African Kipsigis, richer men marry younger wives (of higher reproductive value) and produce more children than poorer men. On the Pacific island of Ifaluk, men who hold political power have more wives and more children than others. The status-reproductive success pattern holds not only in these societies, but in others as diverse as the Meru of Kenya, the east African pastoralist Mukogodo (Cronk 1991b), the agricultural Hausa, the Trinidadians, and the Micronesian islanders (for a review see Low 2000a: ch. 4).

Even in societies in which few physical resources are owned, such as the Yanomamö and Ache of South America and the !Kung of the Kalahari in southern Africa, male striving results in male status, effective in marital negotiations. Among the Yanomamö, coalitions of related men are important (Chagnon 1979, 1988). So male kin available for coalitions represent a resource, and men manipulate kinship terms to maximize their affiliations

with powerful men (this can be a rather general pattern: e.g., Hughes 1988). Further, men can only marry women in lineages that have a particular relationship to their own, so men try to "redefine" their standing in ways that make more women available for mates (e.g., Chagnon 2000). Among the Ache, good hunters have more children than other men (Hill and Hurtado 1996). In quite varied societies, wealth or status and reproductive success are positively correlated for men.

In historical societies, too, marked wealth or status differentials within a population are frequently accompanied by marked fertility differentials. Typically, elite men—landowners or wealthy men—out-reproduced others (e.g., in Krummhörn, Germany: Volland, Siegelkow, and Engel 1991; Volland et al. 1997; Klindworth and Volland 1995; Norway: Røskaft, Wara, and Viken 1992; and Sweden: Low 1989, 1990, 1994; Low and Clarke 1991, 1993). Landowners married at a far higher rate than other men. In the Swedish data, for example, over 90 percent of landowning men in Tuna parish married, compared with approximately 30 percent of non-landowners. Landowners and wealthy men did not themselves marry earlier; rather they married women about 2.5 years younger than the wives of other men. Within parishes, women experienced similar interbirth intervals and age at last birth. Daughters survived better than sons, but there were no class differences in survivorship. The net result was that wealthy men averaged about 1.5 more children than others.² Of course, local complexities were of great interest; in Sweden, for example, the parishes included agricultural, mining, and fishing occupations, as well as external ecological shifts that affected everyone (although they affected the poor more severely than the wealthy).

Age-specific fertility

For other species, the principal predictor of optimal age at first reproduction is extrinsic adult mortality: when adult life is risky, fertility is early (Stearns 1992; Roff 1992; Charnov 1991). There are some clues (e.g., Daly and Wilson 1997) that despite human complexity, we may find similar patterns when we look locally at age-specific life expectancy. A second obvious factor in optimal age at first reproduction is the tradeoff between investment in self versus investment in offspring: having children too early reduces a mother's ability to care for her offspring and to maintain her own condition. This results in the widely observed adolescent subfecundity of traditional societies, in which women typically have their first child at about age 18 or 19 (Lancaster 1986; Hill and Hurtado 1996); in such societies, people are keenly aware that having children too young is harmful (e.g., Hill and Hurtado 1996). There is clear evidence in both traditional and historical societies that resource bottlenecks which produce poor nutrition reduce fertility and increase mortality (e.g., Hill and Hurtado 1996; Scott and Duncan 1999).

In historical populations, marriage conventions typically delayed fertility for at least some women. Access to resources mattered—both for the population as a whole and for an individual relative to others. Marriage rates and age-specific fertility rates in a number of historical populations responded to drought and famine and resulting swings in crop prices (e.g., Wrigley and Schofield 1981; Low 1989; Low and Clarke 1993). Within societies, it is common to find that daughters of wealthier men or landowners married and began having children earlier than daughters of poorer families, whether or not sons did (e.g., Low 1989, 1990; Low and Clarke 1991; 1992; Røskaft, Wara, and Viken 1992; see Low 2000a for a more complete review).

Modern populations exhibit greater complexity. First, certain tradeoffs may no longer exist: nutritional status in some modern developed countries is sufficient to circumvent the lifetime reproductive “penalty” for very early child-bearing. In other species and in traditional societies (Roff 1992; Stearns 1992; Low 1998; Hill and Hurtado 1996), plots of age at first reproduction against intrinsic rate of natural increase show a clear peak: reproducing for the first time too early or too late means one leaves fewer descendants than others. This pattern is not evident in the United States today, however. The other main factor, life expectancy for adults, still matters. Geronimus and colleagues (Geronimus 1996a,b; Geronimus et al. 1996; Geronimus, Bound, and Waidmann 1999) found early reproduction among poor urban black women in the United States to be positively correlated with low life expectancy. In a study of ten Chicago neighborhoods of similar socioeconomic status but differing life expectancy, Daly and Wilson (1997) found that age-specific fertility was earliest for women in the neighborhoods with the shortest life expectancies at birth, and latest for women in neighborhoods with the longest life expectancies. (For a recent review of issues related to age-specific fertility see Ellison 2001.)

Twinning

Producing twins would seem to be an obvious means to increase the number of children a woman has during her reproductive life. If so, why are twins so rare? Haukioja, Lemmetyinen, and Pikkola (1989) found, in pre-industrial Finland, that producing twins did not improve the lifetime reproductive output for women because of high twin and maternal mortality. Anderson (1990) suggested that twinning has not been selected for directly, but rather is the byproduct of the multiple ova that produce twins. He speculated that multiple ova compensate for early embryo losses and increase the probability of survival of at least one zygote. The observed benefit would be shorter inter-birth intervals among women prone to producing multiple ova. Survival of more than one ovum would be an error condition and lead to higher child and maternal mortality.

Gabler and Voland (1994) found that mothers of twins had shorter inter-birth intervals and suffered increased maternal, infant, and child mortality in the eighteenth- and nineteenth-century Krummhörn population of Germany. Nonetheless, mothers of twins showed a reproductive advantage resulting not from the birth of twins but from higher fertility, more than compensating for the costs of bearing twins. The advantage continued into the second generation.

Lummaa, Haukioja, and Lemmetyinen (1999), using data from eighteenth- and nineteenth-century Finland, found no evidence of reduced birth intervals for women bearing twins. Conflicting results regarding the effect of twinning may illustrate a facultative response to eco-demographic differences between populations (Gabler and Voland 1994). Lummaa et al. (1998), comparing two preindustrial Finnish populations, found that where food was abundant and predictable, producing twins resulted in enhanced lifetime reproductive success. Where crop failures and famines were common, bearing twins reduced reproductive success. Studies across time and socio-ecological settings are needed to clarify the reproductive consequences of twinning. Given the rarity of twinning, historical data could play a critical role in providing the sample sizes and time frames needed to assess reproductive patterns.

Child survivorship

A general pattern of improved survivorship of children with increasing family wealth and status existed in nineteenth-century preindustrial societies (Hughes 1986). We found this pattern even within the relatively egalitarian populations of nineteenth-century Sweden, where both sons and daughters showed better survivorship in wealthier families (Low and Clarke 1992). Survivorship of children was, however, sometimes modified by social complexities. Periods of improvement in survivorship did not always follow a clear progression from upper to lower classes, again because of complex social interactions (Sundin and Tedebrand 1981; Nilsson and Sundin 1991). Despite variation, Low and Clarke (1992) found that wealth influenced survivorship beyond childhood as well.

Klindworth and Voland (1995) found that mortality of sons of the elite in Krummhörn, Germany exceeded that of wealthy farmers. While this finding seems to contradict the expected pattern of improved survival with increasing wealth, Klindworth and Voland explain that this anomaly is best understood as a case of local resource competition in which limiting the number of male heirs was required to minimize division of land important to lineage success. This insight is unlikely to occur to researchers not employing evolutionary logic.

Even within modern populations such as the United States, where basic health care is expected to be readily available to all citizens, child sur-

ivorship varies with socioeconomic status and education levels (e.g., Luker 1996: 109–110).

Complications in parental investment strategies

Sometimes parents terminate their investment in a child (through abortion, infanticide, abandonment, adopting-out); sometimes non-parents raise a child (through step- and foster-parenting and adoption). Evolutionary theory is of interest regarding these patterns. Parental withdrawal of investment seems at first obviously counter-selective. In nonhuman species, it is typically not parents, but reproductive competitors who harm offspring; the overwhelming majority of infanticides, for example, are committed by immigrant males, or males who do not belong to the victim's social group (see Hausfater and Hrdy 1984; van Schaik and Janson 2000; see also the review in Low 2000a).

Parents, however, do sometimes kill or abandon children, and this is of interest both from an evolutionary perspective and in terms of policy formulation. Because each infant requires great investment in order to survive and thrive, parental investment tradeoffs can be reproductively profitable in some circumstances and can result in variable investment across children—even to the extent of infanticide. Across cultures, the factors influencing abortion and infanticide include the mother's ability to invest and her other options (Hill and Low 1991), her access to additional resources (family, mate; e.g., Bugos and McCarthy 1984), the child's expected ability to succeed (Bereczkei 2001; Daly and Wilson 1988; Hill and Ball 1996), and the economic and reproductive value of a woman's existing children. In polygynous societies, conflicts of interest may put children at risk (Strassmann 1997, 2000). As women age and their reproductive value declines, termination of investment in their children is less likely (Hill and Low 1991). Thus, abortion, infanticide, and neglect are more likely when circumstances reduce a mother's chance of successful investment.

Child abandonment reflects similar selective pressures. An example in which evolutionary inference is clear from studies lacking any evolutionary perspective is the fact that child abandonment in historical France (Fuchs 1984), Spain (Sherwood 1988), and Russia (Ransel 1988) was related to economic factors and mothers' abilities. Boswell's (1990) overview reveals that, despite great variation in time, country, and other circumstances, 46 percent (29 out of 63 documented cases) of abandonments were related to maternal ability to invest; when resource allocation (16 cases) and offspring quality problems (4 cases) were also considered, selective reasons were apparent in 49 out of 63 cases, or 77 percent. These results are, however, even more striking than the 77 percent figure suggests, for in the remaining 23 percent of cases there were no data explaining the abandonment circumstances beyond that fact that the child was abandoned. Therefore, all cases for which data existed were consistent with the hypothesis of optimal allocation of reproductive effort.

We most often find differential infant mortality associated with ecological and economic fluctuations (Low and Clarke 1991, 1993; Scott, Duncan, and Duncan 1995), and sometimes with social class as well (Scott and Duncan 2000; Hrdy 1992; see Hrdy 1999 for an overview). Cultural patterns can also be relevant. In Sweden during the nineteenth century, women in one far-northern parish did not breastfeed, but used cow's milk, and infant mortality was high. In the mid-1840s the Swedish government sent a doctor along with civil servants to the parish; he instituted a breastfeeding campaign, mostly among the upper class (Brändström 1984); information then filtered down to workers employed in upper-class homes.

These issues might seem local at first, but demographers and other social scientists have become increasingly concerned with them, as they affect both the population at large and the welfare of abandoned children.

Migration

Behavioral ecologists and evolutionary anthropologists are interested in why migration has evolved and how migration correlates with variance in resource availability and individual ability to access resources. Our questions are closely related to the "push versus pull" theories of migration (Grigg 1977). We are also interested in how migration may influence access to marriage partners, degree of genetic inbreeding, lifetime reproductive patterns, and subsequent population growth.

Historical demographic data are particularly useful in this case because the movements of individuals either can be reconstructed from a variety of population sources (Towner 2001) or are explicitly recorded within original records (Low 1989; Clarke and Low 1992; Voland and Dunbar 1997). A small number of studies have focused on dispersal patterns from an evolutionary perspective. While individual differences exist across the populations studied, some useful generalities emerge.

In nineteenth-century Sweden and Ireland, people were most likely to leave areas where the quantity, quality, or dependability of resources was poor (Low 1989; Clarke and Low 1992; Strassmann and Clarke 1998). Migration also varied with individual ability to access resources, and here the pattern is more complex. The migrant stream was composed of two tiers in nineteenth-century Sweden (Clarke and Low 1992) and in New England (Towner 2001). The upper classes possessed resources, skills, and trades that were in themselves mobile, allowing these people to take advantage of opportunities elsewhere, especially in comparison to the land-based resources of farmers. Farm workers, with no right to land, represented the other extreme. They often had little choice but to move in search of better working conditions (Eriksson and Rogers 1978).

Although both men and women left their place of birth, a higher proportion of women migrated in both Sweden (Clarke and Low 1992) and

New England (Towner 1999, 2001). Men tended to dominate long-distance migration (Clarke 1993a). Whereas unmarried people dominated the migrant stream in nineteenth-century Sweden (Clarke and Low 1992), the opposite was true during the same period in New England (Towner 2001). Dispersal may best be understood as a facultative, demographic response to social, ecological, and reproductive options in the local area and beyond (Clarke, Sæther, and Røskaft 1997).

Fertility and proportion of surviving children decreased with an increase in the number of lifetime moves made in the Skellefteå region of nineteenth-century Sweden (Clarke 1993a). Women who moved delayed their first birth by more than three-quarters of a year. Similarly, women movers in eighteenth- and nineteenth-century Krummhörn, Germany married about one year later than nonmovers (Volland and Dunbar 1997).

Migration patterns and rates are a growing concern in the modern world, yet migration is extremely difficult to study in modern populations since the ability to track individuals seldom exists. In this regard, historical datasets offer the rare opportunity to study correlates and consequences of migration. They remain greatly underused.

Violence, aggression, and reproductive success

Lethal conflict—both of individuals and groups during warfare—looks, at first glance, as if it should decrease reproduction. In fact, lethal conflict resembles infanticide and delayed reproduction: in specific environments, for some individuals, potentially lethal conflict is a high-stakes gamble in which there is some probability of winning (greatly increased reproduction) and of losing (death or disability) (see review in Low 2000a: ch. 13). In traditional societies, competition between males can be fierce, and competitive status of all sorts (not only winning conflicts but, e.g., accumulating resources) contributes to men's ability to marry and raise families. Because traditional societies are more likely to be polygynous (e.g., Murdock 1967, 1981), aggressively successful and wealthy men may have many more children than others (e.g., Chagnon 1988; see review in Low 2000a: ch. 4, 13, 14).

There is good evidence that the evolutionary origins of warfare lie in reproductive competition (Low 2000a: ch. 13,14). Women were the cause of warfare (as a result of abductions or failure to deliver a bride) in 45 percent of societies in one major study of 75 traditional societies (Manson and Wrangham 1991). Material resources specified as useful in obtaining a bride were causal in another 39 percent, and in about a third of these, ethnographies specified that richer men obtained more wives than poorer men. Land (clearly useful in establishing a family), livestock for brideprice, adultery, and wife stealing are major sources of conflict cross-culturally (see Low 2000a: ch. 13). In the Standard Cross-Cultural Sample,³ women were at risk of being captured in 66 of 158 societies; in the vast majority of these

cases, women were married or kept as concubines by their captors. In traditional societies, male aggression was clearly linked to reproductive gain.

In historical societies, also, male aggressiveness apparently had family lineage payoffs; military historians characterized medieval warfare as “violent housekeeping” by which groups of related men protected land and resources (Hale 1985). In warfare involving hierarchies of power (i.e., rank and specialization; probably all but tribal ambush warfare), risk has been negatively correlated with prior status and rank. Since at least the Middle Ages in Europe, disenfranchised or low-status men have been at greatest risk in war (see review in Low 2000a: ch. 14). Sons of Portuguese nobles during the fifteenth and sixteenth centuries, for example, would take three-week crusades to nearby, relatively safe locations, while sons of poor families fought in Jerusalem, often dying there (Boone 1983, 1986, 1988). Boone (1986) noted that politically powerful men apparently were aware of the problem of “excess” young males and deliberately chose to send the young men to foreign military campaigns rather than face disruption on the home front.

Today, the combination of evolutionary profit from aggressiveness and current male-biased sex ratios at birth can predispose groups to war. This, too, makes ecological and evolutionary sense (Chagnon 1988; see evidence reviewed in Low 2000a, ch. 13). Young males are societies’ most violent members, and societies with many young adult males are likely to see strife (e.g., Mesquida and Weiner 1999). In many developing countries today the age structure is young, and there is a preponderance of young men with few opportunities. Given the link between aggression and men’s reproductive success in our evolutionary past, this is an enduring demographic concern.

Additional hypotheses of interest

The topics we discussed above should be of interest to demographers of many sorts. In addition, a number of hypotheses are relevant to family historians, anthropological demographers, and other more specialized groups.

Remarriage. In virtually all societies in which remarriage occurs, it is a male affair. Men remarry more often than women, and they more often have families in second and subsequent unions than women do (e.g., Kåår et al. 1998; Low 1991; Low and Clarke 1991). In part, this relates to the difference in each sex’s mate value to the other. In our evolutionary past, and under many conditions today, men’s mate value is resource value and women’s mate value is reproductive value (Fisher 1958: the number of daughters a woman is likely to have during the rest of her life given current age-specific fertility and mortality schedules). Thus the evolutionary background to this pattern seems clear. Few demographers, however, have connected empirical patterns to the functional reproductive consequences.

Differential investment in sons versus daughters is tied to the relative potential reproductive gain from that investment (Trivers and Willard 1973; Charnov 1982). This phenomenon has an interesting relationship to evolutionary theory that is now widely recognized: numerous species adjust the sex ratio of their offspring (e.g., see Bourke 1997). Sex ratio adjustment is not a peculiarly human phenomenon, nor even one requiring conscious choice. Investments can be in the form of physiological investments (Voland 1989, 1990; Cronk 1991b,d, 1993, 2000), general provisioning (Abernethy and Yip 1990; Gaulin and Robbins 1991; Irons 2000), or intergenerational wealth transfer (Smith, Kish, and Crawford 1986; Low 1990; Judge and Hrdy 1992; Hrdy and Judge 1993; Judge 1995; Gaulin, McBurney, and Brakeman-Wartell 1997). In stratified societies with patrilineal inheritance, male-biased investment may be extreme (e.g., Boone 1986, 1988; Betzig 1986; see Low 2000a: 71–74 and 274). Biased investment favoring daughters occurs among peoples with low status relative to their neighbors (Berezkei and Dunbar 1997; Cronk 1991b, d, e, 1993, 2000) whose daughters can “marry up.” Importantly, in some cases, sex biases in investment correlate with patterns of population increase for land-based groups; in expanding populations, sons are valued while in stagnant conditions they represent a cost (Voland 1995; Voland et al. 1997).

These are issues of concern today: extremes of sex-biased investment in countries such as China, India, and Korea create biased adult sex ratios, and brides become rare. Parents in some circumstances appear to respond to the sex ratio of their living children, so the sex ratio of third- and fourth-born children can be quite biased (e.g., in China the sex ratio of third births to families with two daughters is 224.9, and of third births to families with two sons is 74.1; Zeng et al. 1993; Low 2000a: ch. 10).

Illegitimacy. In most societies, marriage is a social precursor of pregnancy, whether the marriage is arranged or simple mate choice; whether it manifests itself in sleeping together in camp or results from years of courtship. Illegitimate status carries both social and reproductive costs in many societies. In nineteenth-century Sweden, illegitimacy rates varied across parishes (Gaunt 1980; Low 1990; Low, Clarke, and Lockridge 1991). In all parishes, however, illegitimate births were concentrated among women of lower socioeconomic status who had fewer means to avoid the social costs. Most births were first children of women who later married. In the Swedish data, paternity was assigned for some illegitimate cases; in all cases, fathers were lower-status men. Nonetheless, illegitimate status did not affect infant and child survivorship or adult reproduction. Illegitimate children were, however, quite likely to leave the parish before maturity (Low 1990).

Care of offspring by persons other than parents falls into two distinct categories: “helpers at the nest” and other relatives, and nonrelated caregivers

or "allomothers." In many societies, a sibling (often an unmarried older daughter) cares for children; such nepotism exists because it enhances net reproduction of the parents sufficiently to compensate for the child's lost reproduction (Emlen 1995, 1997; Davis and Daly 1997). In some traditional societies, women whose first child is a daughter (who will help care for siblings) have more children than others (Turke 1988). In many historical societies, either sons (Volland, Siegelkow, and Engel 1991) or daughters (Low 1991; Clarke 1993b; Hrdy 1999; Scott and Duncan 2000; Clarke 1993a) might forgo marriage to help care for siblings. Especially when resources became constricted, children might face tradeoffs between emigrating (see below) or becoming a helper (Strassmann and Clarke 1998). Grandmothers represent another important relative in child care (Hawkes, O'Connell, and Rogers 1997; Hawkes, O'Connell, and Blurton Jones 1997; Hawkes et al. 1998, 2000). This phenomenon may be related to the evolution of menopause, although Hill and Hurtado (1991) were unable to confirm this in the Ache (see Low 2000a: 112–113).

"Allomothers" (and allofathers) are quite a different story from an evolutionary point of view. In other primates, "allomothers" are often females who capture other females' offspring and injure or kill them—a clear reproductive competitive strategy (see van Schaik and Janson 2000). Because human parenting is expensive, individuals in many societies are reluctant to invest as much in stepchildren as in own children (Stephan 1993; Anderson, Kaplan, and Lancaster 1999; Anderson, Kaplan, Lam, and Lancaster 1999), although there is considerable variation (e.g., Hewlett 1992; Anderson 2000). Children in modern societies with a stepparent are at significantly greater risk of abuse and infanticide than children living with both parents (Daly and Wilson 1988). Stepparents' interests may conflict with those of parents; stepparents are more likely than own parents to abuse or neglect children (e.g., Daly and Wilson 1984, 1985, 1987, 1988). Although Gelles and Harrop (1991), Malkin and Lamb (1994), and Temrin, Buchmayer, and Enquist (2000) have claimed that their studies fail to replicate such a "Cinderella effect," Daly and Wilson (1991, 2001) have identified glaring methodological failures in each of these studies.

Nonetheless, in cultures such as the Ache, in which both men and women have multiple sexual partners and marriage is casual, all men who associate with a particular woman are counted as father and invest in the child (also see Hewlett 1992). Adoption occurs in some nonhuman species and cross-culturally, and represents a phenomenon for which evolutionary theory proposes a unique rationale (e.g., Silk 1980; Dublin 1983). If rearing children is costly, under what circumstances would individuals take on the rearing of children not their own? There should be four circumstances: (1) when a close relative's child is at risk (Silk 1980); (2) when the adopter's status can be raised by adopting the offspring of, for example, a high-status individual (Dublin 1983); (3) when adoption of children gives access to a

mate who is alone and encumbered because of divorce, death of a spouse, or nonmarriage (Anderson 2000; Lancaster and Kaplan 2000); and (4) when proximate cues drive behavior—adopting a child to experience parenthood when pregnancy is not possible. In the first three cases, the strategy is reproductively profitable; in the fourth, it is not.

Longevity and costs of reproduction. Natural selection, by placing priority on successful reproduction, can in theory create negative effects on other life-history processes, including longevity. Although this relationship requires additional study, Lycett, Dunbar, and Volland (2000) examined the relationship using historical data from nineteenth-century Krummhörn, Germany and found that when confounding factors were controlled for (duration of marriage, time spent in fecund marriage), there is a strong negative relationship between longevity and reproduction with increasing economic deprivation.

Opportunities for the future: Merging perspectives

The evolutionary approach to human reproductive behavior has proved highly fertile in its twenty-year history (Irons and Cronk 2000; Gray 2000). Hypotheses and testable predictions from several disciplines converge with those of evolutionary and behavioral ecology in useful ways; this is certainly true in demography (including economic and historical; e.g., Easterlin 1978; Easterlin and Crimmins 1985) and economics (e.g., Becker 1981; Becker and Barro 1988; Becker and Lewis 1974). Yet the approaches remain sufficiently distinct that each can enrich others through thoughtful application.

Of course, no approach is universally effective. Dunbar, Clark, and Hurst (1995), for example, have suggested that evolutionary analysis focused on reproductive costs and benefits may be difficult when applied to historical populations, where limited data render it impossible to assess the actual fitness benefits of alternative courses of action available to an individual in any given case. This difficulty can apply to any retrospective data, modern or historical. Experimental approaches with controls are obviously not possible. Comparative methods (e.g., Harvey, Martin, and Clutton-Brock 1986; Promislow and Harvey 1990; Mace and Pagel 1997) that analyze behaviors of groups of individuals within, or across, populations who face different circumstances have been extremely useful in the biological sciences, and we see increasing use of this approach for demographic problems. These methods also address the important issue of nonindependence of samples. Phylogenetically, of course, humans represent a single species and it can be argued, therefore, that human populations are not statistically independent. Evolutionary scholars seeking to compare patterns across human societies are still struggling to assess the validity and utility of comparative methods

in dealing with this problem (Borgerhoff Mulder 2001)—a problem shared with, though perhaps not widely recognized within, the broad field of demography. Large sample sizes are required for such analyses; historical data are often better able than, for example, data on traditional societies to satisfy this requirement.

Demographers bring much-needed sophistication of analysis (e.g., family reconstitution; see Willigan and Lynch 1982; Sharpe 1990) to complex problems of reproduction. Evolutionary biologists have typically treated these in simpler ways (e.g., game theory, basic statistical analysis). Small samples in traditional societies often preclude sophisticated analysis, but historical datasets are frequently large enough. We suggest that demography courses become part of the training of evolutionary anthropologists and psychologists, and that behavioral ecologists (who typically have courses in life-history theory, a relative of demography) also take human demography courses.

Evolutionary scholars bring critical thinking to the problems of levels of selection and levels of analysis in ways that can help clarify research. For example, it is relatively common for demographers, in interpreting correlations between economic indicators and marital fertility, to infer that people choose to marry or procreate in order to help “manage” population levels (e.g., Viazzo 1989; Wrigley 1978). There are two problems with this. First, parsimony argues for the simplest explanatory hypothesis (Williams 1966, 1992), and it is certainly true that for most couples, marrying and having children in hard economic times is harmful at the individual (as well as the group) level. Second is the related fact that even in hard times, some individuals can reproduce (personally profitable, bad for the group), and we can predict the characteristics of these individuals (e.g., see Hawkes and Charnov 1988). All existing data are inconsistent with a “group benefit” assumption that haunted early demographic work as well as theorizing within evolutionary biology; here is a case in which evolutionary perspectives sharpen the focus of hypotheses.⁴ And the fact that behavioral ecologists, for example, use the comparative method across species can sometimes help in both research design and inference for complex problems in which multiple levels of analysis become important.

These facts mean that additional opportunities exist for fruitful collaboration. Although we have discussed primarily publications that have explicitly used an evolutionary framework for demographic analysis, many studies contain data that could usefully be examined from an evolutionary perspective (e.g., McInnis 1977; Freedman and Thornton 1982; Johnson and Lean 1985; Cain 1985; Knodel 1988; Das Gupta and Bhat 1997). For example, consider how modern changes in fertility, work, and education interact. Combining demographic and evolutionary expertise may yield new insights. In post-demographic transition societies, children require great investment in education and training to become successful, establish themselves, and marry. The biological homologue of these demographic “quan-

tity versus quality" arguments (e.g., Easterlin and Crimmins 1985; Becker 1981; Becker and Lewis 1974; Tilly 1978) is called r-selection and K-selection in reference to the parameters of the logistic equation (MacArthur and Wilson 1967); the predicted result is lower fertility and greater per capita investment in offspring. Thus, the long-standing positive correlation between wealth/status and fertility might disappear.

Modern data are variable. In some cases, the wealth–fertility correlation still holds (e.g., Simon 1974; Essock-Vitale 1984), especially in rural areas. In other cases (Pérusse 1993, 1994) men's sexual access varies with wealth, but contraception means that fertility need no longer result from that sexual access. With small family sizes, men's wealth in some conditions no longer matters to net fertility (though it clearly matters to per capita investment: Kaplan et al. 1995; Kaplan and Lancaster 2000). Similarly, women today may trade reproductive value for resource value, working and delaying fertility.

The investment level required to produce successful offspring varies with environment, specifically with the threshold level of investment required for an offspring's success. Required investment correlates with the competition offspring face, whether this is simply a matter of population density, as in many nonhuman cases (MacArthur and Wilson 1967), of education (Knodel and Wongsith 1991), or of labor market opportunities (Kaplan et al. 1995; see reviews by Low, Clarke, and Lockridge 1992; Low 1993, 2000a: ch. 15, 2000b). But making the investments required by such driving forces does not guarantee the success of the chosen reproductive strategy. Relatively wealthy women who have late and low fertility do not necessarily experience greater net lineage increase or persistence.

In the life histories of other species, we see delayed maturation and late fertility only when these yield a net lineage reproductive profit (e.g., Stearns 1992; Roff 1992; see Low, Simon, and Anderson in press a). The very late and low fertility of highly educated women in developed countries today is almost certainly a social phenomenon that results in down-selection of those women's lineages (Borgerhoff Mulder 1998; Low, Simon, and Anderson in press a, b). Fertility is so low, and so late, in modern Western populations that it is difficult to imagine this as increasing lineage representation or persistence, unless (a) something other than numbers of children (e.g., numbers plus resources controlled) is being maximized and (b) such a strategy could sufficiently reduce unpredictable extrinsic mortality to compensate for very low numbers and long generation time (Low, Simon, and Anderson in press a). That is, such lineages could only gain if they were so well protected from mortality that their persistence was longer than that of other lineages that produced more children, but whose children died at a higher rate. We cannot imagine gathering reliable empirical data sufficient to test this possibility fully, but some recent models may be instructive (Low, Simon, and Anderson in press a, b).

For humans, it looks increasingly as though the decline in fertility that has accompanied industrialization and shifts in education and labor markets has been driven by within-population competitiveness but has gone so far as to become suboptimal from a reproductive point of view (e.g., Pérusse 1993, 1994; Borgerhoff Mulder 1998; Low, Simon, and Anderson in press a).⁵ It is unclear whether the choices by a growing proportion of individuals to maximize physical resources, at the cost of delayed and often lowered fertility, are maladaptive in a biological sense. For the first time, perhaps, we can craft a core theoretical approach to allow us to analyze modern reproductive patterns.

Demographic and evolutionary approaches converge in many respects; they are complementary in offering a rationale for patterns at different levels, including proximate mechanisms (e.g., social forces, satisfaction) and ultimate, evolutionary "strategies" (effects of behavior on lineage success). The real utility of integrating the approaches is twofold. Some predictions do not converge or are not discussed at comparable levels (e.g., the relationship between wealth and fertility today, across versus within populations); and others are entirely unexpected (e.g., sex differences in remarriage, sex ratio selection).

Finally, evolutionary theory proposes broad hypotheses about the conditions that will prompt declines in family sizes—something clearly of interest to demographers, historians, and policymakers (Mace 2000; Low, Clarke, and Lockridge 1992; Low 1993, 2000a: ch. 13, 2000b; Kaplan and Lancaster 2000). Given the complexity of modern conditions, even when we are certain the hypothesis is well crafted, we expect different results under different ecological conditions (Berezkei 1993; Mace 2000; Low 2000b). Teasing out the conditions and theoretical reasons for fertility shifts is clearly useful; and continued dialogue and exchange of theoretical constructs can help us deepen our understanding of today's wide-ranging population issues.

Notes

We greatly appreciate the support of our colleagues in supplying us with reprints and preprints of their recent work. Their cooperation has allowed us to provide an up-to-date review of the literature. We thank Carl Simon for his thoughtful review of a draft of this manuscript.

1 Evolutionary novelty can be a considerable problem in analyses, depending on the question. In our evolutionary past (as in those of all other species), "fitness" (roughly, genetic transmission across generations; see Dawkins 1982: ch. 10) was achieved through effective proximate mechanisms: e.g., individuals who found sex pleasurable, or, in most societies,

men who controlled more wealth or had higher status, were likely to leave more children than others, all else equal (see Low 2000a for a more thorough discussion). Modern environments are novel in evolutionary terms—in this case, because widely available effective contraception has broken the link between sexual activity and fertility. Thus Pérusse (1993, 1994) found that in a modern population of Canadian men, of those who sought multiple partners, wealthier men had more partners—but not more children, because of contraception.

2 In Sweden, the prospects faced by the sons and daughters of wealthy versus poor

men also differed. The strongest pattern was that sons of poor men were likely to leave the parish as children; if they stayed, they were unlikely to marry and were likely to die without acknowledged children. However, the very few sons of poor men who nonetheless became wealthy had the highest reproductive success of all men.

3 The Standard Cross-Cultural Sample (Murdock and White 1969) comprises 158 societies, stratified for geographic region and language group, for which ethnographies are available by qualified ethnographers resident with the society for a substantial period. This sample is used to represent the breadth of cultural diversity and to minimize potentially confounding effects (e.g., geographic location).

4 The notion that individuals will act in ways that are beneficial to the larger group can be traced to the biologist V. C. Wynne-Edwards (1962). He argued that when there was a conflict between what was good for the group and what was good for the individual, group interests would win out. From an evolutionary perspective, then, he envisioned that natural selection, operating at the individual level, would be swamped by group selection. His hypothesis has, however, gained neither logical nor empirical support. Instead, empirical

evidence suggests that any group of altruists will be quickly out-reproduced by genetically selfish individuals, cheaters in the system. Although no longer an accepted concept among evolutionary biologists, the simple group selection approach has gained wide acceptance in the social sciences. Complicating the matter further, a number of more sophisticated evolutionary arguments to explain population-level epiphenomena have emerged and these approaches have, by some authors, also been referred to by the general term "group selection." Low (2000a; ch. 9, including Table 9.1) distinguishes between interdemographic selection (selection operating on isolated local populations) and its variants, culture-gene interactions resulting in the emergence of coalitions and coercion of individuals, and the Wynne-Edwards group selection and population regulation argument. To date, none of the proposals convincingly argues that group-level selection will occur commonly in nature or will exist in stable equilibrium conditions.

5 Note, however, that many studies use a variety of measures and proxies, and few recognize that we may not be defining "environments" and "populations" appropriately (see Low 2000b; Low and Clarke 1993; Low 1993; Low, Clarke, and Lockridge 1992).

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