

Disease and social evolution

Raghavendra Gadagkar

Parasites that cause diseases of varying intensities are ubiquitous in the natural world. However, the role of disease as a factor in shaping the ecology and evolution of their hosts has only recently begun to be sufficiently appreciated. Parasite load has, for example, been shown to be an important parameter that females use to assess the quality of their mates. In response, males are known to evolve elaborate secondary sexual characters to impress upon females their health in general and their ability to resist parasites in particular^{1,2}. An even more profound role that parasites play in modulating social evolution has recently come to light.

In social insects such as ants, bees and wasps (belonging to the order Hymenoptera) males usually develop from unfertilized eggs while females develop from fertilized eggs. This *haplo-diploid* mode of genetics results in curious asymmetries in genetic relatedness. For example, two full-sisters are related to each other by 3/4 rather than by 1/2 as in diploid organisms. Such an asymmetry in genetic relatedness can potentially promote the evolution of social life in these insects. This is because, a female wasp for example, can gain more fitness by rearing her full-sisters (coefficient of genetic relatedness = 3/4) rather than an equal number of offspring (coefficient of genetic relatedness = 1/2)^{3,4}.

Queens in many social Hymenoptera mate with several males and simultaneously use sperm from different males to produce several patriline of daughters (this phenomenon is known as *polyandry*)^{5,6}. Daughters belonging to different patriline would of course be half-sisters of each other with a coefficient of genetic relatedness of 1/4. Fitness gained by rearing half-sisters would obviously be considerably less than that gained by rearing offspring. This habit of multiple mating by the queens should therefore decrease the propensity of the queen's daughter to stay back in her nest and help her raise more daughters. The question therefore is why should queens mate multiply? Would they not be

better off mating with a single male and thus ensuring the cooperation of their daughters? In search of a solution to this apparent paradox people have begun to focus on possible advantages of genetic variability (provided by the presence of multiple patriline) within a colony. Several such factors have been postulated although their involvement in providing a selective advantage for multiple mating has not so far been conclusively demonstrated. For instance, to the extent that task performance in the colony has a genetic basis (and there is some evidence for this^{7,8}) genetic variability provides for more efficient division of labour. A somewhat different kind of argument is that intra-colony genetic variability could provide effective resistance to diseases which might otherwise spread rapidly when all workers in a colony are highly related to each other and thus sensitive to the same parasites^{9,10}.

Recent studies of the bumble bee, *Bombus terrestris* and its intestinal trypanosome parasite, *Crithidia bombi* not only confirm such an advantage for intra-colony genetic variability but demonstrate that disease can have rather complex effects on the dynamics of social evolution¹¹⁻¹³. *Crithidia bombi* spreads from one bumble bee to another through the ingestion by bumble bees of live parasite cells during direct physical contact or through contact with faeces of infected animals. *Bombus terrestris*, living in a temperate environment, suspends colonial life during winter when new queens hibernate while old queens and all workers die. In the following spring, queens emerge from their hibernacula and initiate new colonies. The queen first produce daughters who become workers and later, with the help of this labour force, they produce daughters who mate, hibernate and become queens in the next year. The parasite depends for its continued survival across years, on infecting new queens before they begin to hibernate. Infected queens are likely to pass the infection on to their daughter workers as well as daughter queens because of the possibi-

lity of contacting infection through physical contact as well as contact through faeces within their colonies. Laboratory experiments performed by Shykoff and Schmid-Hempel in Switzerland show that the spread of infection from one bumble bee to another depends significantly on the genetic relatedness between the source and recipient of infection^{11,12}. This suggests a genetic basis for susceptibility and supports the idea that infection would spread rapidly in a relatively genetically homogenous colony compared to a colony with genetically more variable individuals. Given a reasonable chance of their being infected, queens who mate multiply and produce genetically variable daughters should therefore be at an advantage compared to queens who mate singly and produce genetically similar daughters. Disease is thus a potential factor that selects for multiple mating by the queen.

The *Bombus-Crithidia* story has other fascinating ramifications however. In normal uninfected colonies, workers begin by having poorly developed ovaries and spending all their time working for the colony to rear the queen's (their mother's) brood. With time however workers gradually develop their ovaries and towards the end of the colony cycle, virtually revolt against queen-control and begin to lay their own eggs. The success of queens therefore depends upon producing new daughter queens before workers begin to revolt. A queen that dies after producing only workers and no daughter queen gains little, if any, fitness. Curiously, queens seem to benefit from the infected status of their daughter workers. Infection retards the ovarian development of workers and thus keeps them working for longer periods of time and postpones the time of their revolt. Queens therefore have more time to complete the production of their new daughter queens¹³. In principle this should provide an opposing selective force. Since queens benefit from having infected workers and such infection spreads more effectively in genetically similar lines of workers, a queen would be better off mating singly and produce daughters who are all full-sisters of each other. Disease could thus in principle select for single mating instead of multiple mating.

However, there is an unresolved problem here. If workers in a colony are

infected, the queen is bound to be infected too. The parasite which has detrimental effects on workers has similar effects on the queens. Infected queens can start new nests but they lay eggs at a somewhat lower rate compared to uninfected queens. This leads to significantly smaller worker populations in infected laboratory colonies¹³. But, presumably because the laboratory colonies were supplied with unlimited food, this difference in worker populations did not translate into significant differences in the abilities of infected and uninfected queens to produce daughter queens¹³. In nature difference in worker populations between colonies is almost certainly expected to lead to different probabilities of new queen production. Obviously, the critical factor is the magnitude of the disadvantage to an infected queen in nature in terms of reduced probability of producing daughter queens relative to the advantage to her due to the ovarian impairment of her daughter workers which leads to extended cooperation on their part. If the disadvantage of her own infection is greater than the advantage of worker infection then we would expect selection in favour of multiple mating, leading to genetic variability and lower rates of infection. If the disadvantage of her own infection is less than the advantage of worker infection than we would expect selection in favour of single mating leading to genetically similar daughters and consequent high rates of infection of the daughters. All this reasoning is from the queen's point of view because selection on multiple versus single mating is expected to act on the queen—the daughter workers have little say in this matter.

The story does not end there. Multiple mating is only one way of increasing intra-colony genetic variability. The presence of multiple queens either simultaneously or in succession (termed Polygyny) is another way in which intra-colony genetic variability can increase substantially in other social insects^{14,15}. Here it is entirely possible that workers have some say in the matter of the number of queens. In some ants for example, it is well known that workers not only decide how many queens may be reproductively active in their colony but they even decide which individuals may become reproductively active queens¹⁶⁻¹⁹. When selection leading to high or low genetic variability can act on the workers, the differential effects of disease on queens and workers can have effects that may be the opposite of what we have seen above. When both polyandry and polygyny are simultaneously present in colonies of a species^{14,15,20}, i.e. when selection can act on both queens and workers, one might expect a mind-bogglingly complex effect of disease on the dynamics of social evolution.

1. Hamilton, W. D., in *Population Biology of Infectious Diseases* (eds Anderson, R. M. and May, R. M.), Springer-Verlag, Dahlem Konferenzen, New York, 1982, pp. 269.
2. Hamilton, W. D. and Zuk, M., *Science*, 1982, 218, 384.
3. Hamilton, W. D., *J. Theor. Biol.*, 1964, 7, 1.
4. Wilson, E. O., *The Insect Societies*, Harvard University Press, Cambridge, USA, 1971.
5. Page, R. E. Jr., *Annu. Rev. Entomol.*, 1986, 31, 297.

6. Starr, C. K., in *Sperm competition and the evolution of animal mating systems*, (ed. Smith, R. L.), Academic Press, New York, 1984, pp. 427.
7. Page, R. E. Jr. and Robinson, G. E., *J. Insect Physiol.*, 1991, 23, 117.
8. Robinson, G. E., *Annu. Rev. Entomol.*, 1992, 37, 637.
9. Hamilton, W. D., in *Animal Societies: Theories and Facts*, (eds. Ito, Y., Brown, J. L. and Kikkawa, J.), Japanese Scientific Press, Tokyo, 1987, pp. 81.
10. Sherman, P. W., Seeley, T. D. and Reeve, H. K., *Am. Nat.*, 1988, 131, 602.
11. Shykoff, J. A. and Schmid-Hempel, P., *Behav. Ecol. Sociobiol.*, 1991, 28, 371.
12. Shykoff, J. A. and Schmid-Hempel, P., *Proc. R. Soc. London B*, 1991, 243, 55.
13. Shykoff, J. A. and Schmid-Hempel, P., *Behav. Ecol.*, 1991, 2, 242.
14. Gadagkar, R., Chandrashekara, K., Chandran, S. and Bhagavan, S., *Naturwissenschaften*, 1991, 78, 523.
15. Gadagkar, R., Chandrashekara, K., Chandran, S. and Bhagavan, S., in *Queen Number and Sociality in Insects*, (eds. Keller, L. and Cherix, D.), Oxford University Press, 1992, in press.
16. Fletcher, D. J. C. and Blum, M. S., *Science*, 1983, 219, 312.
17. Fletcher, D. J. C. and Blum, M. S., *Science*, 1981, 212, 73.
18. Fletcher, D. J. C., in *Advances in Invertebrate Reproduction 4*, (eds. Porchet, M., Andries, J. C. and Dhainaut, A.), Elsevier, Amsterdam, 1986, pp. 305.
19. Vargo, E. L. and Ross, K. G., *J. Insect Physiol.*, 1989, 35, 587.
20. Muralidharan, K., Shaila, M. S. and Gadagkar, R., *J. Genet.*, 1986, 65, 153.

Raghavendra Gadagkar is in the Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560 012, India

Professor Satish Dhawan attracted our attention to a very perceptive article written by one of our ablest administrators P. N. Haksar. We reproduce below a note by Dhawan as an introduction.

—Editor

In the turmoil—social, political and economic—that India is passing through, nothing stands out as the strife spawned by friction between communities, castes and religion often fomented and manipulated by politicians and their henchmen. There seems to be a growing distrust of reason, a forgetting of the roots of Indian tolerance and adherence to morality. While some members of the Indian intelligentsia have on a few occasions taken courage to speak out against the whipped up frenzy and its disastrous consequences, the Indian Science Community has generally not discussed or taken a public stand in its usual gathering places such as Conferences, Symposia, Congresses, etc. Although many see this phenomenon as a menace not only to the strengthening of the roots of science in India but to virtually all civilized development, few do much about it. Haksar's editorial note [reproduced below] in *Man & Development* is worth reading by all our colleagues. It is a sober and reasoned analysis in the light of history by a respected intellectual who has been active for many decades in the endeavour to help create a modern India which is rational and humane, where the power bestowed by knowledge and status is tempered by wisdom and sensitiveness—he has been in the thick of the fight and yet above it. It is a good, sobering message for all Indian intellectuals.

— Satish Dhawan

Fundamentalism and secularism

P. N. Haksar

In the charmed world of Alice in Wonderland, words can be made to mean anything. Regrettably, outside that Wonderland, words have to be used with utmost care. The context in which a word arises must be understood if we are to avoid unnecessary sorrow and suffering. Ever since human beings began expressing themselves through words and then language, a measure of sacredness has been attached to a 'word'. According to our own tradition, in the beginning there was 'Word' and that word was *Om*. Great care was taken in articulating the vibrant resonance of *Om*. Similar sanctity attaches to a Muezzin's call: "Allah-O-Akbar". In the Christian system of faith and belief, the second person in the Trinity is 'Word'. When a person makes a statement or promise to do something "upon my word", sanctity attaches to that statement.

We have said enough to make the simple point that 'words' have to be used with utmost care. In order to do so, we must understand the context in which each word arose and the shades of meaning which it acquires through the passage of time. All this might sound somewhat pedantic, but the Information Revolution, which is shaking

the world, makes it necessary to point out the dangers involved in our failure to be meticulous, even fussy, about the use of words. In these notes, we are particularly concerned about two words, namely, 'Fundamentalism' and 'Secularism'.

Many dignitaries visiting our shores in recent months, more especially from the United States and the United Kingdom, have warned us about the rise of 'Islamic Fundamentalism'. It is perhaps, their hope that India's social and political climate might be receptive to their warnings. That hope is not without some basis. That is why it is necessary to examine critically the genesis of the word 'fundamentalism'. How did this word arise in the English language? The *Oxford Reference Dictionary* explains it thus:

Strict maintenance of traditional orthodox religious beliefs; a religious movement which developed among various Protestant bodies in the USA after the First World War, based on strict adherence to certain tenets (e.g. the literal inerrancy of Scripture) held to be fundamental to the Christian faith.

The *Encyclopaedia of Social Sciences* elaborates the origins of fundamentalism as follows:

Fundamentalism is the name of an aggressive conservative movement in the Protestant churches of the United States which flourished

during the decade after the World War. It manifested itself chiefly in the Baptist, Disciple and Presbyterian churches but received considerable support from other ecclesiastical groups. It was characterized not only by its conservatism with regard to traditional popular Christian beliefs but also by its aggressive efforts to impose its creed upon the churches and upon the public and denominational schools of the country. Its conservative supernaturalism was expressed in the "five points of fundamentalism" which included the doctrines of the inerrancy of the Bible, the Virgin Birth of Jesus, the supernatural atonement, the physical resurrection of Jesus and the authenticity of the Gospel miracles. The first of these points was interpreted by fundamentalism to apply particularly to the Biblical account of the creation of man in opposition to the theory of evolution, which became the central question of the fundamentalist controversy.

The movement was directed against liberal elements within the churches and against purely scientific or secular interests in American civilization.

Fundamentalism and political conservatism

It may be noted that fundamentalism as it arose in USA allied itself to political conservatism against liberal elements within the churches and against purely scientific or secular interests. Unnormous pressure was exerted on teachers and schools of a large number of States to

Reprinted with permission from *Man & Development*, December 1991.