

Status effects on men's reproductive success

Eric Alden Smitha,b,1

Attempts to gain or maintain status are ubiquitous in human social groups, and are particularly evident among men (1). Status rivalries and maneuvers are a common theme in literary works, and of course are amply described and theorized in the social sciences. Sustained analysis of this topic within an evolutionary framework is comparatively recent, although comparable work on dominance in animal behavior has a longer history (2, 3). The PNAS article by von Rueden and Jaeggi (4) offers important evidence on the evolutionary significance of status acquisition in nonindustrial societies, with a brief comparison with other primates. The authors find a clear link between higher status and various measures of reproductive success, with little effect of subsistence mode but a noticeable difference between strictly monogamous societies and those that practice at least some polygyny.

Before discussing and contextualizing these findings, consider what might be meant by "status." Anthropologists often differentiate between dominance, meaning coercive power (i.e., the ability to inflict costs on others), and prestige, referring to deference freely conferred by others (5). Status may be gained through either channel, although it can be argued that prestige is unique (or at least uniquely important) to humans. In any case, abundant evidence exists that status differences turn on differential skill, strength, intelligence, resources, and generosity (6). von Rueden and Jaeggi (4) subdivide status into measures of "formidability" (size, strength, combat experience), skill (e.g., in resource acquisition), material wealth, and political influence. The authors provide a meta-analysis of data from 33 nonindustrial societies for which individual-level measures of status and reproductive success are available. In keeping with recent trends in evolutionary analyses, statistical analyses are subject to phylogenetic controls, with societies mapped onto a phylogenetic tree constructed from a combination of linguistic and genetic affinities, and effect sizes estimated with Bayesian Markov-chain Monte Carlo methods.

The Egalitarian Hypothesis

Homo sapiens has been in existence for roughly 200,000 y, with roughly 95% of this time spent in

purely foraging (hunter-gatherer) economies (7, 8). Once agriculture arose and spread, hunter-gatherer societies became increasingly rare, and currently only a handful of populations that are primarily subsisting by foraging remain (9). Despite their contemporary rarity, hunter-gatherers retain an important place in anthropological (particularly evolutionary anthropological) research, for reasons implied by the first sentence of this paragraph. Most hunter-gatherer societies known to anthropology are characterized by relatively egalitarian politics, extensive resource sharing, and norms sanctioning aggrandizement, displays of superiority, and stinginess; in a word, status differences are muted (although exceptions exist). In addition, most documented foragers exhibit low levels of polygyny, although it is generally permitted. Given these attributes, von Rueden and Jaeggi (4) note that "the egalitarianism described of many if not most foragers in the ethnographic and archaeological record suggests that status may have been a relatively weak target of selection throughout much of the evolutionary history of modern humans."

To address this "egalitarian hypothesis," one must examine the effects of status on various fitness components contributing to survival and reproductive success (RS). RS is determined by some combination of mate quality, mating success (including duration of reproductive career and number of mates), fertility, and offspring survivorship. von Rueden and Jaeggi (4) do not examine status effects on adult survivorship, but do analyze the components of RS just listed. Their sample includes roughly an equal number of cases across the conventional set of "subsistence modes" (foragers, horticulturalists, pastoralists, and agriculturalists). Analyses fail to reveal any statistically significant differences between subsistence modes in effect of status on RS, although pastoralists did have noticeably higher effect sizes.

In contrast, a sample of 13 primate species (10) analyzed by von Rueden and Jaeggi (4) exhibits about a fourfold higher average effect size of dominance on male RS. Although this latter result should be considered rather preliminary, given the limited size of the primate

^aDepartment of Anthropology, University of Washington, Seattle, WA 98195; and ^bCenter for Studies in Demography and Ecology, University of Washington, Seattle, WA 98195

Author contributions: E.A.S. wrote the paper.

The author declares no conflict of interest.

See companion article on page 10824.

¹Email: easmith@uw.edu.

sample (cf. ref. 11), it does match the generalization that many authors have made, as reviewed in the von Rueden and Jaeggi article (4), that our species exhibits much less reproductive skew than our primate relatives, and supports the common inference that hypersociality in our lineage has transformed (but not eliminated) the dominance system characteristic of higher primates.

von Rueden and Jaeggi (4) conclude that because huntergatherers do not differ from societies with other subsistence modes in degree of status-RS association, "positive selection for traits that facilitate status acquisition (including men's motivation to seek it) did not increase substantially when foragers began domesticating plants and animals" (4). The authors go on to argue that the association between status and reproduction may have been stronger before the spread of agriculture if the egalitarianism of more recent foragers is a consequence of restriction to marginal habitats. However, this conclusion seems premature, if not problematic. First, substantial evidence indicates that the large increase in climate stability in the Holocene led to dramatic changes in huntergatherer lifeways compared with their Pleistocene forebears: broader diets, often higher population densities, lower mobility, probably increased intergroup conflict, and presumably greater control over fixed resources, such as foraging sites (12, 13). This last variable is a strong predictor of political and economic inequality (14) as well as polygyny (15). In sum, there are reasons to think modern foragers are more likely to develop status differences tied to control of resource patches than was the case over most of

In any case, the finding that the "effect of status on men's RS does not differ significantly by subsistence type ... despite subsistence-associated variation in political egalitarianism" (4) is surprising. von Rueden and Jaeggi enumerate several possible explanations for this finding: (i) substantial variation within subsistence categories; (ii) the degree to which status differences result in power and wealth differentials; and (iii) trade-offs between status acquisition and fertility, particularly when offspring quality depends heavily on wealth transmission. These are all reasonable possibilities, supported to varying degrees by extant theory and evidence. The first two explanations point to the need for more direct and fine-grained measures of the factors determining degree of status inequality, such as importance of monopolizable resources (14) and material wealth (16). The third reason is particularly important for complex societies in which not only wealth but human capital are key to status advancement (17).

von Rueden and Jaeggi (4) use a variety of different status measures, constrained by the availability of published quantitative individual-level data. It is encouraging that variation in measure used did not significantly affect the strength of the status-RS association. However, it is worth noting differences in the status measures characteristic of the populations in the von Rueden and Jaeggi sample. Of the agricultural populations, status is measured by material wealth (primarily land) in nearly every case (9 of 11 societies, 92 of 101 measures). In contrast, for foragers (8 societies, 64 measures), only 17% of status measures (from two societies) are wealth-based, whereas the situation for horticulturalists and pastoralists is intermediate (30% and 47% of measures, respectively, being wealth-based). The relative importance of material wealth across these subsistence modes corresponds closely to recent findings on patterns of material wealth importance and intergenerational transmission (16). This correspondence suggests that agriculturalists, and to a lesser extent pastoralists, have status differences that can reliably translate into power differences, whereas foragers and horticulturalists primarily exhibit prestige-based status differences associated with influence rather than coercive power (18). Thus, although subsistence mode may not change the overall magnitude of the effects of status on RS, there are good reasons to suspect it changes the ways in which these effects are realized.

Polygyny Makes a Difference

In contrast to the results concerning subsistence mode, von Rueden and Jaeggi (4) find that polygyny is a strong predictor of status

von Rueden and Jaeggi provide cross-cultural support for three major findings: status effects on RS are much weaker in nonindustrial human societies than in those of other primates, there are no clear effects of subsistence ecology on these effects, and polygyny increases the reproductive pay-off of higher status.

effects on RS. Three of the five RS measures (surviving offspring, fertility, and mating success) show robust positive effects of status in both mating systems. The effect of status on the number of surviving offspring, arguably the most robust measure of RS, is $\sim\!50\%$ greater in polygynous than monogamous populations, whereas wife quality covaries with status only in monogamous ones. The authors also find that status differences have greater effects on mating opportunity and fertility than on offspring mortality (irrespective of polygyny vs. monogamy), with implications for debates about male reproductive strategies I do not have space to discuss here.

von Rueden and Jaeggi (4) do not explicitly define their measure of polygyny, but it appears to be presence/absence. By this very broad measure, 71% of the societies in their sample are classified as polygynous, with frequencies ranging from 45% (agricultural cases) to 100% (pastoralists). Recent research on polygyny has generally attempted to go beyond presence/absence to distinguish the frequency or intensity of polygyny. Accordingly, although von Rueden and Jaeggi (4) classify 63% of their forager sample as polygynous, a set of 30 foraging societies from the standard crosscultural sample finds that 10% are monogamous, 60% are slightly polygynous (1–20% of women married polygynously), and 30% are generally polygynous (>20% of married women) (19). It appears that in von Rueden and Jaeggi's (4) sample, "general" (high-frequency) polygyny is found in all five pastoralist societies plus several others one can characterize as agropastoral. Thus, although their analysis does not find an independent effect of subsistence mode on status-RS relationships, a larger sample of societies that used a more fine-grained measure of polygyny rates might possibly do so.

In conclusion, von Rueden and Jaeggi (4) provide cross-cultural support for three major findings: status effects on RS are much weaker in nonindustrial human societies than in those of other primates, there are no clear effects of subsistence ecology on these effects, and polygyny increases the reproductive pay-off of higher status. Although none of these results are unexpected, von Rueden and Jaeggi have provided the broadest empirical support for them to date. These findings should encourage further research to explore the complex evolutionary dynamics and social mechanisms underpinning status in our species.

- 1 von Rueden C, Gurven M, Kaplan H (2008) The multiple dimensions of male social status in an Amazonian society. Evol Hum Behav 29(6):402-415.
- 2 Chase ID, Tovey C, Spangler-Martin D, Manfredonia M (2002) Individual differences versus social dynamics in the formation of animal dominance hierarchies. *Proc Natl Acad Sci USA* 99(8):5744–5749.
- 3 Smith JE, et al. (2016) Leadership in mammalian societies: Emergence, distribution, power, and payoff. Trends Ecol Evol 31(1):54-66.
- 4 von Rueden CR, Jaeggi AV (2016) Men's status and reproductive success in 33 nonindustrial societies: Effects of subsistence, marriage system, and reproductive strategy. *Proc Natl Acad Sci USA* 113:10824–10829.
- 5 Henrich J, Gil-White FJ (2001) The evolution of prestige: Freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. Evol Hum Behav 22(3):165–196.
- 6 von Rueden CR (2014) The roots and fruits of social status in small-scale human societies. The Psychology of Social Status, eds Cheng J, Tracy J, Anderson C (Springer, New York), pp 179–200.
- 7 Marean CW (2016) The transition to foraging for dense and predictable resources and its impact on the evolution of modern humans. *Phil Trans R Soc B* 371(1698): 20150239.
- 8 Stringer C (2016) The origin and evolution of Homo sapiens. Phil Trans R Soc B 371(1698):20150237.
- 9 Kelly RL (2013) The Lifeways of Hunter-Gatherers: The Foraging Spectrum (Cambridge Univ Press, Cambridge, UK).
- 10 Cowlishaw G, Dunbar R (1991) Dominance rank and mating success in male primates. Anim Behav 41(6):1045-1056.
- 11 Kutsukake N, Nunn CL (2006) Comparative tests of reproductive skew in male primates: the roles of demographic factors and incomplete control. *Behav Ecol Sociobiol* 60(5):695–706.
- 12 Bettinger RL (2001) Holocene hunter-gatherers. Archaeology at the Millenium: A Sourcebook, eds Feinman G, Price T (Kluwer/Plenum, New York), pp 137–195.
- 13 Marean CW (2015) An evolutionary anthropological perspective on modern human origins. Annu Rev Anthropol 44:533-556.
- 14 Mattison SM, Smith EA, Shenk MK, Cochrane EE (2016) The evolution of inequality. Evol Anthropol 25(4):184–199.
- 15 Sellen D, Hruschka D (2004) Extracted food resource defense polygyny in native western North American societies at contact. Curr Anthropol 45(5):707-714.
- 16 Borgerhoff Mulder M, et al. (2009) Intergenerational wealth transmission and the dynamics of inequality in small-scale societies. Science 326(5953):682-688.
- 17 Shenk MK, Kaplan HS, Hooper PS (2016) Status competition, inequality, and fertility: Implications for the demographic transition. *Phil Trans R Soc B* 371(1692): 20150150.
- 18 Smith EA, et al. (2010) Production systems, inheritance, and inequality in premodern societies: Conclusions. Curr Anthropol 51(1):85–94.
- 19 Marlowe FW (2003) The mating system of foragers in the standard cross-cultural sample. Cross-Cultural Res 37(3):282-305.