

Human origins and the transition from promiscuity to pair-bonding

Sergey Gavrilets¹

Department of Ecology and Evolutionary Biology, Department of Mathematics, and National Institute for Mathematical and Biological Synthesis, University of Tennessee, Knoxville, TN 37996

Edited by C. Owen Lovejoy, Kent State University, Kent, OH, and approved April 20, 2012 (received for review January 13, 2012)

A crucial step in recent theories of human origins is the emergence of strong pair-bonding between males and females accompanied by a dramatic reduction in the male-to-male conflict over mating and an increased investment in offspring. How such a transition from promiscuity to pair-bonding could be achieved is puzzling. Many species would, indeed, be much better off evolutionarily if the effort spent on male competition over mating was redirected to increasing female fertility or survivorship of offspring. Males, however, are locked in a “social dilemma,” where shifting one’s effort from “appropriation” to “production” would give an advantage to free-riding competitors and therefore, should not happen. Here, I first consider simple models for four prominent scenarios of the human transition to pair-bonding: communal care, mate guarding, food for mating, and mate provisioning. I show that the transition is not feasible under biologically relevant conditions in any of these models. Then, I show that the transition can happen if one accounts for male heterogeneity, assortative pair formation, and evolution of female choice and faithfulness. This process is started when low-ranked males begin using an alternative strategy of female provisioning. At the end, except for the top-ranked individuals, males invest exclusively in provisioning females who have evolved very high fidelity to their mates. My results point to the crucial importance of female choice and emphasize the need for incorporating between-individual variation in theoretical and empirical studies of social dilemmas and behaviors.

food-for-mating | self-domestication

There are many characteristics that make us a “uniquely unique” species, including those related to morphology, ecology, development, and life history as well as sexual, social, cognitive, linguistic, and cultural traits and abilities (1–4). Both ultimate and proximate mechanisms that were driving their emergence and evolution in hominins are the subject of intensive research efforts and numerous controversies. Recent influential theories link the appearance of some of the unique human features to a major transition in life history strategy that transformed the social structure of early hominins from promiscuous groups to multimale/multifemale groups with strong pair-bonding (4–9). After the new mating system had evolved, a number of subsequent evolutionary transitions became possible. In particular, pair-bonding served as a preadaptation to parental partnership based on the division of labor, which was necessary to offset the disproportionately high costs of raising human children (because of their large brain and delayed maturity). Pair-bonding allowed children to recognize their fathers (and vice versa) on a reliable basis, and subsequently, it led to the emergence of a new type of family that integrated three generations of individuals of both sexes. Recognition of kinship networks simplified the evolution of within-group cooperative behavior, including alloparental care. It also allowed for between-group alliances taking advantage of the bonds between females transferring to other groups and their fathers and brothers remaining in the natal groups.

How such a transition from promiscuity to pair bonding could be achieved is puzzling (4–6, 10–13). The classical explanation of

monogamy in primates—that females’ dispersion across a landscape forces males to associate with individual females (14)—does not work for group-living species with strong within-group dominance hierarchies and high-ranked males largely monopolizing mating (15–18). Also problematic are the suggestions that monogamy was a preferred strategy for reducing the risk of infanticide by strange males (19) and that it emerged because male parental care was indispensable to female reproduction. [Data suggest that paternal care had often evolved after monogamy was already established (20).] Recent discussions, instead, focus on communal breeding (4, 6), mate guarding (6), and food-for-mating transactions (5).

However, an important component is missing from these discussions. Many species would, indeed, be much better off evolutionarily if the effort spent on male competition over mating was redirected to increasing female fertility or survivorship of offspring. However, the fact that there is a higher fitness solution to a particular social (or evolutionary) situation does not imply that this solution will be realized. Realizing such a solution may require crossing fitness valleys and/or finding a way to make it stable to the invasion of various mutants. In the context of the transition to pair-bonding, it has been argued that males are locked in a “social dilemma,” where shifting one’s effort from “appropriation” (i.e., contending with other males for mating success) to “production” (i.e., caring and provisioning) would give an advantage to free-riding competitors and therefore, should not happen (10, 21, 22). In fact, a major challenge for the evolutionary theory is to explain the emergence of group-beneficial behaviors and traits that would be resistant to the invasion of cheaters and free riders (23–25).

Here, I first use simple mathematical models to illustrate the power of the social dilemma faced by males, which results in selective forces strongly opposing the shift from appropriation to production. Then, I propose a general scenario extending and making more specific some of the earlier ideas on how to resolve this dilemma.

Results

I consider a population in which individuals interact in groups comprised of N males and N females. Each male divides his effort between two activities potentially increasing his fitness. One activity is contending for status and dominance with other males in the group. The other activity is directed to females and offspring (e.g., caring for offspring and provisioning or guarding females). I posit that the share S_i of paternity won by male i in direct competition with other males is given by the standard Tullock contest success function of (Eq. 1)

Author contributions: S.G. designed research, analyzed data, and wrote the paper.

The author declares no conflict of interest.

This article is a PNAS Direct Submission.

¹E-mail: gavrilas@tiem.utk.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1200717109/-DCSupplemental.

$$S_i = \frac{m_i^\beta}{\sum_j m_j^\beta} \quad [1]$$

which is extensively used in economics (22) and evolutionary biology (10, 13, 26, 27). Here, $0 \leq m_i \leq 1$ is the fighting effort of male i , and parameter $\beta > 0$ measures the decisiveness of the differences in male fighting effort in controlling the outcome of the competition. Describing the situations where only a few males get most of the matings (which happens in chimpanzees and other species living in hierarchically organized groups) (28, 29) (*SI Appendix*) requires one to assume that β is sufficiently larger than one (e.g., two to four). Using the information in ref. 10, I assume that female fertility is defined by the function (Eq. 2)

$$B(y) = (C + y)^\alpha, \quad [2]$$

where $0 \leq y \leq 1$ is a male's effort to caring or provisioning and $\alpha > 0$ measures the efficiency of males' effort. Parameter C can be interpreted as a female's contribution to her fertility, and it is set to one. If $\alpha < 1$, the males' effort is less efficient than the effort of females; if $\alpha > 1$, there is a synergy between female and male efforts (i.e., the total effect is greater than the sum of the two). It is reasonable to assume that α does not exceed one by too much (10) (*SI Appendix*).

In the communal care model (10), each male allocates a fraction c_i of his effort to caring for offspring ($c_i + m_i = 1$). The male care is distributed randomly among all offspring in the group and increases female fertility by a factor $B(\bar{c})$, where \bar{c} is the average care in the group. In a group with N females, male i wins a share S_i of paternity in competition with other males, and his fitness is $B(\bar{c})S_iN$.

In the mate-guarding model, male i devotes effort g_i to guarding a particular female ($g_i + m_i = 1$). Guarding effort g_i gives a paternity γg_i of the guarded female's offspring, where $0 \leq \gamma \leq 1$ is the guarding efficiency. The total unguarded paternity is $\sum(1 - \gamma g_i) = N(1 - \gamma \bar{g})$, where \bar{g} is the average guarding effort. Male i wins share S_i of this paternity in competition, and his fitness is defined in the second row of Table 1.

In the food-for-mating model, each male allocates effort p_i to provisioning randomly chosen females ($p_i + m_i = 1$). Provisioning at level p_i buys paternity in the amount γp_i , where $0 \leq \gamma \leq 1$ is the efficiency of provisioning to paternity conversion. Provisioning also increases female fertility by a factor $B(\bar{p})$, where \bar{p} is the average provisioning effort in the group. The total paternity assigned in competition is $B(\bar{p})N(1 - \gamma \bar{p})$. The male's fitness is defined in the third row of Table 1, where the first term in the brackets gives paternity bought with food, whereas the second term is paternity won in competition.

The mate-provisioning model is similar to the food-for-mating model, except that each male can provision only one female and each female can be provisioned by only one male. As a result of provisioning, the female's fertility is increased by a factor $B(p_i)$. The total paternity assigned in competition is $\sum_j B(p_j)(1 - \gamma p_j)$.

The male's fitness is defined in the fourth row of Table 1, where the first and second terms in the brackets give paternity of the provisioned female offspring and paternity won in competition, respectively.

These models can be analyzed using a standard invasion analysis (30–32). A common feature of the four models is that, under the biologically most relevant conditions (i.e., small α , relatively large $\beta \sim 2-4$, and large $N \sim 10$) (33, 34), they all predict (Table 1) evolution to a state where all male effort is devoted to fighting ($m_i = 1$). An alternative dynamic, which is the only other possibility in the first three models, is the evolution to a state where all males exhibit an intermediate fighting effort and the rest of their effort goes to caring or provisioning. In the mate-provisioning model, there is also a possibility that the system evolves to a polymorphic state at which a minority of males devotes all effort to provisioning, whereas remaining males devote all their effort to fighting. Such a polymorphic state is analogous to the states observed in producer–scrounger models (35–38); in the present context, “scroungers” are males who do not invest in females but rather, “steal” paternity. However, all these alternatives require α to be large and/or β and N to be small, which seems to be unrealistic under the conditions inferred for hominins. [For example, with $\beta = 3$ and $N = 10$, α would have to be >27 in the communal care model and >18 in the food-for-mating and mate-provisioning models, where in the latter case, I optimistically assumed $\gamma = 1$. With such large α -values, the effect of males on female fertility, defined in the model as $(1 + p)^\alpha$, would have to be enormously large.]

The results summarized in Table 1 assume that groups are formed randomly, which implies low probability of genetic relatedness between individuals. In chimpanzees and likely, hominins, within-group genetic relatedness can be somewhat elevated, because only one sex (females) disperses (39–41). The kin selection theory (23, 25, 42) predicts reduced competition in kin groups. Elevated relatedness does, indeed, reduce between-male competition in the communal care, food-for-mating, and mate-provisioning models. (In the mate-guarding model, relatedness has no effect.) However, in realistic situations, the conditions given in Table 1 will not change substantially (*SI Appendix*).

At the state with $m = 1$, female fertility [$B(0) = 1$] is significantly smaller than the fertility that could be achieved [$B(1) = 2^\alpha$] if all males were to devote all their effort to female provisioning or caring for offspring. Males are forced to invest in appropriation rather than production by the logic of social interactions in a promiscuous group, where investing more in offspring means that there is more paternity for other males to steal (10). Thus, the male's dilemma drives the evolution to a low fitness (payoff) state, which is a feature shared by other social dilemmas (e.g., the Prisoner's dilemma or the public goods dilemma) (23–25).

These results have implications for some recent theories of human origins. In particular, the works in refs. 4, 6, and 8 argue for the importance of communal breeding during the origin of humans. Ref. 6 also argues for the importance of mate guarding

Table 1. Summary of models

Model	Variables	Male fitness	Evolution to $m_i = 1$ if
Communal care (10)	m_i, c_i	$w_i = B(\bar{c})S_iN$	$\alpha < \beta(N - 1)$
Mate guarding	m_i, g_i	$w_i = B(0)[\gamma g_i + S_iN(1 - \gamma \bar{g})]$	$\gamma < \beta$
Food for mating	m_i, p_i	$w_i = B(\bar{p})[\gamma p_i + S_iN(1 - \gamma \bar{p})]$	$\alpha < (\beta - \gamma)(N - 1)$
Mate provisioning	m_i, p_i	$w_i = B(p_i)\gamma p_i + S_i \sum_j B(p_j)(1 - \gamma p_j)$	$\alpha < (\beta - \gamma)(N - 1)$
Pair bonding	m_i, p_i	$w_i = B_i p_i + S_i \sum_j B_j(1 - p_j)$ $B_i = B(p_i)C_i, C_i = 1 - \epsilon P_i^A, P_i = 1 - (1 - f_i)(1 - \gamma p_i)$	<i>SI Appendix</i>

However, after females start developing preferences for being provisioned, the low-ranked males' investments start to pay off. In the model presented here, male provisioning and female faithfulness coevolve in a self-reinforcing manner. At the end, except for a very small proportion of the top-ranked individuals, males invest exclusively in provisioning females who have evolved very high fidelity to their mates. Overall, females are not predicted to become completely faithful, but rather, the level of their faithfulness is expected to be controlled by a balance between selection for better genes (potentially supplied by top-ranked males) and better access for food and care (provided largely by low-ranked males).

Overall, my results confirm the theoretical plausibility of what has been viewed as a critical step in the evolution of our own species—the transition from promiscuity to strong pair-bonding. The model shows that such a sexual revolution could have been initiated by low-ranked males who started provisioning females to get matings; after the process got underway, it would lead to a kind of self-domestication, and the end result is a group-living species comprised of provisioning males and largely faithful females.

The results highlight the importance of considering the joint evolutionary dynamics of male and female traits. The model shows that nonrandom pair formation can have dramatic effects on evolutionary dynamics. The results emphasize the need for incorporating between-individual variation in theoretical and empirical studies of social dilemmas and behaviors; the commonly used simplifying assumption that individuals are identical can significantly bias the conclusions.

The models introduced and analyzed here assume that, initially, both sexes mate promiscuously. It is important to realize, however, that an underlying reason for the male's dilemma as studied here is female promiscuity and the associated risks that the male's investment in production might be stolen by other males. Therefore, some of my results may be relevant for polyandrous species. In polygynous species, male promiscuity may lead to another dilemma for males: whether to invest in obtaining more females or providing better provisioning and care to a smaller number of females. This other version of the male's dilemma between production and appropriation is outside the scope of this work.

The importance of food-for-sex exchanges (5, 43, 51) in chimpanzees has been recently questioned in ref. 52, which argues that the benefits to females of food provisioned by males are small, whereas the role of female selectivity in determining male reproductive success is limited. Population genetic models tell us, however, that even weak evolutionary forces can result in dramatic phenotypic or behavioral changes if they act over multiple generations. A recent metaanalysis (53) shows correlation between male-to-female food transfer and the opportunity for female mate choice. There are some additional anatomical features of humans—bipedalism, hidden ovulation, and

permanently enlarged mammary glands—that are easier to explain in terms of the pair-bonding model than the mate-guarding and communal breeding models (5, 54).

New paleontological data on 4.4-Myr-old fossils of *Ardipithecus ramidus* show that this species already had a reduced sexual size dimorphism and strong reduction in upper canine teeth (5). This finding and a loss of morphological adaptations to sperm competition in humans (5, 55) suggest that strong decline in the intensity of male-to-male conflict, which is one of the consequences of the transition to pair-bonding, happened soon after the hominins/chimpanzees divergence (5). If true, this finding has important implications for the theories of the runaway evolution of human brain size and intelligence over the past couple hundred thousand years. One controversial set of ideas (1, 2, 56–61) coming under the rubric of the “Machiavellian intelligence” or “social brain” hypothesis identifies selective forces resulting from within-group social competitive interactions as the most important factors in the evolution of hominids, who at some point in the past, became an ecologically dominant species (1, 2). These forces selected for more and more effective strategies (including deception, manipulation, alliance formation, exploitation of the expertise of others, etc.) of achieving social success and learning to use them. The social success translated into reproductive success (e.g., more children) (62, 63) selecting for larger and more complex brains. Pair-bonding would significantly decrease the efficiency of selection resulting from within-group competition for mating success. This effect would likely rule out within-group competition as a source of selection for larger brain size and intelligence. An intriguing alternative is selection resulting from between-group competitive and cooperative interactions.

The transition to strong pair-bonding opened a path to intensified male parental investment, which was a breakthrough adaptation with multiple anatomical, behavioral, and physiological consequences for early hominids and all of their descendants (4–6). The establishment of pair-bonding shifted competition between males for mates, which was potentially destructive for the group, to a new dimension which is beneficial for the group—competition to be a better provider to get better mates (64). Pair-bonding provided a foundation for the later emergence of the institution of modern family (65) as an outcome of additional processes, such as wealth accumulation and inheritance (66). Pair-bonding also made possible the recognition of male kin, dramatically expanding the efficiency of kin selection and helping by grandparents, leading to stronger within-group coalitions and alliances (67, 68), and allowing for subsequent evolution of widespread cooperation in general (6, 69).

ACKNOWLEDGMENTS. I thank J. Auerbach, M. V. Flinn, M. Mesterton-Gibbons, K. Page, and reviewers for the comments on the manuscript.

- Alexander RD (1990) *How Did Humans Evolve? Reflections on the Uniquely Unique Species* (Univ of Michigan, Museum of Zoology, Ann Arbor, MI).
- Flinn MV, Geary DC, Ward CV (2005) Ecological dominance, social competition, and coalitional arms races: Why humans evolved extraordinary intelligence? *Evol Hum Behav* 26:10–46.
- Richerson PJ, Boyd R (2005) *Not by Genes Alone. How Culture Transformed Human Evolution* (Univ of Chicago Press, Chicago).
- Hrdy SB (2011) *Mothers and Others: The Evolutionary Origins of Mutual Understanding* (Belknap Press, Cambridge, MA).
- Lovejoy CO (2009) Reexamining human origins in light of *Ardipithecus ramidus*. *Science* 326:74e1–74e8.
- Chapais B (2008) *Primate Kinship: How Pair-Bonding Gave Birth to Human Society* (Harvard Univ Press, Cambridge, MA).
- Chapais B (2010) *Mind the Gap. Tracing the Origins of Human Universals*, eds Kappeler PM, Silk JB (Springer, Heidelberg), pp 19–51.
- van Schaik CP, Burkart JM (2010) *Mind the Gap. Tracing the Origins of Human Universals*, eds Kappeler PM, Silk JB (Springer, Heidelberg), pp 477–496.
- Shultz S, Opie C, Atkinson QD (2011) Stepwise evolution of stable sociality in primates. *Nature* 479:219–222.
- Hawkes K, Rogers AR, Charnov EL (1995) The male's dilemma: Increased offspring production is more paternity to steal. *Evol Ecol* 9:662–677.
- Harada Y, Iwasa Y (1996) Female mate preference to maximize paternal care: A two-step game. *Am Nat* 147:996–1027.
- Iwasa Y, Harada Y (1998) Female mate preference to maximize paternal care. II. Female competition leads to monogamy. *Am Nat* 151:367–382.
- Kokko H, Morrell LJ (2005) Mate guarding, male attractiveness, and paternity under social monogamy. *Behav Ecol* 16:724–731.
- Rutberg AT (1983) The evolution of monogamy in primates. *J Theor Biol* 104:93–112.
- de Waal FBM (2000) *Chimpanzee Politics: Power and Sex Among Apes* (Johns Hopkins Univ Press, Baltimore).
- Nishida T (1997) Sexual behavior of adult male chimpanzees of the Mahale Mountains National Park. *Primates* 38:379–398.
- Newton-Fisher NE (2004) Hierarchy and social status in Budongo chimpanzees. *Primates* 45:81–87.
- Boesch C, Kohou G, Néné H, Vigilant L (2006) Male competition and paternity in wild chimpanzees of the Tai forest. *Am J Phys Anthropol* 130:103–115.
- Palombit R (1999) Infanticide and the evolution of pair bonds in nonhuman primates. *Evol Anthropol* 7:117–129.

20. Brotherton P, Komers P (2003) *Monogamy: Mating Strategies and Partnerships in Birds, Humans and Other Mammals*, eds Reichard U, Boesch C (Cambridge Univ Press, Cambridge, UK), pp 42–58.
21. Hirshleifer J (1991) The paradox of power. *Econ Polit* 3:177–200.
22. Konrad K (2009) *Strategy and Dynamics in Contests* (Oxford Univ Press, Oxford).
23. Frank S (1998) *Foundations of Social Evolution* (Princeton Univ Press, Princeton).
24. Nowak M (2006) *Evolutionary Dynamics* (Harvard Univ Press, Cambridge, MA).
25. McElreath R, Boyd R (2007) *Mathematical Models of Social Evolution. A Guide for the Perplexed* (Chicago Univ Press, Chicago).
26. Reeve HK, Hölldobler B (2007) The emergence of a superorganism through intergroup competition. *Proc Natl Acad Sci USA* 104:9736–9740.
27. Crowley PH, Hwan Baik K (2010) Variable valuations and voluntarism under group selection: An evolutionary public goods game. *J Theor Biol* 265:238–244.
28. Goodall J (1986) *The Chimpanzees of Gombe: Patterns of Behavior* (Belknap Press, Cambridge, MA).
29. de Waal FB (2000) Primates—a natural heritage of conflict resolution. *Science* 289: 586–590.
30. Hofbauer J, Sigmund K (1990) Adaptive dynamics and evolutionary stability. *Appl Math Lett* 3:75–79.
31. Geritz SAH, Kisdi E, Meszéna G, Metz JAJ (1998) Evolutionary singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol Ecol* 12:35–57.
32. Waxman D, Gavrilets S (2005) 20 questions on adaptive dynamics. *J Evol Biol* 18: 1139–1154.
33. Mitani JC (2006) Demographic influences on the behavior of chimpanzees. *Primates* 47:6–13.
34. Hill KR, et al. (2011) Co-residence patterns in hunter-gatherer societies show unique human social structure. *Science* 331:1286–1289.
35. Barnard CJ, Sibly RM (1981) Producers and scroungers—a general model and its implications to captive flocks of house sparrows. *Anim Behav* 29:543–550.
36. Barta Z, Giraldeau L-A (1998) The effect of dominance hierarchy on the use of alternative foraging tactics: A phenotype-limited producing-scrounging game. *Behav Ecol Sociobiol* 42:217–223.
37. King AK, Isaac NJB, Cowlisshaw G (2009) Ecological, social, and reproductive factors shape producer-scrounger dynamics in baboons. *Behav Ecol* 20:1039–1049.
38. Mathot KJ, Giraldeau L-A (2010) Within-group relatedness can lead to higher levels of exploitation: A model and empirical test. *Behav Ecol* 21:843–850.
39. Morin PA, et al. (1994) Kin selection, social structure, gene flow, and the evolution of chimpanzees. *Science* 265:1193–1201.
40. Copeland SR, et al. (2011) Strontium isotope evidence for landscape use by early hominins. *Nature* 474:76–78.
41. Lalueza-Fox C, et al. (2011) Genetic evidence for patrilocal mating behavior among Neandertal groups. *Proc Natl Acad Sci USA* 108:250–253.
42. Hamilton WD (1964) The genetical evolution of social behaviour. I. *J Theor Biol* 7: 1–16.
43. Gomes CM, Boesch C (2009) Wild chimpanzees exchange meat for sex on a long-term basis. *PLoS One* 4:e5116.
44. Strassmann BI (1981) Sexual selection, paternal care, and concealed ovulation in humans. *Ethol Sociobiol* 2:31–40.
45. Gross MR (1996) Alternative reproductive strategies and tactics: Diversity within sexes. *Trends Ecol Evol* 11:92–98.
46. Gagneux P, Boesch C, Woodruff DS (1999) Female reproductive strategies, paternity and community structure in wild West African chimpanzees. *Anim Behav* 57:19–32.
47. Matsumoto-Oda A (1999) Female choice in the opportunistic mating of wild chimpanzees (Pan troglodytes schweinfurthii) at Mahale. *Behav Ecol Sociobiol* 46:258–266.
48. Wrangham R (1993) The evolution of sexuality in chimpanzees and bonobos. *Hum Nat* 4:47–79.
49. Lande R (1981) Models of speciation by sexual selection on polygenic traits. *Proc Natl Acad Sci USA* 78:3721–3725.
50. Gavrilets S (2004) *Fitness Landscapes and the Origin of Species* (Princeton Univ Press, Princeton).
51. Stanford C (1996) The hunting ecology of wild chimpanzees: Implications for the evolutionary ecology of pliocene hominids. *Am Anthropol* 98:96–113.
52. Gilby IC, Emery Thompson M, Ruane JD, Wrangham R (2010) No evidence of short-term exchange of meat for sex among chimpanzees. *J Hum Evol* 59:44–53.
53. Jaeggi AV, van Schaik CP (2011) The evolution of food sharing in primates. *Behav Ecol Sociobiol* 65:2125–2140.
54. Lovejoy CO (1981) The origin of man. *Science* 211:341–350.
55. McLean CY, et al. (2011) Human-specific loss of regulatory DNA and the evolution of human-specific traits. *Nature* 471:216–219.
56. Byrne RW, Whiten A (1988) *Machiavellian Intelligence. Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans* (Clarendon, Oxford).
57. Whiten A, Byrne RW (1997) *Machiavellian Intelligence II. Extensions and Evaluations* (Cambridge Univ Press, Cambridge, UK).
58. Dunbar RIM (1998) The social brain hypothesis. *Evol Anthropol* 6:178–190.
59. Geary DC (2005) *The Origin of Mind. Evolution of Brain, Cognition, and General Intelligence* (American Psychological Association, Washington, DC).
60. Roth G, Dicke U (2005) Evolution of the brain and intelligence. *Trends Cogn Sci* 9: 250–257.
61. Gavrilets S, Vose A (2006) The dynamics of Machiavellian intelligence. *Proc Natl Acad Sci USA* 103:16823–16828.
62. Betzig LL (1986) *Despotism and Differential Reproduction. A Darwinian View of History* (Albion Publishing Company, New York).
63. Zerjal T, et al. (2003) The genetic legacy of the Mongols. *Am J Hum Genet* 71:717–721.
64. Hawkes K (1993) Why hunter-gatherers work. *Curr Anthropol* 34:341–361.
65. Engels F (1884) *The Origin of the Family, Private Property, and the State. Marx/Engels Selected Works* [International Publishers, New York (1972, c1942)], Vol 3.
66. Fortunato L, Archetti M (2010) Evolution of monogamous marriage by maximization of inclusive fitness. *J Evol Biol* 23:149–156.
67. Gavrilets S, Duenez-Guzman EA, Vose MD (2008) Dynamics of alliance formation and the egalitarian revolution. *PLoS One* 3:e3293.
68. Mesterton-Gibbons M, Gavrilets S, Gravner J, Akçay E (2011) Models of coalition or alliance formation. *J Theor Biol* 274:187–204.
69. Boomsma JJ (2009) Lifetime monogamy and the evolution of eusociality. *Philos Trans R Soc Lond B Biol Sci* 364:3191–3207.