

Human Evolution: A Behavioral Synthesis

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The evolution of language probably occurred in concert with the evolution of many of the other traits we associate with being human... [this] suggests that we shouldn't be trying to understand one characteristically human trait in isolation from the others.

Szathmáry and Számadö (2011)

Research in language evolution must be interdisciplinary... even if only by using the pooled knowledge from diverse disciplines to shrink the problem space and rule out solutions which, while plausible enough within the framework of a single discipline, quickly fall victim to counterevidence from another.

Bickerton and Szathmáry (2009)

Darwin's *The Origin of Species by Means of Natural Selection* (1859) is replete with defenses of his theory against the objections of his critics. But two problems plagued Darwin all his life, and for which he did not have an adequate reply. The first was the ostensibly fitness-reducing ornamentation in males of many bird species, most notably the peacock, which held a revered place in English country life. The second was the advanced cognitive capacities in civilized *Homo sapiens*, whose members are capable of prodigious mental feats that appear to have had no adaptive value in human evolution.

To deal with these cases, Darwin seized on the concept of runaway sexual selection, developed at length in *The Descent of Man and Selection in Relation to Sex* (1871). Peacocks have beautiful tails because peahens prefer to mate with heavily adorned males, and the strength of this preference is sufficiently to offset the fitness costs of producing and displaying the ornaments. Similarly, humans

have large brains and exhibit artistic and musical talent because the ladies are better wooed by males who can sing, dance, and offer witty conversation.

Darwin's argument was formalized by Sir Ronald Fisher in his monumental *The Genetical Theory of Natural Selection* (1930), and carefully modeled by population biologists (O'Donald 1962, Maynard Smith 1976, Lande 1981, Kirkpatrick 1982, Pomiankowski 1987, Bulmer 1989, Johnstone 1995). My own conclusion from this literature is that runaway sexual selection can operate only when the cost to the female of choosing on the basis of an attractive but fitness-reducing trait is zero (Gintis 2000a, Ch. 13). Even in this implausible case, weak group selection will disfavor groups whose females favor males with fitness-reducing traits.

For the evolutionary biologist who takes modeling seriously, the implausibility of runaway selection is a godsend. If costly phenotypic traits could reliably arise through a random mutation in the preference ordering of females in a species, the basic explanatory framework of biological selection and adaptation could not be applied confidently to the explanation of phenotypic traits.

There are two alternative explanations of the peacock's tail. The first is that the peacock's ornamentation is a costly signal that he lacks a serious genetic handicap and does not have a heavy parasite load (Zahavi 1975, Hamilton and Zuk 1982, Sosis 2000, Bliege Bird et al. 2001, Bergstrom and Lachmann 2001, Gintis et al. 2001). The second is the sensory bias phenomenon, according to which complex neural networks have an innate preference for sensory diversity and brilliance (Ryan 1985, Ryan 1990, Basolo 1990, Endler and Basolo 1998, Ryan 1998).

Sensory bias does not cover such behaviors as linguistic fluency or musicality. Thus the only plausible sexual selection explanation of the expansion of cognitive capacity in humans is costly signaling. However, there is to my knowledge no costly signaling explanation of this phenomenon. Intelligence and linguistic ability are not correlated with such desirable hidden phenotypic characteristics as loyalty, bravery, honesty, and fairness, and hence intelligence, while costly, does not signal such traits.

1 Sexual Selection is a form of Social Selection

Darwin treated sexual selection as distinct from natural selection. The sexual form of selection, he asserts, "depends, not on a struggle for existence, but on a struggle between the males for possession of the females" (Darwin 1859, Ch. 4). Darwin, like his many followers even today (e.g., Miller, 2001), overlooked the fact that natural selection involves intraspecific competition, not interspecific—the prey is competing not with the predator to avoid being eaten, but with others of his species

to produce more offspring. In this sense, sexual selection is no different from any other fitness-relevant behavior.

More generally, Darwin, like his contemporary runaway selection followers, failed to see that sexual selection is a form of social selection. We know from general sociobiological reasoning that interspecific interactions, if repeated and hence subject to selection, will generally evolve into stereotypic mutually sustaining behaviors that are genetically governed, although possibly involving a superimposed social learning process. It is often assumed that group living is necessary for sociality, but this is not the case. For instance, territoriality in nesting birds is generally supported by the assumption that the resident will fight harder to keep a territory than a non-resident will fight to displace the resident (Gintis 2007, Gintis 2009). This is of course an evolved behavioral predisposition. Similarly, mating practices are evolved predispositions that govern reproduction within a species. Sexual selection is just another word for the effects of these social mating practices.

From this perspective, sexual selection will be subject to selection just as any other social characteristic, and in general, we expect fierce competition within a niche will lead to highly socially efficient mating practices, while the absence of competition will permit the evolution of behavior independent from issues of natural selection (West-Eberhard 1983, Roughgarden 2006). However, the virtual stationarity of hominid population size in the Pleistocene is not supportive of the notion that hominid species had little niche competition. The rather logical conclusion is that the human brain is not the result of any form of sexual selection.

2 The Social Intelligence Model

The expansion of the hominid neocortex in the passage to *Homo sapiens* was only a recent step in the growth of neocortical size in our primate ancestors. There is clearly a close correlation between group size and neocortical size in primate species (Dunbar 1996). According to the social intelligence hypothesis, this larger brain allowed individuals to remember and interact strategically with more individuals (Dunbar 1996, Byrne and Whiten 1988). According to this theory, the benefit of an increase in group size was better protection against predators, but the side-effect of increased group size was heightened problems of coordinating and adjudicating relations among group members, particularly concerning feeding and mating.

The social intelligence theory of neocortical growth does less well in explaining the superior intelligence of apes over other primates. Holding constant group size, monkeys are considerably less intelligent than apes. Of course, chimpanzees and other apes use their intelligence, for using tools and forming alliances, for example,

but it is difficult to justify increased brain size by reference to fitness gains. Perhaps there is some group activity undertaken by multi-male/multi-female ape groups that is beyond the capacity of monkey societies, and that requires enhanced intelligence. It would be nice to know what that might be.

The most plausible hypothesis explaining heightened human intelligence is that hominid groups engaged in forms of fitness-enhancing social coordination that required a large neocortex, and individuals with enhanced cognitive powers were rewarded with extra mating opportunities and offspring protection. A particularly intelligent male who could signal his favorable genetic potential would then be favored by females on costly signaling grounds. This of course is gene-culture coevolution in its most productive form: when individual intelligence has group-beneficial implications, and when a hominid society finds a social arrangement for rewarding individual intelligence, this new cultural arrangement will lead to genetic selection on the basis of intelligence.

According to this theory, human success in hunting and fighting was based on highly flexible cooperation in moderately large groups of loosely related families. This flexible coordination required networked minds and distributed cognition, so that the hunter-gatherer group acted as a superorganism in which social rules rewarded individuals for their sacrifices in developing the skills to contribute to the execution of collective goals. Cognitive ability thus became a social good, costly to develop and sustain in the individual, but contributing to group success. The key question is how hunter-gatherer societies provided fitness-enhancing rewards to its more intelligent members.

3 Human Cooperation as Coalitional Enforcement

The benefits of group living for primates is ostensibly protection against predators. The increased neocortex size of apes appears to be unexplained by either group size, heightened foraging efficiency, or anything else. I take this to be a mystery.

It is clear that humans have several rather stunning capacities not shared by other primates. These include enhanced cognition, a theory of mind, the ability to manipulate counterfactuals, the ability to manufacture complex tools, the capacity to invent novel rules and play games according to these rules (*Homo Ludens*), a strong moral sense, and the ability to use language with syntax. But these capacities are relevant for a single reason: they allow groups of non-kin to cooperate in finding food and protecting themselves against enemies. This ability is absent in non-human multi-male/multi-female primate groups, where the most dominant male would doubtless monopolize a megafauna kill, leaving others at best to beg for scraps. As a result, chimpanzee hunting is restricted to capturing small monkeys

that can be consumed on the spot. Hominid groups fared better in cooperating because they devised a way of countering the hierarchical power of the dominant male, and developed social norms for the division of the kill that did not undermine the incentives for individuals to develop their hunting skills and to participate in collective hunting activity.

Paul Bingham (1999), appears to be the first to propose this model of early human cooperation, using the general term *coalitional enforcement*. “Coalitional enforcement,” he writes, “arose uniquely in humans when the animals that founded the Homo clade acquired the ability to kill or injure conspecifics from a substantial distance. This developed from the evolution of hominid virtuosity at accurate, high-momentum throwing and clubbing. . . This ability dramatically reduced the individual cost of punishing noncooperative behavior by allowing these costs to be distributed among multiple cooperators.” (p. 133)

4 Human Cooperation as Confrontational Scavenging

Several four-legged mammals have adapted their front legs for manipulating food objects, digging, and other pursuits besides locomotion (rats, squirrels, primates). Bipedality freed the hominid front limbs from contributing at all to locomotion, and thereby allowed the skeleton and muscles of the arm and torso to become specialized for something else. That something else was throwing. (Calvin 1983) and Bingham (1999) insightfully analyzed the neural and skeletal correlates of skillful projectile deployment, and paleontologists have since refined this argument considerably. Bingham’s argument that low-cost punishment is at the heart of coalitional enforcement has been supported by mathematical population biological models (Gintis 2000b, Bowles and Gintis 2004, Boyd et al. 2010).

Our understanding of the increased mental capacity of early Homo has been advanced by (Bickerton and Szathmáry 2009b), who argue that early Homo were not hunters, but rather confrontational scavengers of megafauna (i.e., they used rocks and clubs to chase away killers and other scavengers). Because this prey was likely to be rarely found in any one locality, groups would have been forced to divide into several very small hunting parties and disperse widely over a territory. When one group located a prey, it would be obliged to communicate over long distances with the others to draw them to the spot of the prey. From this, both language and abstract ideas could easily have developed.

5 Lethal Weapons

According to our best evidence, the hunter-gatherer societies that defined human existence until some 10,000 years ago were extremely egalitarian, involving widespread sharing in both communal child rearing (Hrdy 2000, 2009) and hunting (Boehm 2000; Boyd and Silk 2002; Bowles and Gintis 2011). Why did the hominid line develop such egalitarian societies? The emergence of settled trade and agriculture some 10,000 years ago laid the foundation for the growth of predatory states and ruling classes based on the ruthless exercise of power. What permitted this reversal of homo Sapiens egalitarianism? Finally, what accounts for the triumph of democracy from the mid-nineteenth century to the present? In all cases, I will argue the key factor was innovation in lethal weaponry.

A comparative analysis of the evolution of primate social organization is the appropriate setting for addressing this question (Silk 2011). Shultz et al. (2011) recently carried out such a study, based on the genetic distances and phenotypic social-structural similarities of 217 extant primate species. They conclude that the earliest primates lived some 72 Mya as solitary foraging individuals who came together only for mating. Multi-male/multi-female aggregations appeared some 52 Mya. We can infer from the social structure of contemporary non-human primate species living in multi-male/multi-female groups that mating was promiscuous and males formed a hierarchical power structure with a single alpha male at the apex. Indeed, all known non-human primates who live in multi-male groups exhibit this living pattern (Chapais 2008). While this social structure is highly stable and has persisted into the present, when suitably stressed it broke down into two social forms in which a social group included only one male. The first, which appeared first about 16 Mya, was the single-male harem while the second, appearing about the same time, was single pair-living.

The last common ancestor of hominids and their closest relatives, chimpanzees, lived some 5 to 7 Mya, but hominids split into two distinct lineages some 2.5 Mya, one group becoming the australopithecines and the other become the early human precursors. The australopithecines line became extinct some 1.4 Mya. It is important to note that the first record of tool use in primates lies in this same range of 2.5 Mya. The crucial point is that while there is widespread, if primitive tool use in non-human primates, only humans are effective in killing at a distance. Most important were sharpened wooden thrusting and throwing spears developed for hunting and contestational scavenging, but quite effective in killing or maiming the strongest male while asleep or otherwise inattentive. Because of these lethal weapons, there was no possibility of maintaining a political hierarchy based on physical prowess alone. The political organization of ape society was destroyed by the presence of primitive lethal weapons.

By contrast, non-human primates never developed weapons capable of controlling a dominant male. Even when sound asleep, an accosted male chimpanzee reacts to hostile onslaughts by awakening and engaging in a physical battle, basically unharmed by surprise attack. In *Demonic Males* (1996), Richard Wrangham recounts several instances where even three or four male chimpanzees viciously and relentlessly attack a male for twenty minutes without succeeding in killing him. The backwardness of chimpanzees in this regard is not simply the lack of the appropriate lethal weapon, but the inability to wield effectively potentially dangerous natural objects, for instance stones and rocks. A chimpanzee may throw a rock in anger, but rarely will it achieve its target.

Bingham (1999) has correctly stressed the importance of the superior abilities of humans in clubbing and throwing projectiles as compared with other primates, citing Goodall (1964) and Plooij (1978) on the relative advantage of humans, and Darlington (1975), Fifer (1987), and Isaac (1987) on the importance of these traits in human evolution. Calvin (1983) argues that humans are unique in possessing the same neural machinery for rapid manual-brachial movements that allow for precision stone-throwing.

The reaction of hominid political structure to the emergence of lethal weapons was, logically, either to sustain leaderless social coalitions, or to find some basis for leadership other than force. The superior survival value of groups with a political structure allowing for flexible coordination of cooperative tasks doubtless led to the demise of many leaderless hominid social formations, and the consolidation of new hominid social relations based on novel forms of social interaction that sustained flexible coordination and cooperation. The more skilled, the more talented, and the more intelligent individuals must have held positions of high social influence and even power in such new arrangements, and since these positions could be held by force, they must have been held by persuasion.

Thus successful hominid social bands came to value individuals who could command prestige by virtue of their persuasive capacities. Persuasion depends on clear logic, analytical abilities, a high degree of social cognition (knowing how to form coalitions and curry the favor of others), and linguistic facility (Plourde 2009). For this reason, the social structure of hunter-gatherer life favored progressive encephalization and the evolution of the physical and mental prerequisites of effective linguistic and facial communication. In short, two million years of evolution in the presence of lethal weapons gave rise to the particular qualities of *Homo sapiens*.

It is surprising that this straightforward argument appears not to have been explored in the literature. In a more general setting Byrne and Whiten (1988) have argued that the increased complexity of social life in primate multi-male groups accounts for the cognitive development of primate species. The lethal weapon argument extends this analysis to explain human exceptionalism in the area of

cognitive and linguistic development. A kindred lethal weapon argument has recently been put forward by Chapais (2009), who notes that the extreme equality of power among individual humans was central to the emergence of pair-bonding (monogamy and occasional polygamy) in hominid species after the collapse of the dominance hierarchy, as the presence of lethal weapons rather leveled the playing-field in the competition for controlling the reproductive capacity of many females.

The centrality of lethal weaponry in promoting egalitarian multi-male/multi-female hominid groups explains the huge cognitive and linguistic advantage of humans over other species not as some quirk of sexual selection (the favorite theory through the ages of Charles Darwin, Ronald Fisher, Geoffrey Miller and many others), but rather as directly fitness enhancing, despite the extreme energy costs of the brain: increased cognitive and linguistic ability entailed heightened leadership capacities, which fellow group members were very willing to trade for enhanced mating and provisioning privileges.

With the development of settled trade, agriculture, and private property some 10,000 years ago, it became possible for a Big Man to gather around him a relatively small group of subordinates and consorts that would protect him from the lethal revenge of a dominated populace, whence the slow but virtually inexorable rise of the state both as a instrument for exploiting direct producers and for protecting them against the exploitation of external states and bands of private and state-sanctioned marauders. The hegemonic aspirations of states peaked in the thirteenth century, only be driven back by the series of European population-decimating plagues of the fourteenth century. The period of state consolidation resumed in the fifteenth century, based on a new military technology: heavily armed cavalry. In this case, as in some other prominent cases, technology becomes the handmaiden to oppression rather than emancipation.

In *Politics*, Book VI part vii, Aristotle writes “there are four kinds of military forces—the cavalry, the heavy infantry, the light armed troops, the navy. When the country is adapted for cavalry, then a strong oligarchy is likely to be established [because] only rich men can afford to keep horses. The second form of oligarchy prevails when the country is adapted to heavy infantry; for this service is better suited to the rich than to the poor. But the light-armed and the naval elements are wholly democratic. . . An oligarchy which raises such a force out of the lower classes raises a power against itself.”

The use of cavalry became dominant in Europe through the success of the Parthians in the Roman-Persian wars that lasted from the late Hellenistic period until the Middle Ages. The Roman’s armored infantry could not stand up to the Parthian cavalry and the Romans adjusted by adopting the practices of their enemies. The increased strategic role of cavalry was enhanced by the emergence of new breeds of horses engineered for the battlefield, and deployed adeptly by the

Germanic invaders and the Islamic warriors. From this, enhanced by the development of the wraparound saddle, stirrup, and spurs, the preeminence of cavalry in the Middle Ages was assured, whence the oligarchic character of European feudalism, which centered around a knightly cavalry.

The history of warfare from the Late Middle Ages to the First World War was the saga of the gradual increase in the strategic military value of infantry armed with longbow, crossbow, hand cannon, and pike, which marked the recurring victories of the English and Swiss over French and Spanish cavalry in the twelfth to fifteenth centuries. Cavalries responded by developing dismounted tactics when encountering infantry, using heavy hand weapons such as two-handed swords and poleaxes. These practices extended the viability of cavalry to the sixteenth century in the French and Spanish armies, but gradually through the Renaissance, and with the rise of Atlantic trade, the feudal knightly warlords gave way to the urban landed aristocracy and warfare turned to the interplay of mercenary armies consisting of unskilled foot soldiers wielding cannon and other weapons based on gunpowder. Cavalry remained important in this era, but even in the eighteenth and nineteenth century, cavalry was used to execute the coup de grace on seriously weakened infantry.

The true hegemony of the foot soldier, and hence the origins of modern democracy, began with the perfection of the hand gun, with its improved accuracy and greater firing rate than the pistols of a previous era. Until that point, infantry was highly vulnerable to attack from heavy artillery. By the early twentieth century, the superiority of unskilled foot soldiers armed with rifles was assured. World War I opened in 1914 with substantial cavalry on all sides, but mounted troops were soundly defeated by men with rifles and machine guns, and thus were abandoned in later stages of the war. The strength of the political forces agitating for political democracy in twentieth century Europe was predicated on the strategic role of the foot soldier in waging war and defending the peace (Bowles and Gintis 1986).

REFERENCES

- Basolo, A. L., "Female Preference Predates the Evolution of the Sword in Sword-tails," *Science* 250 (1990):808–810.
- Bergstrom, Carl T. and Michael Lachmann, "Alarm Calls as Costly Signals of Antipredator Vigilance: The Watchful Babbler Game," *Animal Behaviour* 61 (2001):535–543.
- Bickerton, Kerek and Eörs Szathmáry, *Biological Foundations and Origin of Syntax* (Cambridge, MA: MIT Press, 2009).
- and — , "Confrontational Scavenging as a Possible Source of Language and

- Cooperation,” *BMC Evolutionary Biology* 11,261 (2009).
- Bingham, Paul M., “Human Uniqueness: A General Theory,” *Quarterly Review of Biology* 74,2 (June 1999):133–169.
- Bliege Bird, Rebecca L., Eric A. Smith, and Douglas W. Bird, “The Hunting Handicap: Costly Signaling in Human Foraging Strategies,” *Behavioral Ecology and Sociobiology* 50 (2001):9–19.
- Boehm, Christopher, *Hierarchy in the Forest: The Evolution of Egalitarian Behavior* (Cambridge, MA: Harvard University Press, 2000).
- Bowles, Samuel and Herbert Gintis, *Democracy and Capitalism: Property, Community, and the Contradictions of Modern Social Thought* (New York: Basic Books, 1986).
- and — , “The Evolution of Strong Reciprocity: Cooperation in Heterogeneous Populations,” *Theoretical Population Biology* 65 (2004):17–28.
- and — , *A Cooperative Species: Human Reciprocity and its Evolution* (Princeton: Princeton University Press, 2011).
- Boyd, Robert and Joan Silk, *How Humans Evolved (Third Edition)* (New York: W. W. Norton, 2002).
- , Herbert Gintis, and Samuel Bowles, “Coordinated Punishment of Defectors Sustains Cooperation and Can Proliferate When Rare,” *Science* 328 (30 April 2010):617–620.
- Bulmer, Michael G., “Structural Stability in Models of Sexual Selection,” *Theoretical Population Biology* 35 (1989):195–206.
- Byrne, Richard and Andrew Whiten, *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans* (Oxford: Clarendon Press, 1988).
- Calvin, William H., “A Stone’s Throw and Its Launch Window: Timing Precision and Its Implications for Language and Hominid Brains,” *Journal of Theoretical Biology* 104 (1983):121–135.
- Chapais, Bernard, *Primeval Kinship: How Pair-Bonding Gave Birth to Human Society* (Cambridge: Harvard University Press, 2008).
- , “The Deep Structure of Human Society: Primate Origins and Evolution,” in Peter M. Kappeler and Joan B. Silk (eds.) *Mind the Gap: Tracing the Origins of Human Universals* (Berlin: Springer, 2009).
- Darlington, P. J., “Group Selection, Altruism, Reinforcement and Throwing in Human Evolution,” *Proceedings of the National Academy of Sciences* 72 (1975):3748–3752.
- Darwin, Charles, *The Origin of Species by Means of Natural Selection, 6th Edition* (London: John Murray, 1859).

- , *The Descent of Man and Selection in Relation to Sex* (London: Murray, 1871).
- Dunbar, Robin M., *Grooming, Gossip, and the Evolution of Language* (Cambridge, MA: Harvard University Press, 1996).
- Endler, J. A. and A. L. Basolo, “Sensory Ecology, Receiver Biases and Sexual Selection,” *Trends in Ecology and Evolution* 13 (1998):415–420.
- Fifer, F. C., “The Adoption of Bipedalism by the Hominids: A New Hypothesis,” *Human Evolution* 2 (1987):135–47.
- Fisher, Ronald A., *The Genetical Theory of Natural Selection* (Oxford: Clarendon Press, 1930).
- Gintis, Herbert, *Game Theory Evolving* (Princeton: Princeton University Press, 2000).
- , “Strong Reciprocity and Human Sociality,” *Journal of Theoretical Biology* 206 (2000):169–179.
- , “The Evolution of Private Property,” *Journal of Economic Behavior and Organization* 64,1 (September 2007):1–16.
- , *The Bounds of Reason: Game Theory and the Unification of the Behavioral Sciences* (Princeton: Princeton University Press, 2009).
- , Eric Alden Smith, and Samuel Bowles, “Costly Signaling and Cooperation,” *Journal of Theoretical Biology* 213 (2001):103–119.
- Goodall, Jane, “Tool-using and Aimed Throwing in a Community of Free-Living Chimpanzees,” *Nature* 201 (1964):1264–1266.
- Hamilton, William D. and M. Zuk, “Heritable True Fitness and Bright Birds: a Role for Parasites?,” *Science* 218 (1982):384–387.
- Hrdy, Sarah Blaffer, *Mother Nature: Maternal Instincts and How They Shape the Human Species* (New York: Ballantine, 2000).
- , *Mothers and Others: The Evolutionary Origins of Mutual Understanding* (New York: Belknap, 2009).
- Isaac, B., “Throwing and Human Evolution,” *African Archaeological Review* 5 (1987):3–17.
- Johnstone, Rufus A., “Sexual Selection, Honest Advertisement and the Handicap Principle,” *Biological Reviews* 70 (1995):1–65.
- Kirkpatrick, M., “Sexual Selection and the Evolution of Female Choice,” *Evolution* 36 (1982):1–12.
- Lande, R., “Models of Speciation by Sexual Selection of Polygenic Traits,” *Proceedings of the National Academy of Sciences USA* 78 (1981):3721–3725.
- Maynard Smith, John, “Sexual Selection and the Handicap Principle,” *Journal of Theoretical Biology* 57 (1976):239–242.

- Miller, Geoffrey, *The Mating Mind: How Sexual Choice Shaped the Evolution of Human Nature* (New York: Anchor, 2001).
- O'Donald, P., "The Theory of Sexual Selection," *Heredity* 17 (1962):541–552.
- Plooij, F. X., "Tool-using during Chimpanzees' Bushpig Hunt," *Carnivore* 1 (1978):103–106.
- Plourde, Aimée, "Human Power and Prestige Systems," in Peter M. Kappeler and Joan B.Silk (eds.) *Mind the Gap: Tracing the Origins of Human Universals* (Berlin: Springer, 2009).
- Pomiankowski, A. N., "The Costs of Choice in Sexual Selection," *Journal of Theoretical Biology* 128 (1987):195–218.
- Roughgarden, Joan, *Evolution and Christian Faith: Reflections of an Evolutionary Biologist* (Island Press, 2006).
- Ryan, Michael J., *The Tungara Frog, a Study in Sexual Selection and Communication* (Chicago: University of Chicago Press, 1985).
- , "Sexual Selection, Sensory Systems and Sensory Exploitation," *Oxford Surveys in Evolutionary Biology* 7 (1990):157–195.
- , "Sexual Selection, Receiver Biases, and the Evolution of Sex Difference," *Science* 281 (1998):199–204.
- Shultz, Susanne, Christopher Opie, and Quentin D. Atkinson, "Stepwise Evolution of Stable Sociality in Primates," *Nature* 479 (November 2011):219–222.
- Silk, Joan B., "The Path to Sociality," *Nature* 49 (November 2011):182–183.
- Sosis, Richard, "Costly Signaling and Torch Fishing on Ifaluk Atoll," *Evolution and Human Behavior* 21,4 (2000):223–244.
- Szathmáry, Eörs and Szabolcz Szamadö., "Language: A Social History of Words," *Nature* 456 (2008):40–41.
- West-Eberhard, Mary Jane, "Sexual Selection, Social Competition, and Speciation," *Quarterly Review of Biology* 58,2 (June 1983):155–183.
- Wrangham, Richard and Dale Peterson, *Demonic Males: Apes and the Origins of Human Violence* (New York: Mariner Books, 1996).
- Zahavi, Amotz, "Mate Selection—A Selection for Handicap," *Journal of Theoretical Biology* 53 (1975):205–214.