

DO DIGGER WASPS COMMIT THE CONCORDE FALLACY?

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Abstract. The Concorde fallacy is a notorious theoretical error which tempts economists and evolutionists alike. It amounts to investing further in a project simply because one has invested in it heavily in the past, rather than because of potential future return on investment. Digger wasps, *Sphex ichneumoneus*, disconcertingly appear to behave as if following the Concorde fallacy. Pairs of females fight over jointly occupied nests, provisioned with paralysed katydids. The prior investment by each wasp in the nest is measured as the number of katydids that she has put into it. The true value of the nest is approximated by the total number of katydids there. The evidence suggests that the wasp with the least prior investment is the one most likely to surrender. In a post-hoc attempt at rationalizing this Concorde result, we uncover some of the pitfalls of naive optimality speculations, and recommend analysis in terms of evolutionarily stable strategies.

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The title should not be misunderstood. A fallacy is a theoretical error, and theoretical errors are committed by humans. The Concorde fallacy is a tempting error which an economist might make about optimal business policy: 'A businessman should never say "I have already invested so much in the Concorde airliner . . . that I cannot afford to scrap it now." He should ask instead whether it would pay him *in the future* to cut his losses and abandon the project now, even though he has already invested heavily in it' (Dawkins 1976). Whatever psychological loyalty we may feel toward a project to which we have committed heavy investment in the past, wise policy decisions will be based upon prospects of future returns, and only indirectly upon weight of past commitment. If total profit would be maximized (or total loss minimized) by scrapping the Concorde project now, rather than by pursuing it, then it should be scrapped *regardless of how much has already been invested in it*. A familiar military equivalent is the 'our boys shall not have died in vain' fallacy (Dawkins & Carlisle 1976).

The Concorde fallacy has a biological parallel, an error committed by evolutionary theorists about optimal policy for an individual animal. Just as a businessman who followed the advice of a Concorde-minded economist would lose money as a result, an animal that behaved as if following the policy recommended by a Concorde evolutionary theorist would presumably be less fit than a rival animal following a different policy. It is in this sense that we may ask whether a digger wasp commits the Concorde fallacy. Weatherhead (1979) asks the same question about savannah sparrows, although his approach is very different.

Rationale

The biological version of the Concorde fallacy was first discussed by Dawkins & Carlisle (1976) in a critique of an important and seminal paper by Trivers (1972). Boucher (1977) independently made the same point. Trivers rightly pointed out that either member of a mated pair might exploit the other by deserting, leaving the partner to finish the job of caring for the young. Where he went wrong was in arguing that, at any given time in the development of a brood, the parent who had so far invested least in that brood, usually the father, was the one most tempted to desert. The broader ramifications of this idea have heavily influenced recent biological interpretations of the whole male/female phenomenon, but its rationale is fundamentally Concorde and incorrect. Natural selection will in fact most favour desertion by that parent who has the most to gain in the future by deserting, regardless of who has invested most in the past. Dawkins & Carlisle went on to argue that the true relationship between past investment and selection in favour of further investment would best be predicted by using Maynard Smith's theory of evolutionarily stable strategies. Such an approach has now been taken, with interesting results, by Maynard Smith himself (1977) and, independently, by Grafen & Sibly (1978).

The Concorde fallacy has great psychological appeal. Once one is sensitive to it, one frequently unmask it in verbal discussions of evolutionary theory. Many an unprofitable line of speculation is nipped in the bud by the crushing rebuke 'Concorde!' Against this background, the reader may imagine our own consternation when we happened upon evidence that the digger wasps that we were studying for other reasons (Brockmann et al. 1979; Brockmann 1980

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Brockmann & Dawkins 1979) seemed to be behaving in exactly the way a Concordian theorist would have recommended. This paper tells the story, and finishes with our own attempt to come to terms with the result.

The Facts

The context is not mate desertion, but rivalry between female wasps over nesting burrows. *Sphex ichneumoneus* L. (Hymenoptera, Sphecidae), the great golden digger wasp, is a solitary sphecid wasp, common throughout much of the United States. Brockmann kept almost continuous records of the nest-related activities of 68 individually colour-marked females in three different field sites over a total of six breeding seasons (Brockmann & Dawkins 1979). Each nest (an underground burrow leading to an oval brood cell) is dug by one female, who then provisions it with stung and paralysed katydids (Orthoptera, Tettigoniidae), lays a single egg, seals up the burrow, and begins the cycle again leaving the larva to hatch and feed on the paralysed prey. She will go through this cycle up to about 10 times during her six week season of adult life. Occasionally (5 to 15% of nests, depending on the site) a second wasp moves in and the two jointly provision the nest for a while. They co-provision the same brood-cell, not, as has been reported for other species, different brood cells within the burrow. 'Co-occupation' was rigorously defined (Brockmann & Dawkins 1979) and did not include casual enterings of another burrow, or temporary orientational errors. In a co-occupation, both wasps were fully engaged in provisioning the same burrow, and neither of them had another burrow open at the same time. Co-occupying wasps seldom meet because both spend most of their time out hunting, but when they do meet they fight, and one is usually driven off. In any case only one of the two lays an egg in the brood cell.

Twenty-three fights were seen between females co-occupying nests. They wrestle, rear up and lunge with open mandibles. Fights varied in duration from 2 to 16 min. A fight was defined as beginning when the wasps made physical contact, and as ending when one of them, thereby defined as the loser, left the area. After 18 of the 23 fights the loser never returned to the nest; in 5 cases she returned, many hours later.

The prize, then, is a well-furnished chamber in which to lay an egg, the more fully provisioned the better. A well-'advised' wasp would fight only moderately hard for an empty burrow: even

if she wins she still has to spend several days provisioning it; to lose would cost her only an extra few hours digging or finding a new one. But a nest containing four katydids is ready for egg-laying; the winner of such a prize saves herself days of precious time. The important point is that this is true for both wasps, regardless of who originally dug the burrow and caught the katydids. We would have cried 'Concorde' to any suggestion that an individual wasp should fight for her *own* investment in a burrow rather than for the total quantity of useful investment that was there.

For each of the 23 fights we know how long it lasted, who won, which wasp was the founder and which the joiner, how long each had been associated with the nest, who was larger, how many katydids there were in the nest and who caught them. First, consider who wins fights. Binomial tests (all statistical tests are two-tailed) eliminate obvious 'asymmetries' (Maynard Smith & Parker 1976; Davies 1978): the larger wasp enjoyed no significant advantage ($P > 0.5$), nor did the founder over the joiner ($P > 0.4$), nor did the individual who most recently visited the burrow before the fight occurred ($P > 0.5$). For the 11 wasps who fought more than once, a 2×11 contingency table revealed no significant individual effect on the distribution of wins and losses (χ^2 for 10 $df = 5.33$, $P > 0.8$). Fights, then, are not obvious foregone conclusions: it seems that an individual could determine whether she wins or not by how hard she fights.

Now to test the Concorde theory. Does the combatant who has put most katydids into the nest fight hardest and therefore win? For each fight we compared the number of katydids that the winner had contributed to the nest with the number contributed by the loser (Fig. 1). The effect is a marginal one, but the winner did indeed tend to be the one who had brought most prey to the nest (Wilcoxon Matched-Pairs test, $P < 0.05$).

We cannot convincingly plead that wasps who are good at fighting also happen to be good at hunting: we have already noted the lack of any individual effect on fighting success, and elsewhere (Brockmann & Dawkins 1979) we present an analysis of variance that indicates no individual effect on hunting success. It might be that the individual who has been longest in the nest genuinely stands to gain more by holding on to it than does the intruder: for instance she might be better able to exploit knowledge of local terrain. But a Wilcoxon test on prior time spent

in the burrow by winner and loser shows no significant difference ($N = 19$, $P > 0.20$). As we shall see below, there is strangely little correlation between time spent in a nest and number of katydids caught. It is hard to resist the suspicion that the wasps are behaving as if following the Concorde fallacy. The data on fight durations lead to a similar conclusion.

Fights over well-stocked nests might ideally last longer than fights over empty nests: both combatants have more to gain by winning, in comparison with whatever costs there may be (injury, wasted time, etc.) and therefore both will be less likely to give up. Fight duration did, indeed, turn out to be correlated with the number of katydids in the nest (Kendall $\tau = 0.39$, $N = 23$, $P < 0.01$, Table I). There is nothing necessarily Concordish about this result. But consider what determines how long a fight lasts. It takes two to fight and only one to break it off. Presumably the duration of a fight is determined by the decision of one wasp to leave. That one, by definition, is the loser. On the Concorde hypothesis we should therefore expect the duration of a fight to correlate most strongly with the

number of katydids that the *loser* has contributed to the nest. And, indeed, this is the case ($\tau = +0.55$, $P < 0.0003$). The corresponding correlation between fight duration and the winner's katydid score is only $+0.30$ ($P < 0.05$).

So, the duration of a fight correlates with the total number of katydids in the nest, with the number brought by the loser, and, more doubtfully, with the number brought by the winner. We used Kendall's partial rank technique to eliminate the spurious effects of, for instance, the obvious correlation between the loser's katydid contribution and the total number of katydids in the nest (Table I). Of all the variables that originally appeared to covary with fight duration, only the number of katydids brought by the loser remains convincingly correlated when other effects are held constant ('partialled out'). The individual who has invested least in the nest seems to break the fight off at a moment determined by how much she has invested. This is stark Concordism.

How does the wasp who surrenders know how many katydids she has brought? She is not monitoring the time that has elapsed since she moved into the nest, for this time is correlated neither with the number of katydids she has brought ($\tau = +0.03$) nor with fight duration ($\tau = -0.05$). Evidently 'prior effort' is measured not in units of time but in something more directly associated with catching katydids. She is also not counting the katydids actually in the nest, for she would then take note of the winner's quota as well as her own. Perhaps she is tallying her own stings, or metering the effort of manhandling across difficult country prey nearly as heavy as herself.

Rationalization

How *could* wild animals, in the teeth of natural selection, commit the Concorde fallacy? The question is instructive, for it epitomizes some of the general problems that are raised by the current fashion for interpreting animal behaviour in terms of 'optimality' (McCleery 1978; Maynard Smith 1978; Oster & Wilson 1978). Normative ethology, the study of what animals ought to do in comparison with what they actually do, is easily misunderstood. Above all, it is important to realize that the theory of natural selection itself is not under test; it is assumed. As Maynard Smith (1978) has said, '... we are *not* testing the general proposition that nature optimizes, but the specific hypotheses about constraints, optimization criteria, and

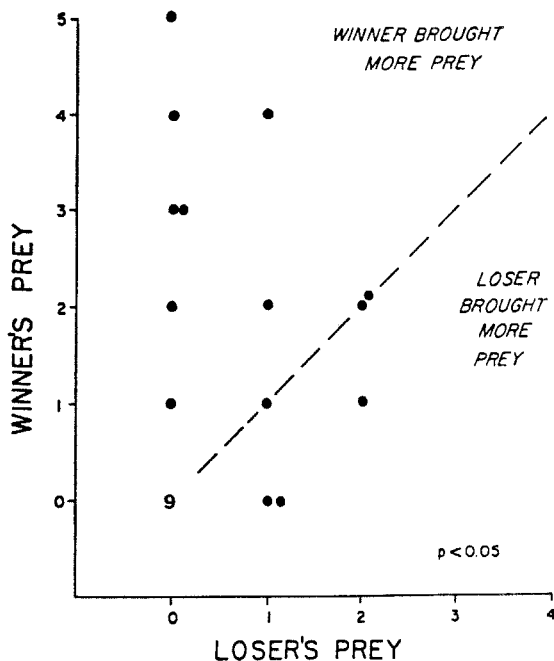


Fig. 1. Number of katydids brought by the winner of each fight plotted against number brought by the loser. (To avoid congestion, the nine fights over empty burrows are represented by a single '9'.)

Table I. Kendall Rank Correlations Between Fight Duration and Various Measures of Prior Investment in a Disputed Nest

Variable correlated with fight duration	τ	P	Variable held constant in partial correlation:				
			Loser's prey	Winner's prey	All prey	Loser's time	Winner's time
Loser's prey	0.55	< 0.0003		0.53	0.45	0.56	0.54
Winner's prey	0.30	< 0.05	0.22		0.09	0.31	0.27
All prey	0.39	< 0.01	0.18	0.29		0.41	0.37
Loser's time	- 0.05	> 0.3	- 0.09	- 0.10	- 0.12		- 0.04
Winner's time	0.17	> 0.1	0.11	0.09	0.07	0.16	

The left two columns give the simple correlation coefficient τ and the associated P value. The other columns give partial correlations when the variable indicated in the column heading is held constant. 'Prey' means number of prey brought by winner, loser or both (all), and 'time' means the amount of time the winner or loser spent associated with the nest.

heredity. Usually we test whether we have correctly identified the selective forces responsible. . .'

An engineer given *carte blanche* on his drawing board could design an 'ideal' wing for a bird, but he would demand to know the constraints under which he must work. Is he constrained to use feathers and bones, or may he design the skeleton in titanium alloy? How much is he allowed to spend on the wings, and how much of the available economic investment must be diverted into, say, egg production? The concept of an optimum is meaningless unless the allowed costs and other constraints are specified. It may be that, given certain plausible constraints, the Concordian policy of the digger wasps is a serviceable rule of thumb. What kind of constraint might be imposed?

We have independent evidence (Brockmann & Dawkins 1979) that these wasps cannot, or at least do not, distinguish an empty, abandoned burrow from one that is occupied by another wasp. This lack of discrimination constitutes one of the main assumptions of a mathematical model of evolutionarily stable nesting strategies, a model with some impressively successful predictions (Brockmann et al. 1979). Now, if a wasp cannot tell an occupied burrow from an abandoned one, it is only to be expected that she might not be able to count katydids in a burrow. The inability to count katydids might be the constraint we are seeking. If a wasp lacks the equipment to measure the true katydid content of a burrow, but can assess her own contribution to it, the Concorde 'fallacy' becomes a good available rule of thumb. There is, after all, a correlation between her own contribution to the katydid content and the true worth of the burrow.

There is no need to regard such a constraint as binding for all time. Great golden digger wasps

probably could, at some cost, evolve the sensory and nervous ability to count katydids in the nest; indeed other species of digger wasps are known to have some such capacity (Baerends 1941). But these *Ammophila* wasps are progressive provisioners, and the selection pressures in favour of the ability to assess the content of the nest could well be strong enough to outweigh the costs. Although *Sphex* individuals might gain slightly from the ability to count katydids, it is likely that the gains would be insufficient to justify the extra expenditure on sensory and nervous equipment.

The Concorde 'fallacy', then, may be an adequate rule of thumb given plausible economic constraints. But we must also remember the important distinction between what a designer thinks of as 'good design', and what is evolutionarily stable (Maynard Smith 1974; Dawkins 1980). A strategy is said to be evolutionarily stable against a specified list of alternatives if, given that the frequency of its use in the population exceeds a critical value, selection favours none of the alternatives. In Maynard Smith's terms, the Concorde strategy could be written: 'surrender when the fight has lasted for a time t which is proportional to the number of katydids that you yourself have put into the nest'. Our intuitive surprise at the wasps' Concordian behaviour must be translated into the precise expectation that this Concorde strategy should be evolutionarily unstable: a population dominated by the Concorde strategy should be invaded by some alternative mutant strategy. But *what* alternative?

Our subjective conviction that an 'ideal' wasp would fight hardest for a burrow that was rich in katydids, regardless of who had caught them, can also be expressed in terms of a precise

strategy, which may be called the 'shrewd economist' strategy: 'fight for a time t which is proportional to the total number of katydids in the burrow'. The shrewd economist strategy, of course, requires the feat of discrimination discussed above. But apart from this the problem with the shrewd economist strategy is that, if everybody pursued it, a great deal of time would be wasted. In each encounter both wasps would surrender simultaneously, after a long fight if the burrow was valuable, and after a short fight if the burrow was not valuable. In practice, presumably, random factors would determine which one surrendered first.

It now becomes clear that the shrewd economist strategy, for all that it originally seemed more 'sensible' than the Concorde strategy, is no more likely to be evolutionarily stable. A population dominated by shrewd economists would quickly be invaded by some other strategy. A simple example of a strategy that would invade is the 'penny-tossing' strategy: 'on a random half of your encounters, give up immediately without a fight; on the remaining half of your encounters persist indefinitely until your rival surrenders'. In a population dominated by shrewd economists, a single penny-tosser would be guaranteed to win half of her fights, at no greater cost than a typical shrewd economist, and she would waste no time over lost fights. A single shrewd economist in a population of shrewd economists would also win half her fights on average, but she would waste large quantities of time over the fights that she lost. Therefore the shrewd economist strategy is not evolutionarily stable against penny-tossers.

The above argument does not necessarily suggest that the penny-tossing strategy is stable either. A population dominated by penny-tossers could itself be invaded, yielding a form of 'war of attrition' (Grafen in preparation). The penny-tossing strategy does not seem, in itself, sufficiently interesting or plausible to justify our pursuing the matter to the lengths of constructing a detailed mathematical model. The penny-tossing strategy has served its purpose of toppling the shrewd economist from his pedestal. It is a task for the future to discover whether there exist plausible constraints under which the Concorde strategy might prove to be evolutionarily stable against realistic alternatives. The present discussion has at least shaken our confidence in

human subjective judgment as to what constitutes 'good design' in biology.

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