cofactor); the majority of the Fe is present in Fe—S clusters that are in a highly reduced state and which are in a less exposed position than is the MoFe cofactor.

A point made by both J. Chatt and R. H. Burris (University of Wisconsin, Madison) was that nitrogenase has different affinities for the substrates N_2, H_2 and C_2H_2 depending on its oxidation state. Since the reduction of C_2H_2 to C_2H_4 is often used to assay nitrogenase activity it follows that it is not straightforward to extrapolate the values obtained from this assay to calculate absolute amounts of nitrogen that are being fixed.

Burris also referred to the fact that in *Rhodospirillum* and in *Azospirillum* the success in isolating the Fe-containing nitrogenase component is variable in different laboratories. It seems that there is an inactive form of the protein which can be activated by enzymatic removal of moieties (possibly adenine) and that the occurrence of the active or inactive forms depends upon the growth medium.

Nitrogenase needs a source of energy and electrons for reducing power. H. Haaker (Agricultural University, Wageningen) proposed that in *Azotobacter vinelandii* and in the bacteroids of *Rhizobium leguminosarum* the transport of electrons to nitrogenase depends upon the electrical component ($\Delta\psi$) of the proton motive force since there was a correlation between the value of $\Delta\psi$ and nitrogenase activity. In free-living nitrogen fixing bacteria, NH_4^+ is a potent repressor of nitrogenase but in the case of *Rhizobium* bacteroids, nitrogenase is relatively immune to NH_4^+ repression. Interestingly, the addition of NH_4^+ to *A. vinelandii* caused a drop in $\Delta\psi$ but the $\Delta\psi$ of *Rhizobium* bacteroids was immune to the addition of NH_4^+.

There are some bacteria that are doubly blessed in that they can fix nitrogen and can obtain the energy for fixation by photosynthesis. J. R. Gallon (University College of Swansea) considered whether in the case of blue green algae, photosynthesis could directly provide ATP and reductant to nitrogenase. Some evidence to support this came from the finding that inhibition of photosystem II rapidly inhibited nitrogenase activity in *Gloeocapsa*. However nitrogenase activity was quickly restored and it was suggested that this recovery was due to the switch on by another, non-photosynthetic, source of energy.

Bacteria that are fixing nitrogen liberate gaseous H_2 due to the reduction of protons by nitrogenase. Many species possess a hydrogenase that can be used to recoup some of the energy that would otherwise be lost. H. J. Evans (Oregon State University) discussed the hydrogenase system in *Rhizobium japonicum* in which the enzyme is sufficiently active to allow autotrophic growth on hydrogen as sole energy source. The fact that when hydrogenase-deficient mutants were used to inoculate soybeans the yields were about 30% less than when wild-type strains were used shows that the hydrogenase system is of real agronomic importance.

The developments in the genetics of nitrogen fixation were discussed by a number of speakers. The most detailed analyses have been on the *nif* gene cluster of *Klebsiella pneumoniae* and these were

Squirrels kill kids but are nice to relatives

from John Krebs

BELDING's Ground Squirrel (*Spermophilus beldingi*) conceals a vicious habit beneath its charming, furry coat. P. W. Sherman has studied a population of 250-300 of these little beasts high up in the Sierra Mountains of California since 1974, and he reported on some of his results at the XVI Ethological Congress.* The squirrels hibernate underground beneath the snow for about 8 months of the year and have a brief reproductive season during the months of May-August. Their life is a tough one as might be expected from such an extreme environment: 54-93% of juveniles and 23-68% of adults die during winter hibernation, and the survivors have to face the dangers of numerous nocturnal (coyotes, and bears) and diurnal (raptorial birds, weasels and coyotes) predators, as well as the risk of being run over by a passing car. These kinds of natural hazards are well known as causes of death in natural populations of many species, but more unusual is the fact that a considerable number of young squirrels die as a result of infanticide. About 8% of all young are dragged from their burrows by adult squirrels and killed before their mothers can come to the rescue. Sherman's detailed analyses of the causes and consequences of infanticide lead him to the following conclusions.

Adult females and yearling males are the commonest killers. Adult females kill when their own young have been destroyed by predators: the bereaved mother moves to a new place (choosing carefully to go to a place less susceptible to predator attack) and tries to kill the young of a mother in the area. If she is successful in killing young the female settles near the burrow of her victims. It seems, therefore, that infanticide by adult females is a form of competition: the female removes potential future competitors by disposing of her new neighbour's young. The young male killers, unlike the adult females, eat their victims, and Sherman suggests that the benefit derived is simply that baby ground squirrel is a good source of protein for a growing lad. A young male's future survival and reproductive success in this highly polygynous species depends heavily on fighting ability and hence body size (Sherman in *Natural selection and social behaviour: recent research and new theory.* (Alexander & Tinkle eds.) Chiron Press 1979).

Thus infanticide is far from being a pathological behaviour shown by a few squirrels under abnormal conditions; it is a normal part of the day-to-day business of competition and survival. Female squirrels with young are highly territorial during the period in which their infants are helpless to defend themselves, and mothers with large territories have the lowest risk of infanticide, which suggests that territory defence might be an anti-infanticide device.

Belding's Ground Squirrels are not, however, universally nasty: close relatives are nice to each other. The squirrel society is matrilineal. Females pass on bits of their defended home area to daughters while males disperse well away from home soon after weaning. Sherman's accurate data on kinship enabled him to show that close female relatives cooperate with each other in a number of ways. They share parts of their territories, do not attack each other very often, and help each other in guarding their burrows against infanticidal intruders. Mothers also put themselves at a demonstrable risk when a predator approaches by giving alarm calls to warn close relatives of the danger (Sherman *Science* **197**, 1246; 1977). Squirrels without close relatives in the vicinity (males and transient females) do not give alarm calls, which is consistent with the fact that they do not stand to make a genetic profit by self-sacrifice.

Sherman's unique and impressive data show that altruism (or nepotism as he prefers to call it) occurs between close relatives. This is to be expected since an altruist's genes are propagated not just through children but also through other relatives, and some would argue that Sherman's data are a good test of the theory of kin selection. In a sense, however, the theory is not testable. It is a logical generalisation of the theory of Natural Selection and is not one of a number of alternative, refutable hypotheses. However, an example of the kind of interesting question which arises from kin selection theory is Sherman's observation (*Nat. Hist.* **88**, 80; 1979) that while mothers, daughters and sisters show nepotism towards one another, more distant relatives such as aunts and nieces or grandmothers and granddaughters do not. As Sherman puts it, the reasons for this limit to nepotism remain an enigma.

John Krebs is a Lecturer in Zoology in the Edward Grey Institute of Field Ornithology, University of Oxford.

*The XVI International Ethological Congress was held in Vancouver, BC, Canada, 18-27 August, 1979.