



across the snow-covered plateau stretches all the way to the horizon, and the sastrugi – ridges in the snow whipped up by the wind – look like waves on a white ocean.

For all that, the South Pole remains one of the remotest places on Earth. The station is dependent on flights from the McMurdo station 3 hours away for everything from food and fuel to heavy machinery, and these can be grounded by bad weather. Serious medical problems require evacuation to New Zealand, a considerable effort during the summer and a near impossibility in winter, when temperatures can reach -75 °C. “You can’t really ever get complacent when you work here,” says area director Bettie Grant. “As soon as you do, this place will reach out and kick your butt.” ●

**“Edward Wilson thinks kin selection is a special, complex kind of natural selection, which it is not”**

# The group delusion

It is wrong to invoke group selection as an explanation for altruism in social insects, says **Richard Dawkins**

EDWARD WILSON has given us a characteristically fascinating account of the evolution of social insects (see page 6 and *BioScience*, vol 58, p 17). But his “group selection” terminology is misleading, and his distinction between “kin selection” and “individual direct selection” is empty.

What matters is gene selection. All we need ask of a purportedly adaptive trait is, “What makes a gene for that trait increase in frequency?” Wilson wrongly implies that explanations should resort to kin selection only when “direct” selection fails. Here he falls for the first of my “12 misunderstandings of kin selection”; that is, he thinks it is a special, complex kind of natural selection, which it is not.

In the true sense of kin selection, offspring are “kin” just as siblings are. Parental care and sibling care both evolve because copies of genes for caring are present in beneficiaries. Genes promoting feeding of larvae by sterile workers are passed on by those larvae – sisters, nephews, and so on – destined to become reproductives. That’s kin selection, and it maintains sterile worker castes in insect colonies. Wilson could not dispute that.

What he does dispute – perhaps correctly – is that eusociality originated through related females clubbing together because of kinship. It could also originate through unrelated females nesting together. But to call this “group selection” is massively confusing. A better approach is John Maynard Smith’s concept of evolutionarily stable strategies (ESS). “Stable” means that when most individuals follow the strategy, no alternative does better. If “breed cooperatively” were a stable strategy for unrelated females, this would furnish a good preadaptation for the evolution of eusociality.

Jane Brockmann, now at the University of Florida, Gainesville, and I explored this with an ESS model developed with Alan Grafen of the University of Oxford, using Brockmann’s fieldwork on solitary

digger wasps, *Sphex ichneumoneus*. When following the “dig” strategy, a female digs a burrow, provisions it with prey on which she lays a single egg, seals the burrow and departs. But burrows may be abandoned and this opens the way for an alternative strategy: “enter” an existing burrow and take it over, saving the time and effort of digging. The disadvantage is that the original owner may not have abandoned the burrow, and you run the risk of a dangerous fight. So the decision whether to enter or dig is a gamble.

With too much entering in the population, not enough new burrows get dug and chances rise that a given burrow will be occupied. Selection would therefore favour digging. With too much digging, many abandoned burrows go begging, and individuals should enter instead. Grafen’s ESS model predicted an equilibrium frequency of digging versus entering with equal benefits to each. Brockmann’s field measurements were rich enough to test this prediction, and it was, with reservations, fulfilled.

Brockmann and I then postulated an ecological “landscape” over which the parameters governing Grafen’s model might vary. A change in ecological conditions might move digger wasps from an “aggressive space” strategy, as used by *S. ichneumoneus*, to “tolerant space” – where diggers benefit from being joined by an enterer. From here there is a smooth gradient to “cooperative space”, where both parties benefit from sharing. Our review of the literature uncovered wasp species that apparently take such intermediate positions. From here, the evolutionary journey to full eusociality is easy.

Revealingly, Wilson’s great book *Sociobiology* allots only four sentences – in the chapter on group selection – to ESS theory. Kin selection is also here, as a form of group selection! Evidently Wilson’s weird infatuation with “group selection” goes way back: unfortunate in a biologist who is so justly influential. ●