

What is a Human Universal? Human Behavioral Ecology and Human Nature

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In 1991 the cultural anthropologist Don Brown bucked anthropology's tabula rasa tradition by identifying over 300 "human universals"—individual and sociocultural traits that are found in every known human society (Brown 1991; universals enumerated in Pinker 2003). The items he identified include both psychological traits (e.g., wariness around snakes, sweets preferred, sexual jealousy) and sociocultural ones (e.g., territoriality, females do more direct childcare, food sharing). Because they are universal, it is plausible that these traits have a biological basis and that they are evolved features of a universal human nature.

What, then, of the many domains where cultures differ? The assumption is often made that human nature is found solely in its universals—in the traits found in every society. A trait that is found in some societies and not others is then assumed to be culturally constructed and without an evolutionary foundation.

Behavioral ecologists hold a different view: because human nature evolved to be flexible in predictable ways, the task of understanding human nature requires that we understand how evolution shaped that variation. The assumption is not just that we evolved to respond flexibly, but that selection shaped the nature and direction of that flexibility. To a behavioral ecologist, then, the predictable, patterned nature of that response is the universal we must understand. In this view, we cannot understand our universal human nature without understanding the variability in its expression.

The concept is clarified by viewing variation as a norm of reaction—the pattern of expression of a genotype across a range of environments. The increase in a person's skin pigmentation as

a function of exposure to sunlight (tanning) is a norm of reaction, as is the percentage of male and female leopard geckos hatched at different incubation temperatures (see figure 1). Although gecko families vary in the strength of their response to temperature, the patterning of the response is similar: it is part of leopard gecko nature for more males to be born when the temperature is warmer, within this range of temperatures. Figure 2 shows another example, from a brilliant study of soapberry bug mating behavior by Carroll & Corneli (1999). A male soapberry bug may stay attached to his mate after mating in order to guard her against other suitors. If there are many more males than females (high sex ratio), this makes adaptive sense: he gains more by keeping other males away than he loses in forgone mating opportunities. But if eager suitors are less numerous (lower sex ratio), he gains little by mate-guarding and should instead leave after mating and search for another mate. The upper figure shows the mate-guarding response of male Oklahoma soapberry bugs (each line is a family of half-sibs) to experimental changes in the sex ratio. Mate-guarding increases as the sex ratio increases. Although each family has a slightly different reaction norm, they are similar enough to indicate a general feature of what we might call Oklahoma soapberry bug nature. An observer will see different behaviors in different environments, but the responsiveness—the shape of the reaction norm curve—is "universal." At least, it is universal in Oklahoma. The lower figure shows that soapberry bug families from Florida do not alter their mate-guarding appreciably, irrespective of experimental changes in the sex ratio. Why not? In Florida, the climate, hence the sex ra-

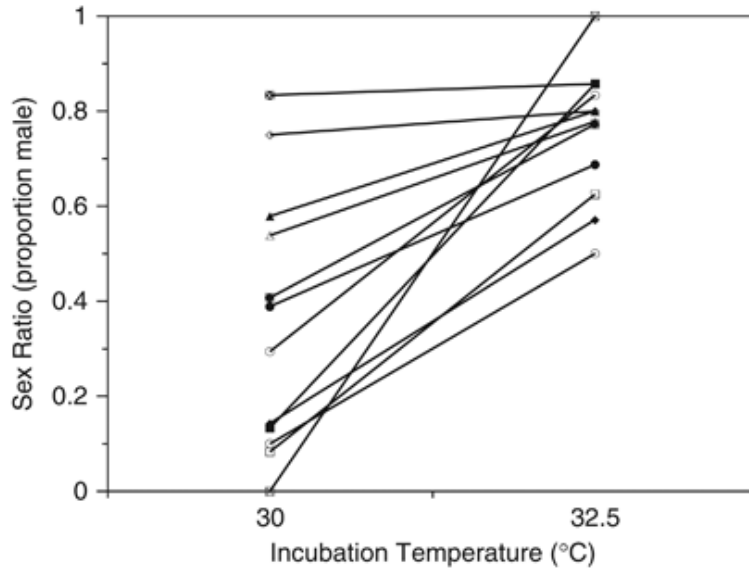


Figure 1: Sex ratio reaction norms as a function of incubation temperature in leopard geckos. Each line connects the sex ratio for a half-sib family (offspring sired by a single male) that was divided between two incubation temperatures. (Rhen et al., 2010)

tion, is less variable than in Oklahoma. In Oklahoma, a facultative (plastic, flexible) response makes adaptive sense, because an individual bug could find himself in a variety of environments and he will reproduce better if he can respond to those changes. For the Florida bugs, living in their equable environment, there is no advantage to such flexibility, and in that population, the flexible response did not evolve (Carroll & Corneli, 1999).

Soapberry bugs occupy a range of environments, but the range is nothing compared to that of humans, who live in every part of the planet and whose environments include novel ones that they constructed for themselves. The principle illustrated in the previous example, therefore, is even more important when discussing human nature. To a human behavioral ecologist, then, human nature is not limited to human universals, as that phrase is usually understood. The human universal is the shape of the response, and the task is to understand how selection pressures shaped it.

This perspective on human nature derives from the anthropologists' knowledge of human variation and the ecological focus of the parent discipline of behavioral ecology. Most human behavioral ecologists were trained as cultural anthropologists, which gives them an unequaled knowledge of the breadth and regularities of human variation. They know, better than anyone, that people living in developed, industrialized states (the usual subjects of human social science) represent only a very small part of the range of human variation, and that those societies are in many respects quite unusual. The nature of the parent discipline of behavioral ecology also shapes their perspective of human nature. Human behavioral ecology's modus operandi is to model optimal outcomes by considering the costs and benefits of different strategies and how they trade off against one another. Doing this forces an explicit consideration of the ecological factors that shape those costs and benefits, and how they vary across environments.

In what follows I will consider examples

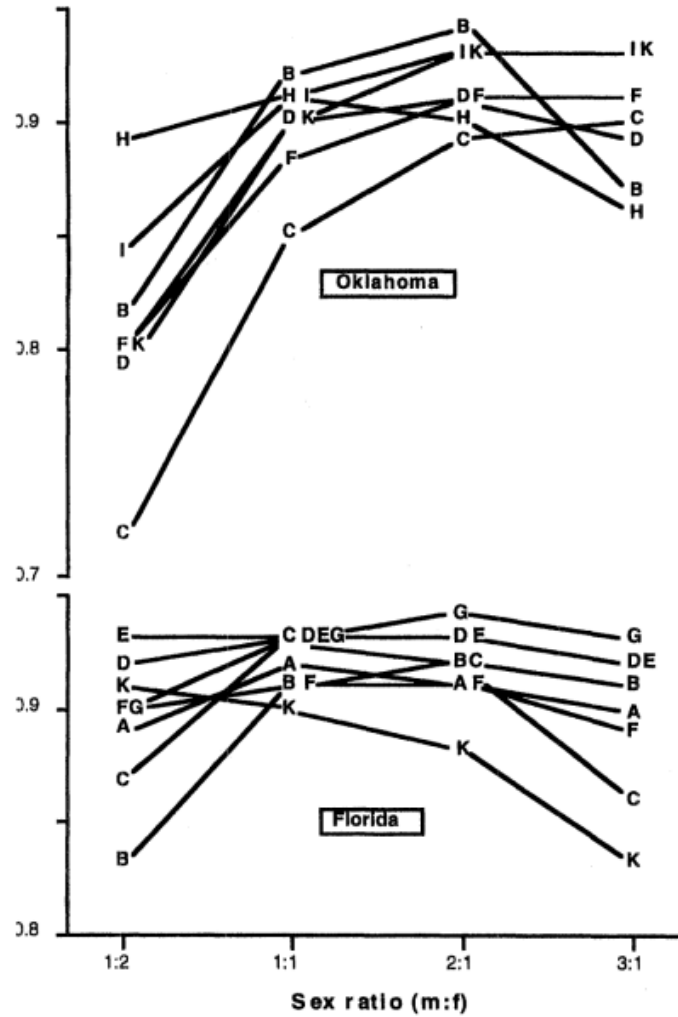


Figure 2: Mate guarding reaction norms as a function of sex ratio in soapberry bugs in Oklahoma (top) and Florida (bottom). (Carroll & Corneli, 1999)

which illustrate the following implications of this view of human nature: (1) human and non-human animal behavior can be understood using the same evolutionary theoretical perspective, and, in some cases, models (hence human nature is seen as part of the evolved natural world), (2) viewing behavioral variation as a reaction norm provides guidance on how policy can address the darker side of human nature, and (3) the individual-maximizing process of natural selection has created a remarkably altruistic, cooperative human nature. I will not, in this essay, attempt to review the field of human behavioral ecology generally, which has been done admirably elsewhere (Borgerhoff Mulder, 2003; Cronk, 1991; Laland & Brown, 2011; Smith et al., 2001; Winterhalder & Smith, 2000). However, several points should be made first about the assumptions under which behavioral ecologists operate.

Human nature, broadly speaking, encompasses the ways in which people think, feel, and act. However, thoughts and feelings are themselves “invisible” to natural selection, since they can only affect survival or reproduction by motivating behavior. An emotion, no matter how strongly felt, is irrelevant to evolution if it does not cause an observable change. For this reason, human behavioral ecologists are largely unconcerned with psychological mechanisms, and focus instead on the behavioral outcomes that selection can act upon.

For somewhat different reasons, human behavioral ecologists also are largely unconcerned with genetic mechanisms. Although biologists studying the behavioral ecology of other species are increasingly interested in the genetic basis of flexible responses, these are difficult to study in people, and we know very little about the genetics underlying human nature and behavior. Human behavioral ecologists therefore typically adopt a “phenotypic gambit” that assumes there has been sufficient genetic variation and time for competing selection pressures to have resulted in the evolution of better-adapted phenotypes. Be-

havioral ecologists who work with humans also typically hold the working assumption (not belief) that the human behavioral differences they observe are the facultative expression of a largely shared genotype.

Finally, human behavioral ecologists assume that human nature is adaptive (fitness-enhancing), and that selection will lead to optimal outcomes. These optimal outcomes are modeled as the best outcome possible given resource constraints and tradeoffs between competing demands. The assumption of optimality is less a matter of belief about human nature than it is a useful working assumption. Behavioral ecologists know, as well as anyone, that people sometimes do maladaptive things (although they do not expect maladaptive outcomes to be common), and they also know the reasons why evolution sometimes leads to sub-optimal outcomes. But it is a reasonable and powerful working assumption in generating and testing hypotheses about the functions of, and selection pressures on, human behavior—hence how human nature came to be. This is best demonstrated by example, so we will consider several, beginning with mating and marriage.

Mating and Marriage: Biological models can explain a lot about human cultural behavior

Marriage is universal, but variable, across human societies, and our understanding of what forms are natural or normal have both moral overtones and policy implications. The ethnographic database makes it clear that human nature encompasses marriages that are both monogamous and polygynous, and even, under very rare and special circumstances, polyandrous. What behavioral ecology adds to this pluralistic view of mating and marriage is the specification that men and women will adjust their mating and marriage choices to environmental circumstances in predictable ways, and that those choices will be optimal from the perspective of enhancing re-

productive success.

What is the optimal number of wives (assuming a man is legally allowed to have more than one)? It depends. Both time and resources are limited and subject to tradeoffs, and these tradeoffs apply across species. If a male spends time guarding one mate, he has less time available to pursue others. If he spends resources (energy or money) trying to attract and monopolize additional mates, he has less to invest in his current offspring. Like the soapberry bugs, therefore, a human male with few alternative mating opportunities may do better to stay with his mate (not only to keep other suitors away but also, in the case of humans, to invest in his offspring and enhance their reproductive success).

This argument has been used to explain differences in mating and marriage among two groups of South American foragers, the monogamous Hiwi and the polygynous Ache. Among the Hiwi, a comparative shortage of reproductive-aged women and lower fertility promotes monogamous pair bonds and men directing more of their resources to provisioning their family, even though that effort has a modest effect on children's survival compared to that of Ache men. Ache men, in contrast, have relatively more opportunities for new matings and added paternity, and so they can gain more reproductive success by searching for new mates, and marriage is less durable than among the Hiwi (Hurtado and Hill 1992; see also Blurton Jones et al., 2000). Cross-national data (Trent & South, 1989) and historical trends (Guttentag & Secord, 1983; Pedersen, 1991) also find that high sex-ratio societies, in which men more than women must compete for mates, are associated with more stable marriages and lower divorce rates.

Mating and marriage decisions are complex, not least because women and men often want different things and the outcome must consider the strategic decisions of both. Where women can choose their own mates, mating patterns may be driven more by female choice. Polygyny can be in a woman's interests if by being the second

wife of a wealthy man she can end up with more resources (after division among wives) than she could by being the sole wife of a pauper. This argument (formalized as the "polygyny threshold" model) was initially developed to explain mating patterns in birds, but was also used successfully to explain who married whom among the agro-pastoral Kipsigis. Borgerhoff Mulder (1990) showed that having co-wives imposes reproductive costs on Kipsigis women, which they try to minimize by judicious marital choices. The Kipsigis women she studied (or their parents acting on their behalf) chose men who had the most acres available after division among existing wives (consistent with the female-choice polygyny threshold model), not the most acres overall (the latter would suggest instead that the wealthiest men were able to control the outcome).

These examples illustrate both limitations and contributions of human behavioral ecology to an understanding of human nature. Because it follows the phenotypic gambit, human behavioral ecology is agnostic about the mechanisms that lead to these patterns, so has little to say about them. Does the choice of mate arise from conscious consideration of the pros and cons of each option? Or from innate preferences, such that fitness-enhancing mates look sexier and more attractive? Or (most likely) both? For the answer to that question, you will need to ask the evolutionary psychologists – it is simply not a focus of human behavioral ecology. Behavioral ecology does show that (1) marriage choices are consistent with models of adaptive behavior (i.e., behavior that enhances the fitness of the people making them), (2) the diversity of mating and marriage patterns is, therefore, not divorced from nature but rather is a predictable manifestation of it, and (3) models from biology, which were developed for other species, are surprisingly successful in explaining these cultural patterns. The last point underlies the fact that human nature is one manifestation of animal nature.

Life history and parenting: what the human behavioral ecology perspective implies about problematic behavior

It is part of human nature for a mother to love her children, but it is also part of human nature that such love is not unconditional. Humans are unusual primates in this respect. The primatologist Sarah Hrdy (2009) has pointed out that in most other primates a mother gives birth only when her other offspring are independent, and unconditional nurture for each new arrival is the norm. This is not true for humans, who differ from other primates in having a long period of childhood dependency together with interbirth intervals that are short compared to those of our closest primate relatives. One result of having to take care of several children simultaneously is that human mothers face allocation decisions most other primate mothers do not, and withdrawal of investment, including even infanticide, is part of the human condition. Another consequence is that human mothers, unlike other primate mothers, need and get help with child-rearing from other relatives (the industrialized world is an exception to this otherwise universal feature).

Behavioral ecologists have shown that a mother's reproductive decisions are sensitive to factors that would maximize the fitness returns on her investment: the condition of the infant, the mother's social and economic support, and her other options. Because a woman's reproductive options diminish with age, the probability that she will terminate investment in an offspring also declines with age. Figure 3 shows this pattern in a population of forager-farmers, the Ayoreo (Bugos & McCarthy, 1984), and modern Canada (Daly & Wilson, 1988). The opportunity costs are greater and the age effect steeper for single women than for married women, since men are less likely to marry a woman with children sired by another man, other things equal. This tradeoff is illustrated in figure 4, which shows that the probability of terminating a preg-

nancy is a linear function of the probability of future marriage (data from England and Wales, Lycett & Dunbar 1999). Views of human nature have implications for policy, since behavior that is pathological is addressed by trying to change the individual, while a normal but undesired aspect of human nature (i.e., one that lies within the norm of reaction of most of the population) is more profitably addressed (if one wishes to) by changing the circumstances that favor it. By viewing behavior such as child neglect and even infanticide as a fitness-maximizing response to resource constraints and competing demands, the behavioral ecologist would be hesitant to label such behavior as pathological, and more likely to suggest that we ameliorate the situation by addressing the constraints and competing demands that made such choices adaptive. She would also be aware that a single mother who struggles without kin help is in an unnatural situation, although a common one in modern industrial societies, and would suggest policies that change the circumstances to resemble those to which we are normally adapted. While models in human behavioral ecology may seem cold-blooded, therefore, the policy implications of its approach are likely to be both humane and progressive.

Generosity

When Dawkins (2006) coined the term "selfish gene" he was describing the fact that any gene that promotes reproductive success in the body it finds itself in will help itself to spread in the population. Genes may be selfish in this sense, but they can spread by promoting altruistic as well as selfish behavior. From Dawkins's gene-centric perspective, a gene that is shared by two individuals through common descent will be favored if those individuals behave altruistically toward each other. Kin selection, which is built on this idea, is the reason many species exhibit behavior that is altruistic (in the technical sense of an act that favors the recipient at some cost to

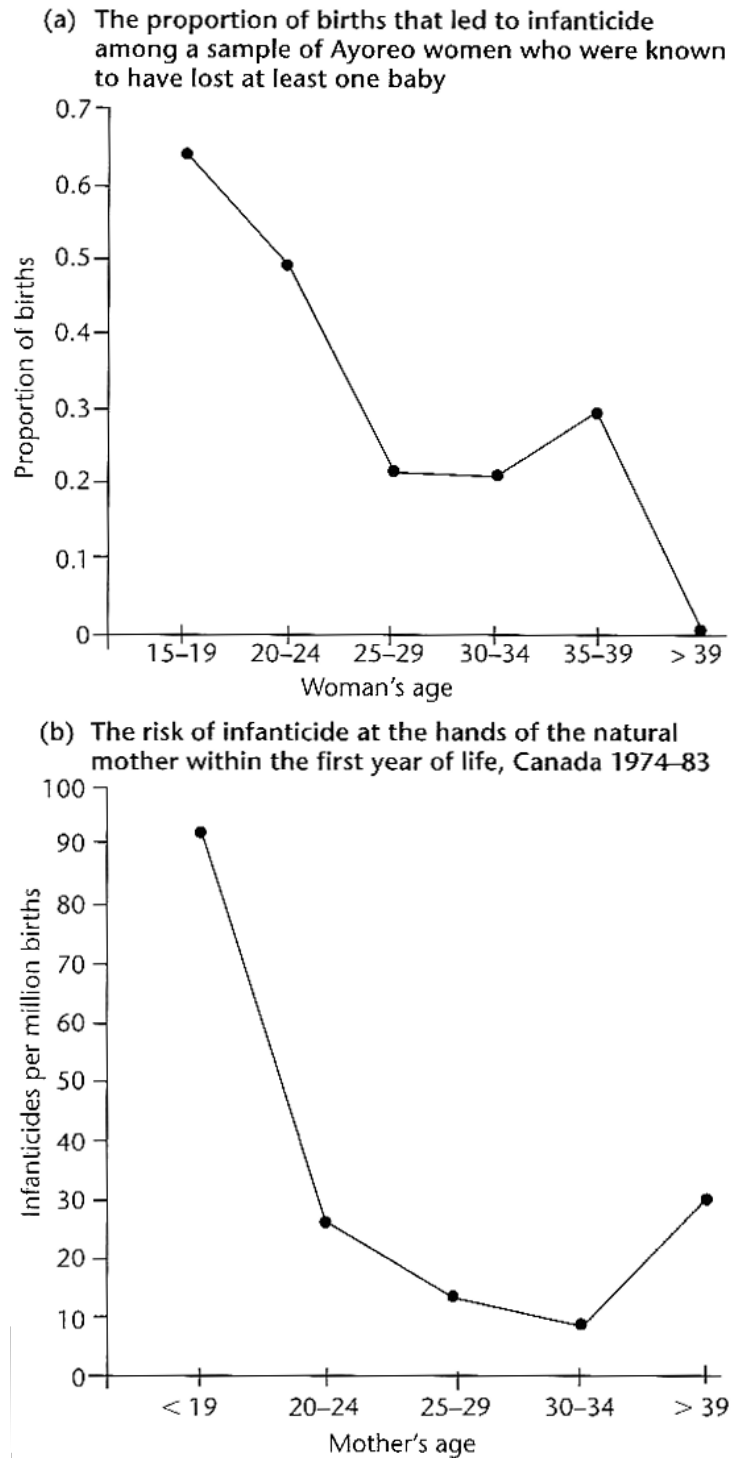


Figure 3: Risk of infanticide as a function of mother's age among (a) the Ayoreo (n=141 births) and (b) Canada (Daly & Wilson, 1988).

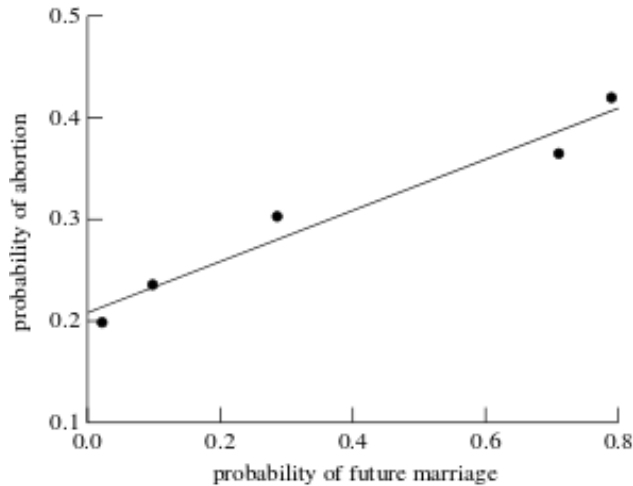


Figure 4: Age-specific probability of abortion plotted against the probability of future marriage during the reproductive life span ((ages 16-40 years) of single women. England and Wales 1991. (Lycett & Dunbar, 1999).

the altruist). Altruism toward kin is an evolved part of human nature also, but humans are unusual in the scope of their unselfish behavior, which is extended far beyond the usual explanatory reach of kin selection. Understanding how selection has favored such behavior is a major part of the recent human behavioral ecology research agenda.

Generosity to non-kin can confer long-term benefits (even though at a short-term cost) if the altruist can be sure that a favor given now will be reciprocated at some future time when he needs the help (reciprocal altruism). Such a system is vulnerable to cheaters, so people are expected to be careful about who they are generous to, limiting their generosity to people who have shared with them in the past or who have a reputation for having been generous with others. Experimental games have shown that decision rules of conditional generosity can out-compete selfish behavior. A second way in which generosity to non-kin can confer benefits to the altruists is through advertising the donor's resources or abilities (e.g., the philanthropist who gets his name on a building).

Both of these explanations, and others, have been evaluated by behavioral ecologists, particularly in the context of food sharing. Supportive evidence for the role of reciprocity comes from evidence that food sharing among both Ache and Hiwi is contingent on past behavior (people share more with those who have shared with them) (Gurven, 2006), and that Ache who produced and shared more than average also received more food when they were injured or sick (Gurven et al., 2000). There is also evidence for sharing as advertisement. Some foragers, especially young males, target hard-to-get and large game, which is shared more widely than other resources. The behavior is costly, but pays indirect fitness benefits, chiefly by enhancing mating opportunities for good hunters, even where the sharing is not contingent (Hawkes & Bliege Bird, 2002; Smith & Bird, 2000; Smith et al., 2003). In the case of both reciprocity and showing off, the generosity is real but ultimately enhances the fitness of the donor. Food sharing is one of Don Brown's human universals, but, like most universals, it is exhibited strategically, and we will not understand human nature without understanding that

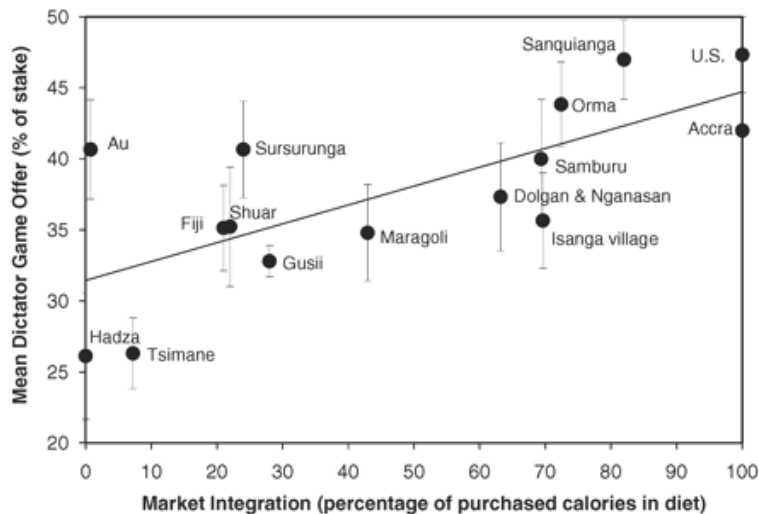


Figure 5: Sharing in the anonymous “dictator game”: Mean offer (as a percent of total stake) by degree of market integration of fifteen traditional societies and the U.S. (Henrich et al., 2010)

variability and the reasons for it.

Explaining variation in generosity is a major focus of research in behavioral ecology. Figure 5 shows how results of an economic sharing game (the “dictator” game) vary with the market integration of the society. In this game, two anonymous players are given a sum of money and one of them (the “dictator”) is given the right to allocate whatever fraction of it he wants to the other (the recipient). The recipient can do nothing to punish the dictator for meager offers, yet in no society do people, on average, fail to give something (the reason for this persistent but uneconomical behavior is still being debated). Interestingly, the two groups with the lowest (least generous) offers are Hadza foragers and Tsimane forager-farmers, both of whom depend heavily on sharing in their daily lives and are far more dependent on it than people in the U.S., who anchor the high end by offering nearly a 50-50 split. Group size is also a strong predictor of generosity in this game, with large groups being more generous. Henrich et al. (2010) reach beyond the usual evolutionary mechanisms and models of behavioral ecology to explain this counter-intuitive result, arguing that large-scale market exchange is

possible only in groups where norms of fairness and trust among strangers have spread through social means. Most of the behavioral ecology research on this topic continues to be agnostic about mechanisms, but this is starting to change. Behavioral ecologists and evolutionary psychologists are working together to understand the evolution of the cognitive specializations that makes us such an unusually cooperative species. Cooperation on a larger scale, involving such phenomena as ethnocentrism, fairness to strangers in market societies, and large-scale warfare, are likely to require the understanding of new mechanisms involving cultural as well as genetic transmission, and this is another new and growing area that is expanding the field of human behavioral ecology. It is also an area of active collaboration between human behavioral ecologists and other social scientists, especially experimental economists. Human behavioral ecologists sometimes grumble that these sister disciplines are largely “ecology free” and give insufficient attention to the real range of human variation, and that evolutionary psychologists in particular give inadequate attention to trade-offs among competing aims, but the trend is clearly

toward an integration of the human evolutionary sciences. Substantive differences in the disciplinary views of human nature stem from historical differences in the populations studied and the models and methods employed, and are likely to be short-lived as these complementary strengths are pooled through collaboration.

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