

## Arms races between and within species

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An adaptation in one lineage (e.g. predators) may change the selection pressure on another lineage (e.g. prey), giving rise to a counter-adaptation. If this occurs reciprocally, an unstable runaway escalation or ‘arms race’ may result. We discuss various factors which might give one side an advantage in an arms race. For example, a lineage under strong selection may out-evolve a weakly selected one (‘the life-dinner principle’). We then classify arms races in two independent ways. They may be symmetric or asymmetric, and they may be interspecific or intraspecific. Our example of an asymmetric interspecific arms race is that between brood parasites and their hosts. The arms race concept may help to reduce the mystery of why cuckoo hosts are so good at detecting cuckoo eggs, but so bad at detecting cuckoo nestlings. The evolutionary contest between queen and worker ants over relative parental investment is a good example of an intraspecific asymmetric arms race. Such cases raise special problems because the participants share the same gene pool. Interspecific symmetric arms races are unlikely to be important, because competitors tend to diverge rather than escalate competitive adaptations. Intraspecific symmetric arms races, exemplified by adaptations for male–male competition, may underlie Cope’s Rule and even the extinction of lineages. Finally we consider ways in which arms races can end. One lineage may drive the other to extinction; one may reach an optimum, thereby preventing the other from doing so; a particularly interesting possibility, exemplified by flower-bee coevolution, is that both sides may reach a mutual local optimum; lastly, arms races may have no stable end but may cycle continuously. We do not wish necessarily to suggest that all, or even most, evolutionary change results from arms races, but we do suggest that the arms race concept may help to resolve three long-standing questions in evolutionary theory.

‘Wonderful and admirable as most instincts are, yet they cannot be considered as absolutely perfect: there is a constant struggle going on throughout nature between the instinct of the one to escape its enemy and of the other to secure its prey’ (Charles Darwin, in Romanes 1883).

Foxes and rabbits race against each other in two senses. When an individual fox chases an individual rabbit the race occurs on the time scale of behaviour. It is an individual race, like that between a particular submarine and the ship it is trying to sink. But there is another kind of race, on a different time scale. Submarine designers learn from earlier failures. As technology progresses, later submarines

are better equipped to detect and sink ships, and later-designed ships are better equipped to resist. This is an 'arms race' and it occurs over a historical time scale. Similarly, over the evolutionary time scale the fox lineage may evolve improved adaptations for catching rabbits, and the rabbit lineage improved adaptations for escaping. Biologists often use the phrase 'arms race' to describe this kind of evolutionary escalation of ever more refined mutual counter-adaptations.

We must not be misled by the language of improvement. As the arms race progresses and predators 'improve', this does not necessarily mean they catch more prey. The prey lineage, after all, is improving too. There seems to be no general reason to expect the average success of animals at out-running or out-witting contemporary enemies, victims, prey or competitors, to improve over evolutionary time. Van Valen (1973) has put this point more generally in his 'Red Queen Hypothesis'. But if modern predators are in general no better at catching modern prey than Eocene predators were at catching Eocene prey, it does at first sight seem to be an expectation of the arms race idea that modern predators might massacre Eocene prey. And Eocene predators chasing modern prey might be in the same position as a Spitfire chasing a jet.

There is some indirect fossil evidence bearing on this. Jerison (1973) measured encephalization quotients of carnivorous and herbivorous mammals from the early Tertiary through to the present. As Gould (1978) summarizes his evidence: 'Both herbivores and carnivores displayed continual increase in brain size during their evolution, but at each stage, the carnivores were always ahead. Animals that make a living by catching rapidly moving prey seem to need bigger brains than plant eaters. And, as the brains of the herbivores grew larger (presumably under intense selection pressure imposed by their carnivorous predators), the carnivores also evolved bigger brains to maintain the differential.' Radinsky (1978) casts doubt on the conclusion that the 'carnivores are always ahead', but his reanalysis of the data does nothing to weaken the conclusion that both carnivores and herbivores grew brainier over the period. He concludes that 'Relative brain size increased independently many times in the evolution of the various orders of mammals. Elucidation of the factors responsible for that major evolutionary trend remains an outstanding problem.' The arms race interpretation favoured by Jerison and Gould seems very plausible to us.

H. B. Cott (1940) made early use of the arms race metaphor to dispose of the then fashionable argument that animal mimicry was too perfect to have been produced by natural selection:

'Before asserting that the deceptive appearance of a grasshopper or butterfly is unnecessarily detailed, we must first ascertain what are the powers of perception and discrimination of the insects' natural enemies. Not to do so is like asserting that the armour of a battle-cruiser is too heavy, or the range of her guns too great, without inquiring into the nature and effectiveness of the enemy's armament. The fact is that in the primeval struggle of the jungle, as in

the refinements of civilized warfare, we see in progress a great evolutionary armament race – whose results, for defence, are manifested in such devices as speed, alertness, armour, spinescence, burrowing habits, nocturnal habits, poisonous secretions, nauseous taste, and procryptic, aposematic, and mimetic coloration; and for offence, in such counter-attributes as speed, surprise, ambush, allurement, visual acuity, claws, teeth, stings, poison fangs, and anticyptic and alluring coloration. Just as greater speed in the pursued has developed in relation to increased speed in the pursuer; or defensive armour in relation to aggressive weapons; so the perfection of concealing devices has evolved in response to increased powers of perception . . . ’

Charles Darwin lived before ‘arms race’ became a fashionable phrase, but he was well aware of the evolutionary phenomenon, and seems to have suspected that it was relevant even to adaptations that appeared to be to the inanimate environment only (Darwin 1859):

‘ . . . the structure of every organic being is related, in the most essential yet often hidden manner, to that of all the other organic beings, with which it comes into competition for food and residence, or from which it has to escape, or on which it preys. This is obvious in the structure of the teeth and talons of the tiger; and in that of the legs and claws of the parasite which clings to the hair on the tiger’s body. But in the beautifully plumed seed of the dandelion, and in the flattened and fringed legs of the water-beetle, the relation seems at first confined to the elements of air and water. Yet the advantage of plumed seeds no doubt stands in the closest relation to the land being already thickly clothed with other plants; so that the seeds may be widely distributed and fall on unoccupied ground. In the water-beetle, the structure of its legs, so well adapted for diving, allows it to compete with other aquatic insects, to hunt for its own prey, and to escape serving as prey to other animals.’

Although we are sympathetic to this view, it is not our purpose to advocate the universal importance of arms races in all evolutionary change. Ours is the more modest aim to suggest that the arms race metaphor leads to new and productive habits of thought about old and familiar material.

We shall organize our discussion around a two-way classification of arms races. An arms race may be interspecific or intraspecific. Cutting across this classification, it may be symmetric or asymmetric. An asymmetric arms race might be called an ‘attack–defence’ arms race. It is one in which offensive adaptations on one side are countered by defensive adaptations on the other. Swords get sharper, so shields get thicker, so swords get sharper still. Most of the familiar biological examples are asymmetric, as in the predator–prey or the parasite–host asymmetry. In a symmetric arms race on the other hand, the parties are becoming better and better at doing the same thing. The possession of 2 megaton bombs on one side provokes the manufacture of 3 megaton bombs by the other side and so on. Sym-

metric arms races are essentially competitive, and biological examples are likely to be found within species, for example in the weaponry of male–male competition for females.

The arms race idea suggests progressive rather than random (Raup 1977) trends in evolution, but we are anxious not to be mistaken as strong partisans for the view that Eldredge & Gould (1972) have dubbed ‘phyletic gradualism’. Conscious that modern palaeontology is in a fast moving and excitingly controversial phase (see, for example, any recent number of *Paleobiology*), we are content as ethologists to wait on the touchline. Although for convenience we shall normally use ‘gradualistic’ language, much of what we say could be rephrased in ‘punctuationist’ terms (Gould 1977). An exception is our treatment of intraspecific symmetric arms races, which does seem necessarily to imply gradual and continuous change.

In all of this discussion it is important to realize who are the parties that are ‘racing’ against one another. They are not individuals but lineages. To be sure, it is individuals who attack and defend, individuals who kill or resist being killed. But the arms race takes place on the evolutionary time scale, and individuals do not evolve. It is lineages that evolve, and lineages that exhibit progressive trends in response to the selection pressures set up by the progressive improvements in other lineages. This raises a problem when we consider intraspecific arms races, for instance that between males and females, for males and females are not two independent lineages: males are descended from females and vice versa. But we shall face that problem when we come to it.

Before developing our two-way classification, we need to consider in general those factors that are likely to favour one side or the other in an arms race.

#### FACTORS FAVOURING ONE SIDE OR THE OTHER IN ARMS RACES

Slobodkin (1974) wrote that ‘while an “evolutionary race” may exist between predators and prey, there is reason to believe that the prey can keep ahead in the race’. It is by no means clear what it might mean to say that one side or the other can ‘keep ahead in the race’. It is probably true that, in any arms race, whenever either side produces a new adaptation it may enjoy something like a period of grace before the other side perfects a counter-adaptation. Individuals will experience this period of grace as a temporary decrease in the adverse effects of the other side. How long the period of grace lasts will depend on the various factors that govern rates of evolution. If one side consistently enjoys longer periods of grace than the other; if, say, the predator lineage is consistently slow to evolve a counter-adaptation to each relatively rapid prey adaptation, it might indeed be reasonable to talk of the prey ‘keeping ahead in the race’.

Slobodkin’s particular reasons for expecting prey to keep ahead in the race against predators can be applied the other way round, and we shall therefore not discuss them in detail. But his argument can be generalized in an interesting way.

It amounts to the suggestion that in an arms race between a specialist and a generalist the specialist will tend to win. The point is essentially the following economic one.

### Water filling algorithm

### Adaptation budgets

Adaptations can be seen as 'costly', and resources that are used up in one adaptation are not available for use in another. A predator species that is adapted to hunt several different prey species is unlikely to be devastatingly effective against any one of them. As far as the individuals of any one prey species are concerned, this might be said to put them ahead in the arms race against this predator species. Similarly, if the prey invest maximally in adaptations for running fast, they may outrun predators which have to invest both in running speed and in adaptations for killing the prey once they have caught them. This is not to say it is in general 'better' to be a specialist than a generalist. In any particular arms race between a specialist and a generalist the specialist may have an advantage. But the generalist, by definition, runs many races and it may make a good living overall.

This kind of economic imbalance is also relevant when there are inequalities in strengths of selection pressures on the two sides. This is the subject of the next section.

### The life-dinner principle (unequal selection pressures)

'The rabbit runs faster than the fox, because the rabbit is running for his life while the fox is only running for his dinner' (Dawkins 1979, after Aesop). There is a built-in imbalance between predator and prey with respect to the penalty of failure. Mutations that make foxes lose races against rabbits might therefore survive in the fox gene pool longer than mutations that cause rabbits to lose races can expect to survive in the rabbit gene pool. A fox may reproduce after losing a race against a rabbit. No rabbit has ever reproduced after losing a race against a fox. Foxes who often fail to catch prey eventually starve to death, but they may get some reproduction in first.

The life-dinner principle does not imply that 'rabbits' under strong selection pressure will win in the sense of driving weaker-selected 'foxes' to extinction. The suggestion is more subtle than this. As we saw in the last section, adaptations of one type, say for running fast, have to be paid for in the form of less perfect adaptations of other types. An illustration of the cost of antipredator adaptations is seen in some kinds of plants which produce chemical defence compounds. Within one species there tends to be a negative relation between investment in defence chemicals and fecundity (Price 1975). If 'foxes' are less strongly selected for running speed than 'rabbits', this means that they can afford to put more resources into other things such as gonads or intraspecific competitive adaptations. We could almost measure the cost of adaptations in 'gonad equivalents'. The life-dinner principle simply implies that, all other things being equal, animals under strong selection for speed will pay relatively more 'gonad equivalents' over to developing

adaptations for running fast. Animals under weak selection for running speed will correspondingly benefit by being able to deploy relatively more resources in gonads or other adaptations.

Parker *et al.* (1972) used something like the life–dinner principle in discussing the origin of anisogamy. They postulated an ancient arms race between small, mobile ‘male’ gametes, and large, well nourished ‘female’ gametes. Selection favoured female gametes that discriminated against male ones, and simultaneously selection favoured male gametes that broke through the female defences. As Williams (1975) put it: ‘This primeval conflict between the sexes was resolved in favor of the males because of more intense selection for male functions. Once the issue was decided, macrogametes abandoned the attempt to unite with other macrogametes and reject sperm.’ Females are under stronger selection pressure because the number of kids they can have is more limited.

The general point here is that where one side in an arms race is under stronger selection pressure than the other, it will tend to have an advantage in that particular arms race. A similar idea was used by Pimentel (e.g. 1968) in his ‘genetic feedback’ theory of population regulation. The life–dinner principle is just one example of a way in which inequalities in rates of evolution may be important in determining the course and outcome of an arms race. A few others are mentioned in the next section.

#### *General inequalities in potential rates of evolution*

Palaeontologists agree that major taxonomic groupings vary in how fast they evolve (Simpson 1953). Stanley (1973) suggests that mammals evolve faster than bivalve molluses because interspecific competition is fiercer for mammals. Schopf *et al.* (1975) feel that the difference may be more apparent than real, and Kauffman (1978) suggests that it is often not even apparent. But if it is true, for whatever reason, that mammals evolve on average nearly ten times as fast as bivalve molluses in terms of observable phenotypes, would this give a mammal a built-in advantage in an arms race against a bivalve mollusc? The suggestion begs a serious question. It implies that bivalves are inherently incapable of evolving fast even when they are under strong selection pressure. But it is equally probable that lineages that evolve slowly do so precisely because they are *not* involved in severe arms races. Bivalves and frogs may have evolved slowly, not because they are incapable of evolving fast, but because they are getting on nicely as they are (Cain 1964).

On the other hand, there are some general reasons why some lineages might be inherently capable of responding to selection pressures more rapidly than others. These do not obviously differentiate mammals from bivalves or frogs, but they are worth brief consideration anyway. Population geneticists recognize various factors that in theory should influence rates of evolution, though any one of them might be ineffectual if other factors happened to be limiting. They include population size and genetic variance (Fisher 1930), tendency of the population to be broken up into semi-isolated sub-populations (Wright 1977), generation time,

presence or absence of sexual reproduction, and perhaps mutation rate and recombination rate. For example, 'costly' though sex undoubtedly is, in the sense that a clone of asexual females is expected in the short term to outcompete sexual rivals within a species (Williams 1975), there can be little doubt that in an arms race a sexual lineage will have a good chance of out-evolving an asexual one (Maynard Smith 1978a).

### Learning

It has often been pointed out that from a functional point of view there is a formal analogy between learning and natural selection (see, for example, Pringle 1951; Lorenz 1966). Both can be thought of as processes by which animals improve over time. In natural selection the improvement is seen only when a lineage of many individuals is viewed over many generations. In learning the improvement occurs during each individual's lifetime.

In an arms race between two non-learning species, one side may enjoy longer 'periods of grace' after producing each new adaptation, for any of the reasons that we have listed. But such periods of grace will be measured in tens or hundreds of generations. In an arms race where the individuals on one side are good at learning, there is a chance that they can cut the other side's period of grace down to less than one generation. On the other hand, the period of grace recurs for the same length of time in each generation, since unless there is cultural transmission every individual has to learn anew.

During the rest of this paper we shall refer back to these ways in which one side or the other in an arms race might have an advantage. We now turn to our two-way classification of arms races, beginning with an example of the most familiar class, interspecific asymmetric arms races.

## DIFFERENT TYPES OF ARMS RACE

### *Brood parasites and hosts: an asymmetric interspecific arms race*

Interspecific asymmetric arms races include those between parasites and hosts, and predators and prey (Edmunds 1974). We shall discuss *brood parasitism* as an example, and shall use the arms race approach to discuss a particular paradox: why cuckoo hosts sometimes seem so clever, in discriminating against poorly mimetic eggs, and at other times seem so stupid in feeding young clearly different from their own (Zahavi 1979). Less anthropomorphically, how can a host provide the fastidious selection pressure that shapes the impressively accurate cuckoo egg mimicry, and a few days later be fooled by a cuckoo nestling which seems completely unlike its own young, and which may, indeed, be very much larger than the host itself?

The first thing to say is that the selection pressure in favour of discrimination by hosts is obviously stronger early in the incubation period than late. A host who realizes she has been duped as soon as the cuckoo egg is laid can destroy it immediately, or desert and begin a new nest having lost only a short time. When

a baby cuckoo is old enough to impress humans as grotesquely different from the host's natural children, a host who at this point detects it gains little in comparison to one who continues to feed it; perhaps she gains only a few days, and it may be too late in the season to breed again anyway. She might even do better to finish the job and gain experience in the skills of parenthood. (We are tempted to go further and suggest that hosts who have little to lose might complete the rearing of cuckoos out of spite to other potential hosts, but unfortunately the idea seems theoretically unworkable.) Even if some of these suggestions are helpful, they only quantitatively mitigate our wonderment at the host's 'stupidity'. It still remains mysterious.

We prefer to think that the fundamental answer to the paradox lies in a subtle application of the arms race concept. When a human behaves in a way which is manifestly bad for him, for instance when he continually takes poison, we may explain his behaviour in at least two ways. He may not realize that the substance that he is drinking is poison, so closely does it resemble a genuinely nutritious substance. This corresponds to the host bird being fooled by the cuckoo's egg mimicry. Or he may be unable to save himself because of some direct subverting influence of the poison on his nervous system. Such is the case of the heroin addict who knows the drug is killing him, but who cannot stop taking it because the drug itself manipulates his nervous system. We have argued elsewhere that much of animal communication might profitably be regarded as akin to manipulation (Dawkins & Krebs 1978). There are indications that the orange gape and loud begging calls of the baby cuckoo have a supernormal effect (Wickler 1968). Could it be that the host can no more resist the supernormal manipulative power of the cuckoo nestling than the junkie can resist his fix, or than the brainwashed prisoner can resist the orders of his captor, however much it would benefit him to do so? Perhaps cuckoos have put their adaptive emphasis on mimetic deception at the egg stage, but on positive manipulation of the host's nervous system at the late nestling stage.

This is not a new idea. Wickler (1968) quotes Oskar Heinroth as having referred to the cuckoo as a 'vice of its foster parents' since they respond like 'addicts' to the supernormal stimulus. But the 'addiction' or 'manipulation' hypothesis has one outstanding difficulty which may be solved by an application of the arms race principle. It may be believable that an individual foster-parent could be hypnotized, addicted, or otherwise manipulated into feeding a cuckoo nestling which obviously bears no resemblance to one of her own. But surely, it will be said, over evolutionary time natural selection would put a stop to that: selection would favour hosts who have nervous systems resistant to the manipulation. Yes, but exactly the same thing could in theory be said of mimetic deception: mimicry cannot possibly evolve, because selection will always favour individuals who are not fooled by it! This, of course, is where the arms race idea comes in. Any nervous system can be subverted if treated in the right way. Any evolutionary adaptation of the host nervous system to resist manipulation by cuckoo nestlings simply lays itself open

to counter-adaptation by the cuckoos. Selection acting on cuckoos will work to find whatever chinks there may be in the hosts' newly evolved psychological armour. Host birds may be very good at resisting psychological manipulation, but cuckoos might become even better at manipulating.

It does indeed seem easy to imagine that cuckoos might have a built-in advantage in their arms race with their hosts. The 'life-dinner principle' could apply: a cuckoo in the nest has *got* to manipulate its host successfully or it will surely die; its individual foster-parent will benefit somewhat if it resists manipulation, but it still has a good chance of future reproductive success in other years even if it fails to resist this particular cuckoo.

On the other hand, there is also evidence that under some conditions hosts may eventually get the upper hand. Systematic tests of the ability of various species of bird to discriminate against cuckoo eggs show that many non-parasitized species are excellent discriminators. Jourdain (1925) even suggested that non-parasitized species of European passersines are better discriminators than species used by cuckoos as hosts. While it is possible that cuckoos have simply avoided parasitizing species that are good discriminators, it is also possible that the good discriminators are species that used to be parasitized in the past. On this theory, cuckoos successfully parasitize a species for a while, then give it up when that host species becomes too good at discrimination. Maybe successive host species win their private arms race against cuckoo eggs, and the cuckoos then turn to new, 'evolutionarily naïve' victims. As C. E. Davies has pointed out to us in this connection, it may be significant that among the British gentes of cuckoo, which parasitize different species of host, egg mimicry ranges from nearly perfect in the meadow pipit gens to virtually non-existent in the hedge sparrow gens. Rothsteins' (1975a, b, 1976) evidence on the brown headed cowbird (*Molothrus ater*), an American brood parasite, can be interpreted in a similar way.

Our suggestion that cuckoos manipulate their hosts is not an alternative to the classical supernormal stimulus interpretation. Rather, we are providing a functional explanation of the host's maladaptive behaviour, instead of leaving it as an unexplained limitation of the nervous system.

The drug analogy is especially apt for insect parasites that use chemical means to coerce their hosts into acts that are profoundly damaging to their own fitness. The ant *Monomorium santschii* is a workerless parasite of *Monomorium salomonis*. An *M. santschii* queen enters a host nest in the same way as many other parasitic ants. But unlike parasitic queens of other species who directly kill the host queen, *M. santschii* achieves the same result by more subtle means. The host workers kill their own mother and adopt the usurper instead (Wilson 1971). It does not seem to be known why they do this, but we must infer that the parasite queen exerts a direct hold over their nervous systems. It might well be correct to label her weapon a pheromone, but it is probably more illuminating to think of it as a formidably powerful drug. In line with this interpretation, Wilson (1971) writes of symphylic substances as being 'more than just elementary nutritive substances

or even analogues of the natural host pheromones. Several authors have spoken of a narcotizing effect of symphylic substances.' Wilson also uses the word 'intoxicant' and quotes a case in which worker ants under the influence of such a substance became temporarily disorientated and less sure of their footing.

Those who have never been brainwashed or addicted to a drug find it hard to understand their fellow men who are driven by such compulsions. In the same naïve way we cannot understand a host bird's being compelled to feed an absurdly oversized cuckoo, or worker ants wantonly murdering the only being in the whole world who is vital to their genetic success. But such subjective feelings are misleading, even where the relatively crude achievements of human pharmacology are concerned. With natural selection working on the problem, who would be so presumptuous as to guess what feats of mind control might not be achieved? Do not expect to see animals always behaving in such a way as to maximize their own inclusive fitness. Losers in an arms race may behave in some very odd ways indeed. If they appear disorientated and unsure of their footing, this may be only the beginning.

#### *Intraspecific asymmetric arms races*

The very idea of an arms race between members of the same species would have been considered quite revolutionary until a few years ago. Now we accept the idea even for parents and offspring, and members of a mated pair. In both cases R. L. Trivers (1972, 1974; Trivers & Hare 1976), building on the pioneering work of W. D. Hamilton (e.g. 1964, 1971) has been largely responsible for revolutionizing our way of thinking. We here concentrate on the arms race between parents and their children (Trivers 1974; Alexander 1974; Macnair & Parker 1978, 1979; Parker & Macnair 1978, 1979; O'Connor 1978).

Probably the most clearly worked out example of parent-offspring conflict is the case of sex ratios in social Hymenoptera (Trivers & Hare 1976; criticized by Alexander & Sherman (1977) and by Macnair (1978)). The example is particularly illuminating. The adaptation under discussion is that of the ratio of investment in male versus female reproductive offspring of the colony. We will consider only cases where there is a single queen who is the mother of all other individuals in the colony. If the queen has practical power over sex determination and parental investment, as would be expected if sociality evolved by parental domination (Alexander 1974; Michener & Brothers 1974), the evolutionarily stable investment ratio will be 1:1 as in the classical theory (Fisher 1930). But Trivers & Hare showed that, if the workers exert practical power over investment in young reproductives, the evolutionarily stable ratio will be 1:3. The difference results from the haplodiploid system of genetics which occurs in Hymenoptera (Hamilton 1964). Provided they are full sisters to the reproductives, workers are three times as closely related to female reproductives as to male ones. Since workers are sisters to the young reproductives in question, and the queen is the mother of the reproductives, the theory predicts a direct conflict between queens and workers.

This is a complex and subtle idea. It is misleading to think simply in terms of two

rival ideal sex ratios, one for the queen and one for the workers; 1:1 and 1:3 are optimal ratios only in a particular sense. If the ratio of investment in the population as a whole is 1:1, selection will penalize queens who depart from it, and will favour workers who invest in only females rather than workers who invest 1:3. If the ratio of investment in the population as a whole is 1:3, selection will penalize workers who deviate from it, and will favour queens who lay only male eggs rather than queens who invest 1:1. From the present point of view the important fact is that there is no sex ratio that is stable if both queen and workers exert practical power over the ratio of investment in male and female reproductives.

Trivers & Hare concluded that, in most of the monogynous ant species that they studied, the workers seemed to have won the arms race and produced something close to the 1:3 ratio. The reason for victory, they suggested, is that the workers have more practical power: the workers actually look after the brood and are in a better position than the queen to control the amount of food given to male and female larvae. But there may be another more fundamental genetic reason related to the life-dinner principle, for worker 'victory'. This is that, when the sex ratio is 1:3 and workers are full siblings to reproductives, genes in workers are apparently being propagated more efficiently than genes in the queen would be at any conceivable sex ratio; conversely, when the sex ratio is 1:1, the 'optimum' from the queen's point of view, genes in the queen are only being propagated as efficiently as genes in workers. The queen's optimum, 1:1, is as good for the workers as it is for the queen. But the workers' own optimum, 1:3, is even better for them. Therefore genes for worker adaptations to outwit their mother have a built-in advantage over genes for queen adaptations to outwit her sterile daughters. Notice, incidentally, that these ideas go against the spirit of much of the language commonly used in discussions of social Hymenoptera, 'altruistic submission' by workers, for instance, and 'parental domination' by a 'super-beneficiary' queen.

Trivers & Hare's conclusions have been called into serious question by Alexander & Sherman (1977). The factual part of the argument will remain unresolved until more data have been obtained. But on the theoretical side there seems no doubt that Trivers & Hare's analysis is essentially correct (Charnov 1978), and not incompatible with Alexander & Sherman's alternative hypothesis.

We come now to the characteristically difficult aspect of intraspecific arms races. In an interspecific arms race like that between predator and prey, two entirely separate genetic lineages coevolve in parallel, mutually countering one another's adaptations, but in an intraspecific arms race the 'lineages' which are racing against each other are not really lineages at all. The genes that programme the development of queen behaviour are present in workers, and the genes that programme the development of worker behaviour are present in queens. All females are equipped with the same conditional rule or 'strategy' (Maynard Smith, this symposium): 'If fed like a queen invest 1:1 in male and female productives; if fed like a worker, invest 1:3', or whatever it is. Counter-adaptations and counter-counter-adaptations can still evolve in the arms race between queens and workers.

But it is an arms race between two branches of the same conditional strategy, not an arms race between two independent lineages with separate gene pools. We might see an organ in worker ants which is properly regarded as an adaptation for outwitting queens, and another organ in queens which is an adaptation for outwitting workers. Yet every female is genetically equipped to be either a queen or a worker.

This is a rather startling idea, which applies also to the arms race between males and females (Trivers 1972). As Parker (1979) has put it: '...selection can act in opposition on the two sexes. Commonly, for a given type of encounter, males will be favoured if they do mate and females if they don't'. We can therefore expect to find adaptations in males for overcoming female resistance, and counter-adaptations in females (Williams 1966). But unless the genes controlling these adaptations are carried on sex chromosomes, they will all have spent half their history in male bodies and half in female bodies.

To put the point in an exaggeratedly fanciful way, imagine that blueprints of Russian missiles spent half their time in Pentagon files, and blueprints of American counter-missiles spent half their time in Moscow! The analogy has now clearly gone too far, but a more realistic argument along these lines was developed by Alexander (1974). Briefly, he suggested that parents must always win the conflict against their offspring, because all children aspire to become parents. Any adaptation that helps a child to outwit his parents comes back and kicks him in the teeth when his own children use it against him. There seems no obvious reason why Alexander's argument should not be reversed (Dawkins 1976), and appropriate mathematical models (Macnair & Parker 1978; Parker & Macnair 1978) have failed to uphold it. The way to handle the problem is to postulate an asymmetric conditional strategy: 'if young do X, if old do Y', and see whether that conditional strategy is evolutionarily stable.

But we are here making the more general point that we need to think about whether, simply because only one genetic lineage is involved rather than two, intraspecific arms races will have quite different consequences from interspecific ones. One possible approach to answering the question would be along the lines of recent game theoretic analyses of aggressive behaviour for the special case where the combatants are genetic relatives (Treisman 1977; Grafen 1979; Maynard Smith 1978b).

#### *Interspecific symmetric arms races*

The subject of discussion here is competition between species, a major pre-occupation of ecologists. We shall make no attempt to review this important subject, which is well covered in ecological text books. Here we are concerned simply to fit the topic into our two-way classification of arms races, and to point up some contrasts with other types of arms race.

When we look at a predator and its prey, or a parasite and its host, we seem to see numerous adaptations in each for foiling the adaptations of the other. Is this ever the case for interspecific competitors? Do we ever say of an organ or a behaviour pattern that it is an adaptation for outcompeting a rival species? By

analogy with  $r$  and  $K$  selection, selection for mechanisms that prevent hetero-specific competitors from gaining access to limited resources (called interference as opposed to exploitation competition) has been called  $\alpha$ -selection (Emlen 1973). A well known ecological textbook published in 1978 states that 'The major evolutionary problem with  $\alpha$ -selection is that the technique of interference will often affect members of the same species as well as members of competing species, so that competitive ability is achieved only by a reduction in the species' own values of  $r$  and  $K$ . An example would be a shrub which produces chemicals to retard the germination and growth of competing plants but which may suffer from auto-intoxication after several years.' By failing to distinguish individual autointoxication from intoxication of rival members of the same species, the author seems to fall victim to the implicit group-selectionism that lurks beneath the surface of much ecological writing. Nevertheless he is right that there are formidable problems in the way of interpreting any adaptation as a consequence of selection for inter-specific competitive ability.

For example the suggestion by McKaye (1977, but see Coyne & Sohn 1978), that the cichlid fish *Cichlasoma nicaraguense* has been selected to rear predators of a severe competitor, could work only under very special circumstances. It is not enough that the presence of the predator in the lake benefits the species *C. nicaraguense* indiscriminately. Each foster-parent must benefit as an individual from the individual predators that it rears. This could happen if there is strong site attachment, as McKaye himself recognizes.

We may generalize this lesson. Unless there are special reasons to the contrary, we must expect that any individual who takes steps to reduce the competitive effectiveness of an interspecific rival is as likely thereby to help a conspecific rival as to benefit himself. To characterize selection for interspecific competitive adaptations as ' $\alpha$ -selection' is to miss the main point. The competition coefficient  $\alpha$  is a measure of the impact of one species on the population size of another species. An adaptation that simply alters the population size of another species will not be favoured unless it benefits an *individual* possessing the adaptation as compared with another individual of the same species not possessing the adaptation. The coefficient  $\alpha$ , like any other population parameter, conceals the individual-level interactions which really matter.

As we would expect from this argument, the most clearly recognizable adaptations for interspecific interference competition are those that directly benefit the competing individual: cannibalism by *Tribolium* beetles of interspecific rivals (Park 1962) benefits the individual cannibal not only by removing a competitor (this advantage also applies to the rest of the population) but also because the cannibal gains extra food. Apparent adaptations to interspecific competition are probably often extensions of intraspecific competitive adaptations. For example, Picman's (1977a, b) intriguing observation that nesting long-billed marsh wrens (*Telmatodytes palustris*) search out and peck eggs in nearby nests of other marsh wrens and of different species cannot be thought of as a purely interspecific

adaptation. The same argument can be applied to interspecific territoriality (Cody 1974).

Even when adaptations to outcompete rival species do evolve, they will be unlikely to lead to prolonged and progressive arms races in the way predator-prey adaptations do. It is more probable that selection will favour evasion of competition, by niche separation. The theoretical question of how interspecific competition leads to niche separation and consequent reduction in competition has been analysed by Lawlor & Maynard Smith (1976) and Roughgarden (1976). They confirm the intuitive notion that individual level selection will favour species divergence. Direct evidence for evolutionary divergence as a result of competition comes from studies of 'character displacement' (Brown & Wilson 1956; Fenchel 1975; but see Grant 1972).

#### *Intraspecific symmetric arms races*

Intraspecific competition between individuals is the primary driving force of Darwinian evolution. Even adaptations to avoid being eaten by predators have evolved because individuals with such adaptations outcompeted conspecific individuals without them. This does not mean that all the arms races that we have so far discussed should truly be subsumed under the current heading. Improved crypticity in prey insects is truly the product of an interspecific arms race against bird predators in the following sense. If we could wave a wand and freeze evolution in the predators, further evolution of cryptic perfection in the prey would decelerate towards an optimum compromise with competing selection pressures and would eventually stop. It is because predators *evolve* that prey lineages go on evolving improved antipredator adaptations.

Nevertheless there are true intraspecific arms races, arms races that would continue even if with our magic wand we could freeze evolution in predators and all other species. An obvious example comes from male competition for females. Imagine a species in which large size is an advantage in male-male competition but not an advantage from any other point of view. It is entirely reasonable that competition will favour males that are slightly larger than the current population mode, *whatever the current mode may be* (Simpson 1953). This is a recipe for progressive evolution of the kind that we expect from an arms race. It is a true symmetric arms race, such as we shall probably never see in interspecific competition. Incidentally, female size may be 'dragged upwards' by selection for increased male size (Maynard Smith 1977).

An arms race of this kind could also be a recipe for eventual lineage extinction. It is plausible that many selection pressures will favour a fixed optimum, say a length of 10 cm, while sexual selection or other selection pressures favour a relative optimum: slightly larger than the current mode, whatever the current mode may be. If the 'relative' selection pressure causes the lineage to evolve sufficiently far away from the optimum size set by the 'absolute' selection pres-

sures, the lineage will become increasingly vulnerable to extinction, until it is finally finished off by a comparatively minor environmental crisis.

This argument is not necessarily confined to the case of sexual selection. Hallam (1975) provides data relevant to this point for Jurassic bivalves and ammonites that exhibit Cope's Rule: the individuals get larger over evolutionary time. There is great variation in the rate at which they get larger. In the 60 palaeospecies surveyed by Hallam, the range was from 16 millidarwins to 3690 millidarwins (1 darwin was for practical purposes defined as a doubling in size per million years, but see Hayami 1978). Each of these lineages also had a *longevity*, measured from the time of its first appearance in the fossil record until its disappearance and presumed extinction. When the logarithm of the rate of evolution of a lineage, measured in millidarwins, was plotted against the logarithm of its longevity, measured in millions of years, a negative correlation was obtained. (It has been pointed out that Hallam's original way of plotting this relation may have exaggerated it since both axes are functions of one variable, lineage duration. But later analysis (Hallam 1978) shows that the negative correlation remains even after this possible artefact is removed.) It appears that the faster a lineage evolves large size, the sooner it goes extinct. This suggests, though of course it does not prove, that it is the large size itself that, in some sense, caused the extinction.

Hallam's own interpretation of his result is that selection, for whatever reason, in favour of large body size tends to lead to smaller population size and hence greater vulnerability to random extinction. Our suggestion, that the increased size is due to an intraspecific arms race in which selection favours individuals who are slightly larger than the current mode, and that the extinction is due to divergence of actual size from an absolute optimum, is compatible with Hallam's. Both may be true.

For these molluscs it is not obvious what the 'relative' selection pressure might have been. Ammonites are known to have been sexually dimorphic so sexual selection is conceivable for them. For bivalves, on the other hand, something analogous to Harper's (1977) suggestion for trees is more plausible. A tree that is competing for light will benefit by being slightly larger than its neighbours, however large they are. Similarly the filter-feeding current of a bivalve might be improved if the bivalve physically stands out above its neighbours.

By the way, it is an interesting suggestion that the explosive increase in brain size in our own relatively recent ancestors may have been the product of what amounts to an intraspecific arms race; the weapons being improved in this arms race were the skills of social manipulation and deception, countermanipulation and counterdeception (Trivers 1971; Humphrey 1976).

In concluding our two-way classification, we can summarize the most important general points as follows:

(a) Asymmetric interspecific arms races may result in what appears to be maladaptive behaviour, such as the feeding of cuckoos by hosts.

(b) Asymmetric intraspecific arms races may be fundamentally different from similar races between species, because the parties share a common gene pool.

(c) Symmetric interspecific arms races are likely to lead to evolutionary divergence rather than progressive escalation.

(d) Symmetric intraspecific arms races could lead to gradual progressive evolution and even extinction.

We now turn to a general question which applies to all arms races.

#### HOW DO ARMS RACES END?

It is most unlikely that any single statement will suffice to describe how all arms races end. In this section we consider four general classes of endpoint, as follows. One side may drive the other to extinction; one side may reach a definable optimum, thereby preventing the other side from reaching its optimum; both sides may reach a mutual local optimum; or the race may persist in a theoretically endless limit cycle. Of these, the first two can be considered as ways in which one side 'wins'.

##### *One side wins*

The obvious way for an arms race to end in victory for one side is for the other side to be driven to extinction. This would be analogous to the laboratory observation by Pimentel *et al.* (1965) of a decline in housefly numbers brought about by an evolved increase in blowfly competitive ability. If a predator or parasite drove its victims extinct, it might as a result soon suffer a similar fate. Pathogens or parasites would at first sight seem likely candidates for this because, as Haldane (1949) said, '...microscopic and sub-microscopic parasites can evolve so much more rapidly than their hosts that the latter have little chance of evolving complete immunity to them'. Presumably he was thinking of their short generation time which, as suggested above, might give an advantage in any arms race. Most parasitologists believe, however, that parasites do not drive themselves to extinction through their own success. Instead they regard the long-term evolutionary trend as being a reduction rather than an escalation of the arms race: '...it is widely accepted that the longer an association (between parasite or pathogen and host) has been in existence in the evolutionary sense, the more likely it is to be a relationship unaccompanied by excesses on either side' (Sprent 1962). While we doubt the implicitly group-selectionist interpretations sometimes found in the parasitology literature, there may be other reasons for the parasite-host arms race not ending in extinction. For instance Pimentel's (1968) 'genetic feedback' or our own 'life-dinner principle' might be applicable here. Perhaps the best studied case history of an evolutionary arms race between pathogen and hosts is that between Australian rabbits and the introduced Myxoma virus. The evolution of a host-virus equilibrium has involved both a decline in viral virulence and an increase in host immunity (Burnet & White 1972).

The second way in which one side in an arms race can be said to 'win' is illustrated by Trivers & Hare's (1976) work on hymenopteran sex ratios, already mentioned. They concluded, in effect, that in many species, workers have won the arms race against queens. Whether or not they are right in this case, they have demonstrated in theory how it can be possible to assign victory to one side or another. They did it by making clear quantitative predictions that the evolutionarily stable investment ratio if the workers have practical power should be different from the ratio if the queen has practical power. Here the two 'optima' are incompatible. But as the next section shows, there may be cases of mutually compatible stable endpoints.

#### *Equilibrium endpoints*

The coevolution of plants and their pollinators is sometimes said to be an example of pure mutualism: plants give nectar 'in return' for having their pollen transferred to the stigma of another individual. But it is more realistic to think of a mutually exploitative arms race. Plants should be selected for meanness, to maximize the benefit derived from pollen transfer per unit of nectar cost (Heinrich 1975), while bees are designed to maximize their efficiency at harvesting nectar, measured as net nutritive gain per unit time (Pyke 1978, 1979a, b). Pyke shows us how both bees and plants might achieve a local optimum of efficiency, which could be a stable endpoint for the arms race.

Pyke studied the pollination of monkshood (*Aconitum columbianum*) and *Delphinium* by bumblebees, *Bombus appositus*. The flowers of both plants grow in a tall spike, the bottom flowers being older, larger, and female while the upper flowers on an inflorescence are smaller, younger, and male. The lower flowers tend to produce more nectar, so the bee gets the highest net reward per unit time at the bottom of each inflorescence. The bee's optimal harvesting strategy is probably to start at the bottom of each plant, and work its way upwards (without revisiting flowers) until the expected gain from staying in the same inflorescence drops to the gain expected by moving to the next plant (Charnov 1976; Pyke 1978). The bees do approximately this. At the same time the plants seem to have positioned their male and female flowers in such a way as to benefit from these bee movements. A bee arrives at the female flowers at the base of an inflorescence having just come from the male flowers at the top of the previous plant, so the chance of cross-fertilization is high.

Pyke goes further and suggests that the plants may practise a subtle form of exploitation of the bees' foraging behaviour. It might be thought that the optimal movement rule for a bee within an inflorescence would be to visit the flowers in the spiral sequence in which they are arranged, starting at the bottom and moving spirally upwards. However, Pyke's detailed observations of bee movements showed that instead the bee moves vertically up the inflorescence. It therefore misses some of the nectar-rich female flowers near the bottom of the spike, but Pyke was able to show that there is also a saving of time for the bee in flying directly upwards. This is because sideways moves cost more time than vertical moves. Calculations

show that the bee cannot increase its net food intake per unit time by adopting any obvious rule other than moving straight upwards.

How might the plant benefit by the bees' vertical movement rule? Pyke suggests that bees normally do not carry enough pollen to fertilize every female flower on a plant. If the bee visited every single flower in the spiral sequence it would run out of pollen while still taking nectar from female flowers. This would be unfortunate for the plant. So it seems that the spiral arrangement of flowers might be no accident but a coevolved design feature maximizing the amount of outcrossing per unit of nectar expended. The coevolutionary race appears to be at a stable point in that a bee could not do better by adopting a new movement rule given the current structure of the plants, and a plant could not do better by adopting a different structure given the current behaviour of the bees.

A. Grafen has suggested to us that arms race theory may come to provide the dynamic counterpart to Maynard Smith's (1974) 'game' theory of evolutionarily stable states. But not all 'games' end in stable solutions.

#### *Cyclic endings*

Parker & Macnair (1979) and Parker (1979) have suggested that parent-offspring arms races and intersexual arms races may end neither in unilateral victory nor in stable equilibrium but in unresolvable cycling. In a genetic model of parent-offspring conflict, Parker & Macnair postulate a dominant 'conflictor' gene which causes children to demand more investment than the parental optimum (see also Macnair & Parker 1978, 1979; Parker & Macnair 1978). This is countered by the evolutionary spread of a 'suppressor' gene in parents, which causes them to apportion investment equally, regardless of the solicitations of individual young. The model assumes that 'conflictor' behaviour has a cost, and when most parents are 'suppressors' this cost is sufficient to reverse the former direction of selection on children: non-conflictor genes spread and the cycle resumes from its starting point. As Parker & Macnair emphasize, other models suggest that the parent-offspring arms race could, under other assumptions, end in evolutionary equilibrium. A similar example from pathogen-host arms races is given by Clarke (this symposium).

For the case of sexual conflict, Parker (1979) develops an endlessly cycling model which may be applicable to asymmetric arms races generally. We shall, indeed, illustrate his idea in a different context, that of an arms race between a prey and its predator. We follow Parker in thinking of it as a 'game', but our players are predator and prey rather than male and female. Each individual player pays a fixed, irretrievable cost. For example, the prey pay the cost of growing to a large size in order to be hard to swallow. And the predators pay the cost of growing to a large size too, the better to swallow them. There ensues an 'evolutionary chase' in which individuals on both sides pay successively higher costs as they get bigger and bigger. For each side there is an upper limit, determined by the value of 'winning', beyond which they will not further escalate the cost paid. The central idea is that this upper limit may be different for the two

sides, for instance because of the 'life-dinner principle'. If the prey have a higher limit than the predators, what this would mean is that the prey are selected to invest further resources in getting bigger while analogous resources in the predators' case are diverted to other adaptations, say in growing more sexually attractive.

Parker's model suggests that the party that can afford to pay the higher cost will do so, whereupon selection will favour a rapid reduction in the cost paid by the other side. It will abruptly become smaller again, diverting more resources to other purposes. Theoretically this could lead to a return to the start of the cycle by both sides, though it remains to be seen whether anything like this happens in nature, and game theory suggests that in any case there may be a way out of the endlessly recycling chase.

As an aside, e.s.s. enthusiasts may like to note the essential difference between Parker's unstable game and the classical 'war of attrition' of Maynard Smith (1974). In the war of attrition both players pay the price 'bid' by the loser. In Parker's game, both pay the price they bid themselves. Growth to a particular size exacts irretrievable costs (see also Rose, in preparation).

#### CONCLUSION

Even more than when we began writing this paper, we are conscious of how superficial our understanding of evolutionary arms races is. What was planned as a short paper could, and probably should, be expanded into a book. We have tried to raise interesting questions even if we have not answered them. We come away with the feeling that the arms race concept could eventually provide the key to resolving some outstanding problems in evolutionary theory. We shall mention just three.

First, the idea that one side in an arms race might enjoy a built-in advantage over the other, say because of the 'life-dinner principle', could be used to account for many cases in which animals or plants appear to act against their own best interests. As in our example of the cuckoos manipulating their hosts, organisms on the losing side of an arms race may be manipulated into maximizing someone else's inclusive fitness rather than their own (Dawkins 1978; Dawkins & Krebs 1978). The arms race idea provides one positive reason (there are, of course, many more; Maynard Smith 1978*b*; Gould & Lewontin, this symposium) for avoiding naive perfectionism when we look at individual adaptation.

Secondly, the arms race concept may help to resolve the old controversy over whether lineages drive themselves to extinction through progressive evolution. The orthogenetic idea that evolution has its own inexorable internal momentum forcing lineages beyond the limits of natural selection is obviously absurd. But orthodox natural selection, *if there is an arms race*, can generate the kind of runaway process that looks like orthogenesis, and which might eventually hasten extinction of the lineage.

Thirdly, a related point, evolutionists repeatedly return to the question of whether there is any biological law which, in Maynard Smith's (1970) words, '...might enable us to put an arrow on time in evolutionary processes, as the second law of thermodynamics enables us to put an arrow on physical processes'. As Gould (1977) has argued in a stimulating historical essay, this is one of the 'eternal metaphors of paleontology'. He himself confesses to an anti-'directionalist', pro-'steady-statist' bias. He backs this up with evidence from the invertebrate fossil record although, as we have seen, he is prepared at times to offer directionalist interpretations of vertebrate history (Gould 1978). Maynard Smith, too, concludes on theoretical grounds that it is not easy to find a good basis for the commonsense feeling that there is temporal polarity in evolution, an arrow pointing in the direction of increasing complexity and even improved adaptedness.

Directionalist common sense surely wins on the very long time scale: once there was only blue-green slime and now there are sharp-eyed metazoa. But this is not the issue. Over the shorter term, say within the Cainozoic, is there a general trend which could in any sense be called improvement? Whatever attempts might be made to answer this question empirically, we suggest that even if there are no other theoretical reasons to expect such trends, arms races provide one.

If adaptation were solely to the inanimate environment, it is easy to believe that evolution would simply track Darwin's 'elements of air and water' in their random walk through time. Selection would be stabilizing until a change in the climate or an accidental geographical displacement introduced a brief interlude of directionality. Each such directional interlude would seem to be as likely to reverse as to continue the previous one. But in fact consistent directionality is introduced because the environment of any one evolving lineage includes other evolving lineages. Above all, it is because adaptations in one lineage call forth counter-adaptations in others, setting in motion the unstable evolutionary progressions we call arms races.

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