

exclusive birthright, while remaining blind to the sacred mysteries of artistic creation. But Miller has never exactly set the world of medicine on fire. What he is famous for these days is directing operas — not a profession in which scientific discipline is much of a *sine qua non* — and being on TV. The scientific element in *On Reflection* is not excessively taxing (try reading Michael Baxandall's book about shadows in eighteenth-century painting, *Shadow and Enlightenment*, Yale University Press, 1995). But throughout the project he shows a disappointing narrowness of response to the art works he discusses, seeming to think that a picture is only ever about one thing, taking no account of the childish pleasure that even the best artists sometimes take in pushing paint around, disregarding art-historical factors that are thumpingly relevant to certain works.

From this show you would never, for example, know that Parmigianino's self-portrait in a convex mirror reflects not only the difficulty of making flat ones at the time, but also that various sixteenth-century artists, for various reasons, reacted against the Renaissance ideal of verisimilitude in painting; nor that Tennyson's "Lady of Shalott" was a sort of leitmotiv among the later Romantics, for whom the image of someone condemned to see life through a mirror symbolized the tragic unreality of experience mediated by art. There are also basic errors of observation; you cannot see much of yourself if you stand in a pool, as Miller says Rembrandt's girlfriend can, partly because the water would be disturbed by your presence, and partly because your reflection would be grotesquely foreshortened. In any case, Hendrijke is plainly not looking straight downwards in the picture; the reflective surface confers a tenderly erotic mood on the picture, but not in any strictly literal way.

Moreover, the pivotal importance of the mirror as a kind of private symbol among artists of the goals and limitations of what they are striving to do is largely overlooked. A dingy print of Velázquez's "Las Meninas", a picture of what the king and queen of Spain saw while he worked on their portrait in around 1656, and one of the most fascinating pictures about seeing and representing things ever painted, is in the show. Miller notices that the mirror on the back wall reflecting the royal couple is made to seem shiny and scuffed with incident white light — that, in his terms, it is an imperfect reflection. But the shininess of the mirror makes us aware that it is surrounded by pictures, which seem grimy and indistinct, but which can be seen to include paintings by Rubens of mortals punished for claiming that their skill in the arts rivalled the gods (an interesting foil to the bravura self-portrait in the foreground). Velázquez is often cited as an example of a court painter whose life was effectively one of imprisonment (one of his closest friends at court was the king's dwarf).

Among the many levels on which "Las Meninas" works, one is surely a glumly brilliant analogy between the gifted but trapped artist and the mirror, which gives a perfect image but has, as it were, no say in the matter, being a passive redirector of whatever light an object throws at it. The fact that the mirror represents the imperious gaze of Velázquez's masters reinforces this sense of his predicament; the better he does his job, the more literal and reductive the result. It is surely this desire on the part of artists to do more than compete with the dumb mirror which would lead to their break from representation at the start of this century. □

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What two legs can learn from four legs

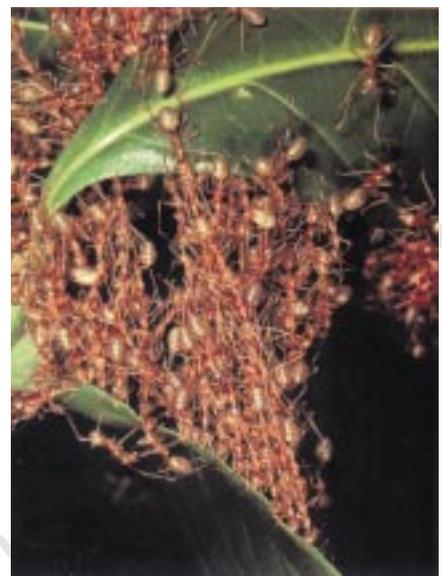
Foundations of Social Evolution
by Steven A. Frank
Princeton University Press: 1998. 268 pp.
\$49.50, £35 (hbk), \$16.95, £13.95 (pbk)

Cooperation Among Animals
by A. L. Dugatkin
Oxford University Press: 1998. 221 pp.
£45, \$65

Martin A. Nowak and Karl Sigmund

From Aristotle's *Zoon Politicon* to George Orwell's *Animal Farm*, philosophical and literary discussions of human social life have often alluded to its beastly side. Conversely, research on animal societies has brought science close to areas traditionally reserved for philosophy and the humanities — too close for comfort, some seem to think. It was all very well to derive convenient morals from animal fables. But a vocal in-group of biologists, a few of them best-seller writers, claim that our moral sense and our civic virtues are actually inherited from animals. These two books by A. L. Dugatkin and Steven Frank studiously avoid the minefield of human social evolution, but draw a considerable amount of their appeal from the resonances animal societies have with our own.

This holds particularly for issues of altruism and mutual help. Darwin saw in animal cooperation a "special difficulty" for his theory. Subsequent cohorts of evolutionary biologists have blown, in turn, hot and cold about the prevalence of selfishness in nature. The last generation, which set out to take the altruism out of altruism, was guided by two shining beacons, William D. Hamilton's "Genetical evolution of social behaviour" (*Journ. Theor. Biol.* 7, 1–52; 1964) and Robert Trivers's "Evolution of reciprocal altruism" (*Quart. Rev. Biol.* 46, 35–57; 1971). The former was based on kin selection: genes for helping relatives will spread, since relatives are diluted copies of oneself. The latter was



Pulling together: Asian weaver ants, *Oecophylla smaragdina*, cooperate in nest building.

based on reciprocity: help your helper and you help yourself. Both approaches were never meant to exclude other possibilities, and are, in particular, mutually compatible. Nevertheless, most of the subsequent contributions can be placed in one tradition or the other. This is the case with the two books at hand, despite the fact that both propose a synthesis. Dugatkin follows Trivers, Frank follows Hamilton, and they synthesize in different ways.

The books complement each other in another respect. Frank's work on the foundations of social evolution explores issues of method in a highly original, almost idiosyncratic manner, whereas Dugatkin's book opens a wide perspective on the sizeable literature dealing with field observations and lab experiments on animal cooperation.

Dugatkin manages to place more than 1,000 papers in context without getting flustered or entangled. This is due to the book's clear organization: there are separate chapters on cooperation in fishes, in birds, in non-primate mammals, in non-human primates and (no, not in humans) in social insects. In each chapter, there are sections devoted to different types of activities: grooming, foraging, anti-predator behaviour, and so on. And, in each section, the data are dissected according to the "four pillars of co-operation", categories of explanation described by Dugatkin in a clear and brisk theoretical introduction. These are, in addition to kin selection and reciprocal altruism, trait group selection and byproduct mutualism.

Group selection (in D. S. Wilson's sense) is not meant to imply a 'good for the species' type of argument, but is based on the benefits that devotion to a clique can confer to individuals. Dugatkin's treatment is fair and sympathetic, avoiding the confusing megasell so rampant with this issue. Byproduct

mutualism holds when the best one can do for oneself also happens to be best for the other. Most theoreticians fail to be excited by this type of cooperation which can obviously not be threatened by cheating, and byproduct mutualism has been branded a solution without a problem. But the concept may account for most instances of cooperation, as emerges from Dugatkin's empirical chapters.

Based on joint work with M. Mesterton-Gibbons (*Quart. Rev. Biol.* **67**, 267–281; 1992), Dugatkin describes all four categories in terms of a single game, the Cooperator's Dilemma, which is an extension of the notorious Prisoner's Dilemma. We are not sure whether this provides the neatest classification of the many facets of cooperation. But it certainly helps Dugatkin to focus a large part of his book on one crucial aspect — the rank order of the payoff values, which are measured in reproductive success. Empirical results on this issue are hard to get, and even in the best-studied case — predator inspection in fish — consensus has not been achieved.

Dugatkin gives an excellent description of this debate, which originated in an ingenious mirror experiment by Manfred Milinski (*Nature* **325**, 433–435; 1987), and of similarly contentious issues. But he shies away from entering the thicket of data and speculation on human cooperation, explaining his reluctance by the huge amount of work which has been done in this area by experimentalists with no evolutionary background. We think that his book might change this state of affairs, and suggest it as required reading in psychology classes.

Frank's book centres not on data, but on theories and even more on methods. It views natural selection as fitness maximization, and mostly deals with how to keep count of fitness, that is, contributions to the future of the population. This is to a large extent a question of book-keeping — how best to invest in future offspring, how to include the contributions of relatives, and so on — and it can lead, depending on social context and interactions, to real brain-teasers. Frank's treatment is based on his dexterous use of the Price equation, which states that the change in the average value of a character is proportional to the covariance of character and fitness (*Nature* **227**, 520–521; 1970). In the hands of Price (a brilliant and tragic figure who killed himself in 1974), and later in those of Hamilton and Franks, the covariance formula worked like magic, shedding light on such diverse topics as R. A. Fisher's fundamental theorem of natural selection, group selection arguments, or Hamilton's concepts of inclusive fitness and population viscosity.

Frank shows, for instance, that relatedness can be used as a measure both of genealogical kinship and of information about social partners. His applications are

not confined to the usual topics of social evolution, but range from parasite virulence to cytoplasmic incompatibility. One third of the book deals with sex allocation, the division of resources between daughters and sons. It allows Frank to elaborate on his three 'exchange mechanisms': reproductive value, kin selection and marginal value. In spite of such examples, the book is heavily slanted towards theory. Its use of techniques from many fields of genetics, statistics and economics makes it a demanding read. But it is worth the effort. Frank's 'how to' approach will certainly shape future modelling of social interactions. Both books are essential reading for those interested in the evolution of cooperation. □

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Fungus not always a bogeyman

Magical Mushrooms, Mischievous Molds
by George W. Hudler
Princeton University Press: 1998. 248 pp.
\$29.95, £22.95

David L. Hawksworth

In 1986, India's foremost mycologist C. V. Subramanian remarked that fungi touch on every facet of our life and progress on Earth. Unseen, misunderstood, or regarded with suspicion, we cannot escape their influence. George Hudler from Cornell University, New York state, explains why in this most readable book. The multifarious topics tackled range from the beneficial to the harmful, and are approached by eclectic examples, albeit with a US bias. He admits he had a dilemma about what to include; I would

share the problem. Stories about potato blight and the Irish famine, the cereal disease ergot and witches, reindeer and radioactive lichens, bread, wine, mycotoxins, mycoses, and devastating tree diseases are all here.

No mention is made of *Pneumocystis carini*, the fungal lung infection causing pneumonia in so many people with AIDS, but did you know that the singer Bob Dylan was critically ill with histoplasmosis? Medicinal products have an appropriately high profile, but what of Ronald Hare's hypothesis on the origin of Fleming's first penicillin-producing isolate? The spores may have originated on the floor below Fleming's laboratory, where Charles La Touche was working on cultures from damp Victorian London basements.

Companies active in pharmaceutical bio-prospecting today recognize that fungi are so poorly known that locally obtained isolates can be as bioactive as ones from exotic tropical sites. A fungus that produces cyclosporin (used as an immunosuppressive drug) turned up only a few miles from Ithaca, in Cornell's own backyard.

In Asian culture, some fungi are legendary for their health benefits. Notable examples are *Ganoderma lucidum* (reishi) and *Lentinula edodes* (shiitake), which give rise to antitumour activity by enhancing the immune system, and are credited with many other medicinal properties. Their metabolites are the subject of ongoing research. Shiitake is now readily available in Western supermarkets, together with about 30 other species, and fungi merit a heightened profile in our diets from both health and ecological perspectives. Largely grown on crop residues, mushrooms are underestimated as potential players in the sustainable use of resources. A lack of imaginative recipes has limited their profile among gastronomes, but this is being rectified by *Hope's Mushroom Cookbook* (Mad River Press, 1993) in the United States, and *Patricia's Mushroom Cookery*, to be published by MycoNova this autumn in the United Kingdom.



Feel the itch: several fungi infect human skin. This one, *Microsporum gypseum*, causes ringworm.