



Figure 1. Stability diagram of phases in the $K_2O-Al_2O_3-SiO_2-H_2O$ system.

decrease in particle size was also reported⁹ in alluvial soils of Haryana and Uttar Pradesh.

The study reveals that aridity of climate and sodicity have played a vital role in the distribution of K in the soil and different fractions.

1. Somasiri, S. and Huang, P. M., *Soil Sci. Soc. Am. Proc.*, 1971, 35, 810.
2. Dubey, D. D., Gupta, S. and Sharma, O. P., *J. Indian Soc. Soil Sci.*, 1986, 34.
3. Richards, L. A. (ed.), *Agricultural Handbook 60*, US Dept Agriculture, Washington, D.C., 1954.
4. Jackson, M. L. *Soil Chemical Analysis*, Prentice Hall India, New Delhi, 1967.
5. Kiely, P. V. and Jackson, M. L., *Proc. Soil Sci. Soc. Am.*, 1965, 29, 159.
6. Marshall, C. E., *The Physical Chemistry and Mineralogy of Soil*, vol. II, John Wiley and Sons, New York, 1977.
7. Choudhari, J. S. and Jain, S. V., *J. Indian Soc. Soil Sci.*, 1979, 27, 123.
8. Malavolta, E., *Potassium in Agriculture* (ed. Munson, R. D.), American Society of Agronomy, Crop Science Society of America and Soil Science of America, Madison W.I., USA, 1985.
9. Maheshwari, R. K. and Sekhon, G. S., *Clay Res.*, 1985, 4, 1.
10. Sparks, D. L. and Jardine, P. M., *Soil Sci. Soc. Am. J.*, 1981, 45, 1094.
11. Sparks, D. L. and Huang, P. M., *Potassium in Agriculture* (ed. Munson, R. D.), American Society of Agronomy, Crop Science Society of America and Soil Science Society of America, Madison, W.I., USA, 1985.
12. Jardine, P. M. and Sparks, D. L., *Soil Sci. Soc. Am. J.*, 1984, 47, 45.
13. Fanning, D. S. and Keramidas, V. Z., in *Minerals in Soil Environments* (eds. Dixon, J. B. and Weed, S. B.), Soil Science Society of America, Madison, W.I., USA, 1977.
14. Huang, P. M., in *Minerals in Soil Environments* (ed. Dixon, J. B. and Weed, S. B.), Soil Science Society of America, Madison, W.I., USA, 1977.

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The haplodiploidy threshold and social evolution

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Workers in eusocial insect species help in rearing their siblings and other genetic relatives instead of producing their own offspring. The multiple origins of such eusociality in the Hymenoptera have been ascribed to haplodiploidy because this genetic system makes a female more closely related to her full sisters than she would be to her offspring. To test this so called haplodiploidy hypothesis, I first assume that workers are capable of investing in their sisters and brothers in the ratio that is optimal for them. I then define a *haplodiploidy threshold* as that value of genetic relatedness between workers and their sisters such that they have a weighted average relatedness to the brood they rear of 0.5 and thus have the same fitness as solitary nesting females. Using 177 published estimates of relatedness between sisters in social hymenopteran colonies, I show that in 29 out of 35 species studied, there is not even one estimate of relatedness that is significantly higher than the haplodiploidy threshold. I conclude therefore that the multiple origins of eusociality in the Hymenoptera cannot be ascribed solely to the genetic asymmetry created by haplodiploidy.

EUSOCIAL insects such as termites, ants and many species of bees and wasps exhibit three characteristic features namely, overlap of generations, co-operative brood care and caste differentiation into fertile reproductive castes and sterile worker castes^{1,2}. These sterile worker castes present an obvious challenge to Darwin's theory of natural selection³. The seminal work of Hamilton^{4,5} was the first serious attempt to meet this challenge. Hamilton developed the concept of inclusive fitness and showed that fitness can also be gained by helping genetic relatives in addition to or, indeed, instead of producing offspring.

One reason for the instant appeal of Hamilton's ideas was that the haplodiploid genetic system found in the insect order Hymenoptera creates an asymmetry in genetic relatedness such that full sisters are more closely related to each other (coefficient of genetic relatedness, $r=0.75$) than a female would be to her offspring, ($r=0.5$). In the light of this, it is striking that eusociality is known to have arisen at least eleven times independently in the Hymenoptera compared to only twice (once in the termites and once in the naked mole rat) outside that insect order^{2,6}. This idea that the genetic asymmetry created by haplodiploidy can promote the evolution of eusociality in the Hymenoptera may be termed the haplodiploidy hypothesis.

There are however at least two hurdles that have to

be overcome before the haplodiploidy hypothesis becomes plausible. The first is that although hymenopteran females are related to their full sisters by 0.75, they are related to their brothers merely by 0.25. A hymenopteran worker who rears equal numbers of sisters and brothers has therefore no advantage over a solitary nest foundress because her average relatedness to the brood she rears is equal to 0.5. Trivers and Hare⁷ suggested that this hurdle can be overcome if workers discriminate between their sisters and brothers and bias their investment in favour of sisters. A combination of Fisher's sex ratio theory^{8,9} and Hamilton's kin selection theory^{3,4} predicts that a ratio of investment between female and male broods which is equal to the ratio of relatedness to the two classes of brood is evolutionarily stable from the worker's point of view¹⁰⁻¹⁵. There is however considerable controversy about whether investment is under the control of workers and whether workers in fact achieve the ratio of investment that is optimal for them¹⁶⁻¹⁸.

The second hurdle is that many hymenopteran females mate with more than one male, store sperm in their spermathecae and produce different patrines of daughters who are related to each other by 0.25 (ref. 19-22). This again reduces the inclusive fitness that workers can potentially gain. Whether the genetic asymmetry created by haplodiploidy is by itself sufficient to allow workers to have more inclusive fitness than solitary foundresses thus depends on their relatedness to their sisters and on their ability to skew investment in favour of sisters. A number of estimates of genetic relatedness between sisters in hymenopteran colonies have now been published. However an objective test of whether the genetic asymmetry created by haplodiploidy by itself can select for worker behaviour has not been performed. To test the *haplodiploidy hypothesis* I first assume that workers are capable of investing in their brothers and sisters in the ratio that is optimal for them, namely, in the ratio of their genetic relatedness to their sisters and brothers. I then compute the threshold relatedness to sisters required for workers to obtain a weighted mean relatedness to siblings of 0.5 and thus break even with solitary foundresses.

The optimum number of females that a worker should rear relative to every male reared is given by r_f/r_m where r_f is her mean relatedness to female brood and r_m is the relatedness to male brood. When workers successfully skew investment between females and males in the ratio $r_f/r_m:1$, their weighted mean genetic relatedness to the brood they rear is given by

$$\bar{r} = [(r_f^2/r_m) + r_m] / [(r_f/r_m) + 1]. \quad (1)$$

In an outbred hymenopteran population where workers rear mixtures of sisters and brothers, r_m is expected to be 0.25 and the relatedness between a

solitary nesting female and her offspring is expected to be 0.5.

To thus solve eq. (1) for $\bar{r}=0.5$, I rewrite it as

$$16r_f^2 - 8r_f - 1 = 0. \quad (2)$$

Eq. (2) yields a value of 0.604 for r_f . This means that a genetic relatedness between workers and their sisters of 0.604 is required if workers are to gain as much fitness as solitary individuals *inspite of skewing investment between sisters and brothers* in the ratio that is optimal for them. I will call 0.604 the *haplodiploidy threshold*.

Most published estimates of genetic relatedness are accompanied by standard errors and it is therefore possible to ask if these estimates are significantly greater than the haplodiploidy threshold. Of 177 such estimates (spread over 35 species) of relatedness between sisters, only 22 estimates are significantly higher than the haplodiploidy threshold ($P < 0.05$). Of these, 5 pertain to ants, 4 to primitively eusocial bees and 13 to primitively eusocial wasps. Of 20 species of highly eusocial hymenopterans studied only three have at least one estimate significantly higher than the haplodiploidy threshold (Table 1). I conclude from this that the *genetic asymmetry created by haplodiploidy is by itself insufficient to maintain the highly eusocial state*. Of 15 species of primitively eusocial hymenopterans studied only 3 have at least one estimate significantly higher than the haplodiploidy threshold (Table 1). I conclude from this that the *genetic asymmetry created by haplodiploidy is by itself insufficient to promote the origin of eusociality*.

Thus only 6 out of the 35 species of social hymenopterans studied have at least one estimate of genetic relatedness between sisters that is high enough for haplodiploidy by itself to select for worker behaviour. It is therefore quite unreasonable to ascribe the multiple origins of eusociality in the Hymenoptera solely to the genetic asymmetry created by haplodiploidy. In computing the haplodiploidy threshold I have assumed outbreeding. This appears to be reasonable for most species used in the analysis. I have also assumed that

Table 1. A test of the haplodiploidy hypothesis.

Group	No. of species for which estimates of genetic relatedness between sisters, with standard errors, are available	No. of species for which at least one estimate is significantly greater than the haplodiploidy threshold
Ants	15	3
Vespine wasps	2	0
Swarm-founding wasps	3	0
Primitively eusocial bees	2	1
Primitively eusocial wasps	13	2
Total	35	6

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workers are capable of skewing investment between female and male brood in the ratio that is optimal for them. This may or may not hold. If it does not, then I am giving an unfair advantage to the haplodiploidy hypothesis. But that is just as well because it makes my falsification of the haplodiploidy hypothesis more robust.

1. Michener, C. D., *Annu. Rev. Entomol.*, 1969, **14**, 299.
2. Wilson, E. O., *The Insect Societies*, Harvard University Press, Cambridge, 1971.
3. Darwin, C., *The Origin of Species*, Collier Books, New York, 1859, p. 268.
4. Hamilton, W. D., *J. Theor. Biol.*, 1964a, **7**, 1.
5. Hamilton, W. D., *J. Theor. Biol.*, 1964b, **7**, 17.
6. Trivers, R., *Social Evolution*, The Benjamin/Cummings Publishing Company, California, 1985.
7. Trivers, R. L. and Hare, H., *Science*, 1976, **191**, 249.
8. Fisher, R. A., *The Genetical Theory of Natural Selection*, Oxford University Press, Oxford, 1930.
9. Charnov, E. L., *The Theory of Sex Allocation*, Princeton University Press, Princeton, 1982.

10. Oster, G., Eshel, I. and Cohen, D., *Theor. Popul. Biol.*, 1977, **12**, 49.
11. Macnair, M. R., *J. Theor. Biol.*, 1978, **70**, 449.
12. Craig, R., *Am. Nat.*, 1980, **116**, 331.
13. Uyenoyama, M. and Bengtsson, B. O., *Theor. Popul. Biol.*, 1981, **20**, 57.
14. Charnov, E. L., *Am. Nat.*, 1978, **112**, 317.
15. Joshi, N. V. and Gadagkar, R., *J. Genet.*, 1985, **64**, 41.
16. Alexander, R. D. and Sherman, P. W., *Science*, 1977, **196**, 494.
17. Nonacs, P., *Q. Rev. Biol.*, 1986, **61**, 1.
18. Boomsma, J. J., *Am. Nat.*, 1989, **133**, 517.
19. Page, R. E. Jr., *Annu. Rev. Entomol.*, 1982, **31**, 297.
20. Starr, C. K., *Sperm Competition, Kinship and Sociality in the Aculeate Hymenoptera* (ed. Smith, R. L.), Academic Press, p. 427.
21. Gadagkar, R., *Proc. Indian Acad. Sci., Anim. Sci.*, 1985, **94**, 587.
22. Muralidharan, K., Shaila, M. S. and Gadagkar, R., *J. Genet.*, 1986, **65**, 153.

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Effect of dietary citrate in reducing housefly resistance to insecticides

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Toxicity of four insecticides, permethrin, bromophos, malathion and lindane, to citric acid-fed houseflies was studied up to F₂ generation using topical application. The results indicated a gradual fall in LD₅₀ values of all the four insecticides thereby suggesting a role of citric acid in reducing insect resistance to insecticides.

CHEMICAL substances fed to insects through diet have a bearing on insect life-span and agility which can alter

the insect resistance to insecticides. Also marked age and stage variations in resistance to insecticides are noted in insects. Thus the resistance is negligible in embryonic stage, high in larval stage and again low in pupal stage. After adult emergence, depending upon the species, the resistance increases initially, remains stable and declines with age^{1,2}. Since the resistance declines with age and an age-associated increase in citric acid has been reported in musca and cerialitis³, we decided to study the effect of citric acid feeding in altering housefly resistance to insecticides. We fed citric acid to houseflies through diet up to F₂ generation and studied the toxicity of four insecticides, permethrin (Indian Explosives), malathion (Cyanamid India) bromophos and lindane (E. Merck, India), to these citric acid-fed

Table 1. Toxicity of four insecticides to citric acid-fed houseflies.

Insecticides	Houseflies*	Regression equation	LD ₅₀ (ng/fly)
Permethrin	Normal	$y = 1.1319 + 2.6131 x$	30.0
	Fed CA for 3 days	$y = 0.8021 + 3.149 x$	21.53
	CA-fed F ₁ generation	$y = 3.2806 + 1.3876 x$	17.35
	CA-fed F ₂ generation	$y = 0.188 + 5.0305 x$	10.75
Bromophos	Normal	$y = 0.3323 + 2.145 x$	150.0
	Fed CA for 3 days	$y = 1.6481 + 1.7021 x$	93.15
	CA-fed F ₁ generation	$y = 1.2128 + 2.1167 x$	61.55
	CA-fed F ₂ generation	$y = 0.1963 + 3.015 x$	39.19
Malathion	Normal	$y = 2.1718 + 0.8773 x$	1674.0
	Fed CA for 3 days	$y = 1.0627 + 1.3374 x$	878.8
	CA-fed F ₁ generation	$y = 2.2678 + 0.9826 x$	603.3
	CA-fed F ₂ generation	$y = 2.086 + 1.1132 x$	414.6
Lindane	Normal	$y = 1.1976 + 1.1888 x$	1580.0
	Fed CA for 3 days	$y = 1.1835 + 1.3136 x$	804.2
	CA-fed F ₁ generation	$y = 0.7989 + 1.5512 x$	510.9
	CA-fed F ₂ generation	$y = 1.3845 + 1.4225 x$	348.1

*3 to 4 days old female flies were used.
CA, Citric acid.