since Liebllich *et al.*, found a small but definite difference in elution of the tumour α subunit during gel filtration compared with the pregnancy subunit. A slightly increased molecular weight could account for this discrepancy, although glycoproteins often behave abnormally during gel filtration chromatography. Weintraub *et al.* (*J. clin. Invest.*, **56**, 1043–1052; 1975) showed similar abnormal properties for α subunits secreted by the Gha-Go cell line. In gel chromatography the Gha-Go subunit behaved as a protein of 27,000–30,000 apparent molecular weight, significantly higher than the α subunit found in pregnancy (23,000–24,000 apparent molecular weight). Thus,

there seems to be an increase in the size of α subunit made by tumours. It may be that this material represents a precursor form present only transiently in the production of normal α subunit and HCG by placental cells. Interestingly, the Gha-Go tumour α subunit could not form biologically active HCG when incubated with HCG β subunit and tested in a rat testis radioreceptor assay. By contrast HCG α subunit from pregnancy urine combined efficiently with HCG β subunit to reconstitute 95% or more of the expected HCG activity under the same conditions. It seems therefore that tumour α subunits may be defective in a stage leading to functional HCG molecules. The mole-

cular basis for the difference is presently unknown. It is possible that the α subunits are degraded in some way by tumour-specific proteases, although this seems unlikely from their apparently greater molecular size compared with the subunit of pregnancy urine. Their amino acid compositions are also very similar to pregnancy α subunit except for small differences in some residues, particularly valine, phenylalanine and half cystine. Perhaps further analysis by peptide mapping or comparison of carbohydrate contents might suggest the structural differences between biologically active α subunit and the apparently inactive product of tumour cells. □

As a general rule, animals settle disputes with other members of the species by means of ritualised displays rather than by physical violence. In contests for food, territories and mates, raised crests and songs serve as substitutes for teeth and claws, and the loser retreats unscathed. This much is well known, but it is less clear why the ritualised communication system does not break down because of cheating. It is easy to imagine that the winner of a ritualised fight could save itself the risk of future harassment by killing the loser, yet even animals with powerful jaws or horns rarely do this; instead they play by the rules. Similarly, if a dominant individual claims a territory by, for example, loud song, why do submissive individuals not bluff their way to success by singing?

The first attempt at a formal theoretical analysis of these problems was made a few years ago by John Maynard Smith (*Nature*, **246**, 15; 1973; *On Evolution*, Oliver and Boyd, 1972). Using game theory, Maynard Smith was able to analyse why physical violence (which he calls escalated fighting) does not replace the 'conventional' system of ritualised signals. His method of analysis was to look for an evolutionarily stable strategy, or ESS. An ESS is defined as a strategy which, when it is used by the majority of individuals in a population cannot be bettered by any alternative rare 'mutant' strategy. The 'strategies' which Maynard Smith considered included such alternatives as 'hawk'—an individual which always escalates—and 'mouse', which only plays the conventional game and retreats at the first sign of violence. He then assigned payoffs for winning, losing, getting injured in an escalated fight and so on, and used these values to construct a payoff matrix for each strategy against all others, including itself. It is intuitively clear that the

hawk strategy does very well against a mouse, but does poorly in a population made up mainly of other hawks, because the risk of injury is high, so it is not an ESS. Only in the extreme case where losing a contest means certain death, say from starvation, will hawk persist as the best strategy. Otherwise the most likely ESS, for a wide variety of payoff values, was a mixed strategy of mainly ritualised display, but with escalation in retaliation to violence by an opponent. Fortunately, this seems to be the

Why don't animals cheat?

from John Krebs

common pattern of contest in real animals. In another model Maynard Smith (*J. theor. Biol.*, **47**, 209; 1974) showed that if a species has no method of escalating (because it does not possess dangerous weapons) so that the main cost involved in a contest is time, the ESS is again a mixed one with the distribution of persistence times given by the expression $(1/v) \exp(-x/v)$ where v is the value of winning and x the persistence time.

In a recent paper, Maynard Smith and Parker (*Anim. Behav.*, **24**, 159; 1976) have taken the analysis a step further by considering combats in which there is an asymmetry. In the real world two contestants will rarely be identical; one may be larger than the other, or may have more to lose, say because it has invested effort beforehand in establishing a territory.

In the latter case, where the payoffs are unequal, it is an ESS for the individual with more to lose (the territory holder for example) to invest more in the contest. Although there is a 'paradoxical' ESS in which the intruder invests more, Maynard Smith and Parker show that this ESS

is unlikely to occur in nature, because, unlike the common sense ESS, the 'paradoxical' strategy cannot invade a hypothetical ancestral population which ignores the asymmetry. In the other type of asymmetry, where differences such as size give an indication of the probable outcome of an escalated fight, the ESS depends on how accurately each individual assesses its own size in relation to that of the opponent, and how good size is as an indicator of the outcome of a fight. It turns out that size, or some other such cue, will be used as a conventional means of settling a contest if the contestants estimate it with certainty, even if it is a poor predictor of the outcome of a fight. The ESS will be "always retreat if you think your opponent is larger, always escalate if you think he is smaller, and do something intermediate if he is the same size".

This automatically leads one to consider the question of bluffers. If it is an ESS for animals to use features such as size to settle asymmetric contests, can bluffers, individuals with the equivalent of padded shoulders, spread through the population? Maynard Smith and Parker conclude that bluff will always tend to spread but it is probably limited by the ability of other individuals to detect the difference between bluff and real fighting ability.

At the moment, this new approach to analysing ritualised contests is still in the theoretical stage, but some data seem to support the theory. Male dung flies (*Scatophaga stercoraria*) competing for females at newly deposited cowpats show the negative exponential distribution of persistence times predicted by the 'no escalation' model. Although this in itself is not a very surprising result, the fact that males with different persistence times have an equal chance of mating suggests that the distribution is in fact an ESS.