

Sex versus non-sex versus cheaters

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Cheating is known to be a potential threat to cooperation. We examine the fitness of a cheater allele in an asexual-haploid versus a sexual-diploid population using three different models. The first model depicts small cooperative groups in which the altruist and cheater are distributed randomly, the second simulates large cooperative groups with varying degrees of spatial aggregation and the third simulates a hymenopteran society with cheater workers. In all the models sex helps stabilize cooperation. The results are not affected by dominance or recessiveness of the cheater allele. In either case, sexual diploidy increases the variance across groups and thus enhances group selection. As a result sex and cooperation can coevolve under conditions when cooperation offers substantial fitness gains and cheaters threaten cooperation. The model predicts that cooperation should be more common in sexually reproducing organisms than asexuals. Among organisms where diploid as well as haploid life-cycle stages are present, cooperation should be seen more commonly in the diploid stage.

EVEN after several decades of theoretical development, all the factors and forces behind the evolution of cooperation have perhaps not been unearthed. The same can be said about evolution of sex. Both the processes are likely to have evolved under a variety of selective forces and their interactions in a complex way. Perhaps a number of selective forces are yet to be identified and their effects elucidated.

A major problem in the evolution of cooperation has been the possibility of cheaters exploiting the cooperators. Cheaters have been demonstrated in natural populations^{1,2}, and shown to enjoy substantial fitness gains over altruistic ones^{2,3}. This problem has been modelled and discussed extensively^{1,4-7}. The known anti-cheater mechanisms include group selection⁶ or policing⁸. We suggest here that sexual diploidy can enhance the anti-cheater effects of group selection and thereby help stabilize cooperation. Almost all theories for the advantage of sex revolve around genetic recombination^{9,10}. Maynard-Smith and Szathmary¹¹ suggest, on the other hand, that recombination may be a later stage in the evolution of sex, syngamy without recombination preceding it. In all the models used below, recombination is not a necessary step. Diploidy arising out

of fusion of two haploid cells or gametes is sufficient to give an advantage in cooperation, as the models show. We use the word sex here to denote sexual diploidy independent of recombination. We model cooperation between cells or individuals in three different situations and show that over a variety of conditions, sex and cooperation can evolve together.

The first model considers cooperation in a small group of individuals, the number being four in the results shown. If the size of the cooperative group is small, chance alone can give rise to some groups with a greater proportion of altruists and some groups with greater proportions of cheaters. The number of cheaters in these groups is assumed to be binomially distributed. In the absence of cooperation, each individual has a baseline fitness of one. Complete cooperation of all members in a group gives a group benefit of 'a'. In a mixed group, the benefit of cooperation is decided by the fraction of altruistic individuals. The cheaters in a group derive an additional individual benefit 'b', which is also proportional to the number of altruists in the group. Sexuals and asexuals form separate cooperative groups in this model. In the sexual population the four individuals form two random pairs, mate and divide mitotically to form four diploid individuals that engage in the group cooperative act. The behaviour of a heterozygote is decided by the dominant allele. At the end of the cooperative act the diploid cells undergo reduction division. The resultant populations disperse randomly again to start a new turn of the cycle. From each group the reproductive success of a genotype is the product of the frequency of the group, the proportion of the allele in that group, the fitness of an individual within a group and the group fitness that is a function of the proportion of altruists in that group.

Accordingly, when the altruist allele is dominant:

$$\begin{aligned}
 P &= d(p^4(1+a) + 4p^3q \cdot 0.75(1+a) + 6p^2q^2 \cdot 0.5(0.33(1+0.5a) + 0.67(1+a)) + 4pq^3 \cdot 0.25(1+0.5a)), \\
 Q &= d(4p^3q \cdot 0.25(1+a) + 6p^2q^2 \cdot 0.5(0.33(1+0.5(a+b)) + 0.67(1+a))) + 4pq^3(0.5(1+0.5(a+b)) + 0.25(1+0.5a)) + q^4), \\
 P1 &= h(p1^4(1+a) + 4p1^3q1 \cdot 0.75(1+0.75a) + 6p1^2q1^2 \cdot 0.5(1+0.5a) + 4p1q1^3 \cdot 0.25(1+0.25a)), \\
 Q1 &= h(4p1^3q1 \cdot 0.25(1+0.75(a+b)) + 6p1^2q1^2 \cdot 0.5(1+0.5(a+b)) + 4p1q1^3 \cdot 0.75(1+0.25(a+b)) + q1^4),
 \end{aligned}$$

where

p is the proportion of altruist alleles in the sexual population, q the proportion of cheater alleles in the sexual population, $p1$ the proportion of altruist alleles in the asexual population, $q1$ the proportion of cheater alleles in the asexual population, d and h are the fractions of sexuals and asexuals in the total population.

P , Q are the resultant populations of altruists and cheaters in the sexual population and $P1$, $Q1$ are those in the asexual population. They are normalized by dividing by $P + Q$ and $P1 + Q1$ to get the p , q , $p1$ and $q1$ for the next generation. d and h are normalized similarly.

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When the cheater allele is dominant, the phenotype expression changes and the model is modified as follows:

$$P = d(p^4(1 + a) + 4p^3q(0.5(1 + 0.5a) + 0.25(1 + 0.5(a + b)))) + 6p^2q^2(0.5(0.33(1 + 0.5a) + 0.67) + 4pq^3(0.25)),$$

$$Q = d(4p^3q(0.25(1 + 0.5(a + b)) + 6p^2q^2(0.5(0.33(1 + 0.5(a + b) + 0.67)) + 4pq^3(0.75) + q^4)).$$

The model assumes no fitness difference in the sexual and asexual genotypes, except that arising from cooperation and cheating. Sex brings about a difference in the proportion of individuals that cheat and thus creates a fitness difference.

Simulations show that if the group benefit of cooperation is moderate to large, cheaters do not go to fixation despite individual advantage. This is due to group selection that, in this case, may be called dynamic group selection since unlike classical group selection, there is random mixing of individuals in the model; nevertheless, selection acts at the group as well as individual level. If the group benefits of cooperation are too large compared to the benefit of cheating, the cheaters quickly become extinct. Once the cheaters are extinct, there is no fitness difference between sexuals and asexuals and they coexist. If the benefit of cheating is disproportionately larger than the group benefit of cooperation, the altruists become extinct and the sexual and asexual cheaters coexist. At comparable values of a and b ; however, altruists and cheaters coexist sufficiently long and under such conditions the sexual population outcompetes the asexual one (Figure 1 *a*). If the cheater allele is recessive, it is not expressed in a heterozygote and therefore the proportion of individuals that cheat is much smaller in a sexual population. This confers an advantage to the sexual population. Surprisingly, results are similar if the cheater allele is dominant. This is likely since the cheater allele is expressed more frequently than its allelic proportion in a sexual population. The groups in which the cheater allele occurs at a higher proportion, fail to cooperate and have a smaller group fitness. On the other hand, in groups with a small proportion of cheater alleles, the cheater phenotype is heterozygous and therefore the advantage of cheating is shared by the altruist allele as well. Moreover, the disproportionate expression of cheating increases the variance in the phenotypic proportions of cheaters, which is an ideal situation for group selection to operate. As a result, the sexual population experiences a steep decline initially. However, the cheaters decline more rapidly than the altruists due to group selection. Following decline of the cheater allele, the sexual population performs better than the asexual one and eventually predominates (Figure 1 *b*).

The ratio of group benefit of cooperation to individual benefit of cheating influences the outcome of the simulations. Assuming the altruist allele to be dominant, at $a/b > 5$, the cheater becomes extinct fast and then the sexual and asexual populations coexist; between 1 and 5, only the

sexual altruists survive; between 0.1 and 1, altruist and cheater coexist in the sexual population and asexuals are driven to extinction; between 0.001 and 0.1, only the sexual cheaters survive and at $a/b < 0.001$, the altruists become extinct quickly and the sexual and asexual cheaters coexist. Assuming the cheater allele to be dominant, at $a/b > 3$, sexual and asexual altruists coexist; between 1 and 3, only sexual altruists survive; between 0.01 and 1, the sexual altruist and cheater coexist and at $a/b < 0.01$, the sexual cheater is the only survivor.

Let us now consider the second model. With cooperation among larger groups, if assemblage of individuals is random, cheaters invade and go to fixation in both sexuals and asexuals. We have shown earlier that if there is some level of spatial aggregation, altruist and cheater can

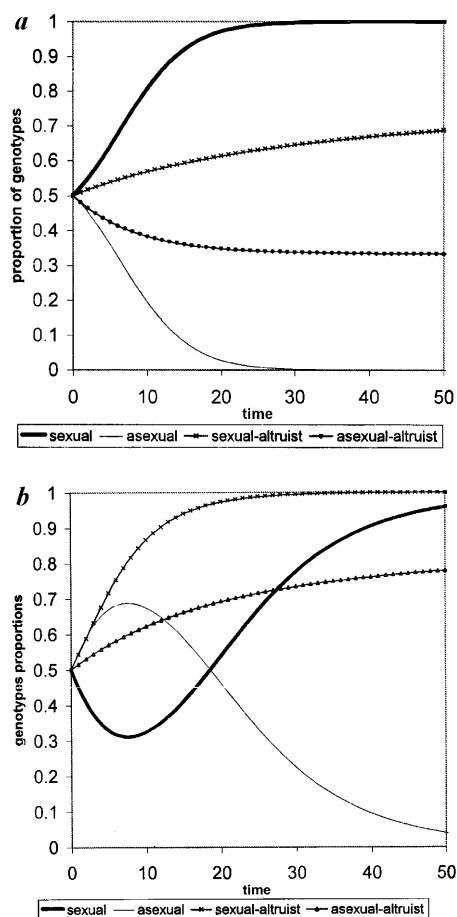


Figure 1. Population dynamics of sexual and asexual cooperating populations in the first model. Proportions of sexual and asexual populations and proportion of altruists in each are shown. Initial frequency of all the alleles is equal in the data shown, the end results were insensitive to the initial proportions of sexual and asexual. *a*, Altruist allele being dominant: Expression of cheaters is suppressed in heterozygotes giving an advantage to the sexual population. The stable population is sexual in which the altruist and cheater alleles coexist. Parameters used here are $a = 1$ and $b = 1$. *b*, Cheater allele being dominant: Sexual population suffers heavy loss initially due to overexpression of cheater in the population. However, the proportion of altruists in the sexual population increases to improve the fitness of the sexual population later on. Here $a = 1$ and $b = 0.4$.

coexist in a stable or stably oscillating proportion⁶. We model here an 'n' person cooperation with varying degree of spatial aggregation. Spatial aggregation is generated using Matapurkar and Watve algorithm developed for modelling altruist cheater dynamics in the slime mould, *Dictyostelium*⁶. In this model, a number of cells are randomly scattered over a defined area. Each cell takes a few random walk steps and divides. This, after a few generations, results in a population consisting of partially intermingling clones of cells. The degree of intermingling depends upon the initial cell density and the number of random walk steps. The population is then divided into a number of quadrats and the population in a quadrat forms one cooperative group. In this algorithm it is possible to control the degree of spatial aggregation by varying the number of random walk steps. We generalize the *Dictyostelium* model here, in which the reproductive success of the group as a whole is directly proportional to the fraction of altruists in the group in addition to the baseline success. Similar to the first model, we take the baseline success as 1 and the benefit of cooperation as *a*. The cheaters in the group get an added advantage *b*. Asexual and sexual cells in a quadrat form two separate cooperative groups. The group fitness of the asexuals is decided directly by the proportion of altruists in the group. The sexual population on the other hand, undergoes random pairing and mating. The behaviour of each heterozygous diploid cell is now decided by the dominant allele and the group fitness calculated accordingly. At the end of the cooperative act, the diploid cells undergo reduction division. The resultant populations disperse randomly again to start a new turn of the cycle.

Simulations show that the sexuals wipe-off the asexuals when the relative fitness gain due to cooperation is large and the cheaters perpetuate sufficiently long. When the random walk steps are few, the distribution of proportion of cheaters in a group is highly aggregated and group selection drives the cheaters to extinction in both sexual and asexual populations. On the other hand, when the cell dispersal is close to random and/or the advantage of cooperation is small, the cheaters go to fixation in both the populations. In either case, there is no fitness difference between sexuals and asexuals once the cheater allele either becomes extinct or gets fixed. With moderate levels of aggregation altruists and cheaters coexist⁶ and under such circumstances, sexuals gain a fitness advantage owing to mechanisms similar to the first model (Figure 2).

In the third model we depict a typical hymenopteran society consisting of a diploid queen who lays eggs; the fertilized eggs giving rise to diploid workers and the unfertilized ones giving haploid males. The males are solitary while the female workers cooperate at various levels. Certain worker bees and ants are known to lay haploid (male) or parthenogenetic diploid (female) eggs¹², and these are considered in our model to be cheaters. We model the reproductive success of altruist (*A*) and cheater (*a*) alleles in a diploid worker society in comparison with a hypotheti-

cal population with haploid workers (Table 1). For simplicity of the model, we consider that the cheater workers lay only haploid eggs.

The group benefit of cooperation (*g*) is obtained in direct proportion to the altruists in a colony. The cheater workers lay eggs with a frequency *h* to give haploid males. The cost of rearing the cheater workers is shared by the entire colony and therefore there is a corresponding reduction (*i*) in the group fitness in proportion to the cheaters. In the hypothetical haploid worker society, the fertilized eggs are assumed to undergo reduction division before giving rise to a worker so that the total gene pool remains the same as in the diploid worker society. The next generation frequencies are calculated from Table 1 as illustrated in the following two examples.

(i) Homozygous altruist queens coming from a diploid worker colony, altruist allele assumed dominant:

$$Q_{xx} = mx(1 + a)q_{xx} + (0.5 mx(1 + (mx + 0.5 my) a - 0.5 my c)q_{xy}).$$

(ii) Cheater haploid males coming from a diploid worker colony, altruist allele assumed dominant:

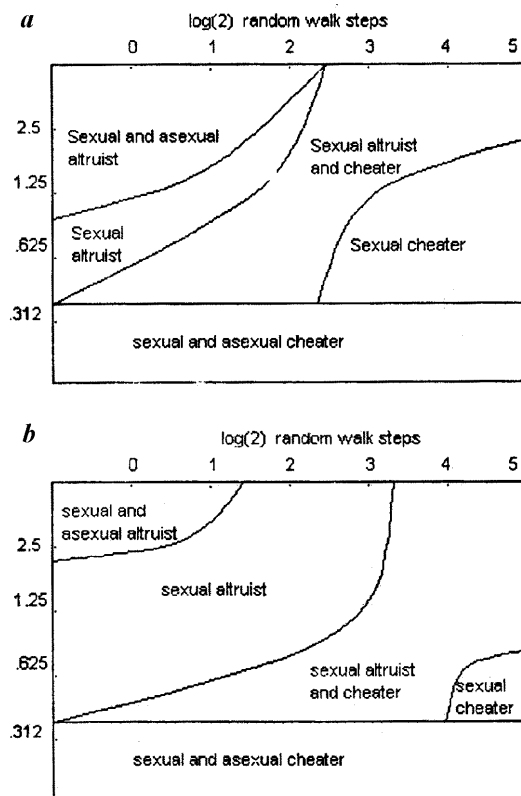


Figure 2. Parameter space over which different genotypes evolve in the second model. The number of random walk steps that govern the degree of aggregation is on the x-axis. The y-axis denotes the ratio of group benefit of cooperation to the individual benefit of cheating. **a**, Altruist allele dominant, and **b**, cheater allele dominant. Interestingly, the pattern remains the same although the precise areas of advantage change. Simulations began with a population of 100 spores each of sexuals and asexuals, each having an equal proportion of altruists and cheaters distributed over an area of 100 × 100 units.

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$$My = (1 + mx g - my i) qyy + (1 + (mx + 0.5 my) g - 0.5 my i) 0.5 qxy + (1 + (mx + 0.5 my) g - 0.5 my i) 0.5 my h qxy + (1 + mx g - my i) my h qyy.$$

All other frequencies are calculated similarly and then normalized as in the first model.

The results of the simulation are similar to the first and the second models (Figure 3 a and b). Whenever there are comparable benefits of cooperation and cheating and the altruists and cheaters coexist in the population, the diploid worker genotype outcompetes the haploid one.

Sexual diploidy in these models enhances group selection. This happens even when the cheater allele is dominant, since in groups having smaller proportion of cheaters, majority of cheaters are heterozygous and the advantage of cheating that they derive is shared equally by the altruist allele. Whereas in groups with cheater majority, homozygous altruist is rare and therefore the fitness of the entire group is small. As a result, cheaters are rapidly driven to extinction or exist in proportions much smaller compared to the asexual population. The other role sex plays is to increase the phenotypic variance across groups and this works in both dominant and recessive conditions. Increase in variance between groups helps group selection. In all the

models, no fitness difference between the sexual and asexual populations is assumed, except that gained by cooperation. Therefore evolution of sex in the model is solely due to the altruist cheater dynamics. On the other hand, wherever cooperation stabilizes, sex is the major stabilizing force. Under no conditions can the asexual altruist alone stabilize. Similarity of results in all the models demonstrates the generality and robustness of this principle.

The results of all the models suggest that sex helps stabilize cooperation and therefore cooperation can be expected to be more frequent in sexual species. On the other hand, the need for cooperation can act as a selective force for the evolution of sex. Both sex and cooperation are multidimensional processes and a variety of selective forces must be involved in their evolution. The model is not incompatible with any of the existing models for the evolution of sex as well as cooperation. Cooperation is certainly not the sole driving force behind evolution and maintenance of sex and vice versa. The interaction of the two processes, nevertheless, could have helped stabilize both.

Two testable predictions of the model are (i) altruism should be seen more frequently in sexually reproducing organisms compared to asexually reproducing organisms,

Table 1. Proportion and fitness of altruist (A) and cheater (a) alleles in a hymenopteran society; 1b the workers are assumed to be haploid arising after meiosis in fertilized eggs

| Altruist dominant – workers diploid | | | | | | | |
|--|-----------------------------------|---------------|---|---------------------|--------------------------|--------------------------------|--------------------|
| Parental Queen | | | | | | | |
| | AA (qxx) | | Aa (qxy) | | | aa (qyy) | |
| Workers | AA (mx) | Aa (my) | AA (0.5 mx) | Aa (0.5 mx) | aa (0.5 my) + 0.5 my) | Aa (mx) | aa (my) |
| Progeny queens | AA (mx) | Aa (my) | AA (0.5mx) | Aa (0.5 mx) | aa (0.5 my) + 0.5 my) | Aa (mx) | aa (my) |
| Progeny males | A (qxx) | | A (0.5 qxy) | | | a (0.5 qxy) | |
| Males from cheater workers | 0 | | A (0.5 my) | | | A (my) | |
| Group fitness | (1 + g) | | 1 + (mx + 0.5*my)*a – (0.5*my*i) | | | 1 + mx*a – my*I | |
| Altruist dominant – workers haploid (after meiosis in fertilized eggs) | | | | | | | |
| Parental Queen | | | | | | | |
| | AA (qxx) | | Aa (qxy) | | | aa (qyy) | |
| Workers | A (0.5 + 0.5 mx) | a (0.5 my) | A (0.25 + 0.5mx) | a (0.25 + 0.5my) | | A (0.5 mx) | a (my + 0.5 mx) |
| Progeny queens | AA (mx) | Aa (my) | AA (0.5mx) | Aa (0.5mx) | aa (0.5my) + 0.5my) | Aa (mx) | aa (my) |
| Progeny males | A (qxx) | | A (0.5*qxy) | | | a (0.5*qxy) | |
| Males from cheater workers | (0.5 my) | | (0.75my + 0.25mx) | | | (my + 0.5 mx) | |
| Group fitness | 1 + (0.5 + 0.5*mx)*g – (0.5*my*i) | | 1 + (0.25 + 0.5*mx)*g – (0.25 + 0.5*my)*i | | | 1 + 0.5*mx*g – (0.5*mx + my)*i | |

mx, Proportion of A males; my = Proportion of a males; x, Proportion of A alleles in queens and y, Proportion of a alleles in queens. Initially, Qxx = x², Qxy = 2xy and Qyy = y². The new generation proportion of males and queens is calculated by multiplying the probabilities of each genotype by the group fitness and normalizing. Only the altruist dominant case is shown.

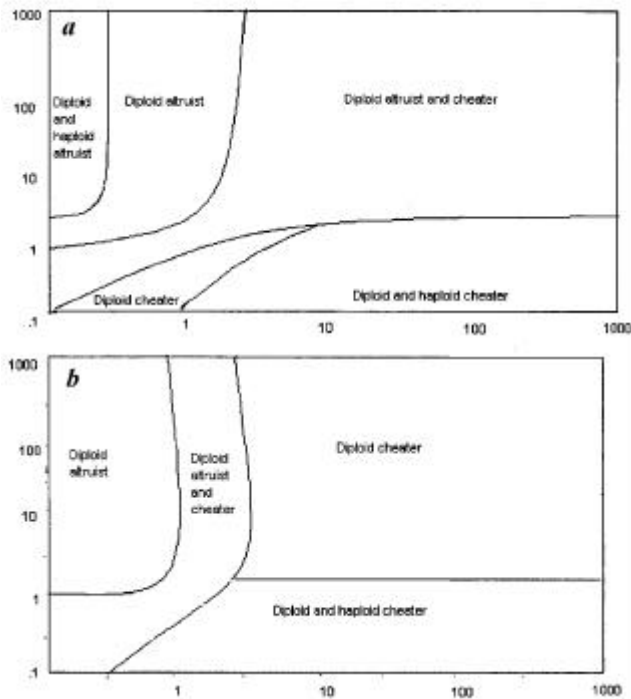


Figure 3. Parameter space (denoting group benefit of cooperation on the x-axis and individual benefit of cheating on the y-axis) over which different genotypes evolve in the third model. *a*, Altruist allele dominant and *b*, cheater allele dominant. Like the second model, the patterns are similar in both altruist and cheater dominant cases, although the underlying mechanisms are different.

and (ii) among organisms which have diploid and haploid stages in their life cycle, cooperation should be more common in the diploid stages than the haploid ones. Just a few examples of altruism, cooperation or eusociality are known among predominantly asexual taxa, particularly prokaryotes. The renewed interest in the social life of microorganisms might bring out a number of novel examples of cooperation in bacteria¹³. At this stage, therefore, the available data are inadequate to test the first prediction quantitatively. Among the well-known examples of sociality in microorganisms are fruiting body formation in Myxobacteria and slime moulds. In both the examples, cheaters have been shown to occur frequently in natural populations (Watve, M. G., unpublished)¹⁻³. Sexual reproduction is not known in Myxobacteria, but is known to occur in *Dictyostelium*¹⁴. Studies on sexual reproduction in *Dictyostelium* are scanty, but apparently the ratio of cells sacrificed per spore produced is much larger in sexual spore formation compared to asexual spore formation¹⁴. In basidiomycetes and ascomycetes, more complex stages showing a greater degree of division of labour among cells and a greater proportion of sterile cells are diploid and the simpler stages haploid. These examples fit well into the predictions of the model, qualitatively. It is difficult to test the prediction quantitatively with available data. However, the picture in hymenopterans is clearcut, in that all cooperative stages are necessarily diploid, while no haploid stage is known to cooperate.

Another speculation arising out of the model is that primitive multicellularity might have been similar to that seen in cellular slime moulds, where polyclonal cooperation could be inevitable. This might have been the right situation for sex and cooperation to coevolve leading to an association between multicellularity and sex. Such an association might have persisted in spite of the nature of multicellularity as well as that of sex changing in the course of evolution. As a result, the unicellular taxa are predominantly asexual and the multicellular ones have a large proportion of sexually reproducing species.

1. Buss, L. W., *Proc. Natl. Acad. Sci. USA*, 1982, **79**, 5337–5341.
2. Strassmann, J. E., Zhu, Y. and Queller, D. C., *Nature*, 2000, **408**, 965–967.
3. Velicer, G. J., Kroos, L. and Lenski, R. E., *Nature*, 2000, **404**, 598–601.
4. Axelrod, R. M., *The Evolution of Cooperation*. Basic Books, New York, 1984.
5. Armstrong, D. P., *J. Theor. Biol.*, 1984, **109**, 271–283.
6. Matapurkar, A. K., and Watve, M. G., *Am. Nat.*, 1997, **150**, 790–797.
7. Kessin, R. H., *Nature*, 2000, **408**, 917–918.
8. Frank, S. A., *Nature*, 1995, **377**, 520–522.
9. Kondrashov, A. S., *J. Hered.*, 1993, **84**, 372–387.
10. Barton, N. H. and Charlesworth, B., *Science*, 1998, **281**, 1986–1990.
11. Maynard-Smith, J. and Szathmari, E. *The Major Transitions in Evolution*, W. H. Freeman & Co. Ltd, Oxford, 1995.
12. Gadagkar, R., *Curr. Sci.*, 1997, **72**, 950–956.
13. Crespi, B. J., *TREE*, 2001, **16**, 178–183.
14. Bozzone, D. M. and Bonner, J. T., *J. Exp. Zool.*, 1982, **220**, 391–394.

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Fuzzy rule-based system for prediction of direct action avalanches

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Rule-based systems are widely being used in decision making, control systems and forecasting. In the real world much of the knowledge is imprecise, uncertain, ambiguous and inexact in nature. Fuzzy logic offers a better way to represent complicated situations in terms of simple natural language.

Here an attempt has been made to develop a rule-base for prediction of direct action avalanches of Chowkibal–Tangdhar road axis (Jammu and Kashmir) in Indian Himalaya using fuzzy logic. The condition

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