

Evolutionarily Stable Nesting Strategy in a Digger Wasp

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Two alternative “strategies” will not coexist in a population unless on average they are equally successful. The most likely way for such an equilibrium to be maintained is through something equivalent to frequency-dependent selection. Females of the digger wasp *Sphex ichneumoneus* (Sphecidae) nest in underground burrows. They usually dig and provision these by themselves but occasionally a nest is jointly occupied. The two wasps fight whenever they meet and in the end only one of the two females lays an egg in the shared nest. Two models based on the theory of mixed evolutionarily stable strategies were developed and tested on comprehensive field data from two North American populations of these wasps. The first model proposes two strategies called *founding* and *joining*. Founders start burrows alone, but they are more successful when they are joined by a joiner. At equilibrium founders and joiners are equally successful, which amounts to an amicable, sharing relationship. The predictions of this amicable model are decisively rejected by the data. The second model proposes two strategies called *digging* and *entering*. Diggers dig their own burrows but they often have to abandon these burrows because of temporary unsuitability. Enterers move in later, thereby exploiting abandoned burrows as a valuable resource. They do not distinguish an abandoned burrow from one that is still occupied. Therefore sharing of burrows arises as an unfortunate byproduct of selection for entering abandoned burrows, and Model 2 is not an amicable model. Its quantitative predictions are impressively fulfilled in one population, though not in another population. This is one of the only examples yet known of a mixed evolutionarily stable strategy in nature. Yet the word strategy itself can confuse, and this paper tries the experiment of substituting “decision”, defined as a moment at which the animal commits future time to a course of action.

1. Introduction

A fashionable idea in modern ethology is that there may coexist among the animals of one population more than one alternative strategy for achieving the same functional end. For instance male crickets (*Gryllus integer*) have been divided into “callers” and “satellites” (Cade, 1978). Callers sing to attract females. Satellites do not sing, but lurk close to a caller and intercept females

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as they approach him. Some male mammals appear to avoid fighting for harems and concentrate on "sneaking" copulations instead. Gadgil (1972) gave examples and made an important theoretical point which is still too frequently overlooked and which nowadays may be subsumed under the theory of evolutionarily stable strategies—ESS (Maynard Smith & Price, 1973; Maynard Smith, 1974; Maynard Smith & Parker, 1976; for a simple account see Dawkins, 1976). This is that if the two strategies are genuine functional alternatives which coexist in the population for an appreciable time they must on average be equally successful. If they were not, natural selection would soon remove the inferior one from the population. In many of the alleged examples in the literature (see Dawkins, *in press*) this rigorous condition is probably not met: either, one of the two is in the process of disappearing through natural selection, or they are not truly two alternative strategies at all but one "conditional strategy" such as "if large, fight; if small, sneak". Yet there may still be one or two authentic cases of equally successful alternative strategies maintained in a state of evolutionary stability (Parker, 1978). Here we present clear evidence of such a case.

It is too much to expect that the costs and benefits of the two alternatives should just happen to balance up exactly. The agency most likely to maintain evolutionary stability in the long term is equivalent to the frequency-dependent selection long ago invoked by Fisher (1930) in his theories of the sex ratio and of balance in mimic populations. The idea is that when the two strategies exist in the population at a particular equilibrium frequency relative to one another they prosper equally. If the proportion in the population should drift away from equilibrium, selection favours whichever strategy has temporarily drifted down in frequency. So the equilibrium is restored.

It is one of the strengths of ESS theory that it manages to apply the same mathematics to two quite different kinds of equilibrium. One is balanced genetic polymorphism. The other is the possibility that each individual might use two alternative behaviour patterns in random order but with relative frequencies stabilized by natural selection. "Sneak with probability 0.7, fight with probability 0.3" is a single mixed strategy. If it is evolutionarily stable this means that, when more than a critical number of individuals is following it, no other strategy, such as "sneak with probability 0.6" or "sneak with probability 0.8" does better. The important point is that evolutionary stability may be achieved by any combination of polymorphism and mixed strategy that leads to the correct equilibrium ratio of behaviour patterns in the population as a whole. A polymorphism of pure fighters and pure sneakers in the correct ratio would be just one end of a continuum, the other end of which would be a uniform mixed strategy.

But this leads us into a terminological difficulty. What are we going to label

“a strategy”? We referred to calling in crickets as a strategy, and satellite behaviour as another. But in that case we must use “ESS” to stand for “evolutionarily stable *state*” (Taylor, in press), because it is not one strategy that is stable but the state of balance between two of them. If, however, we have a mixed strategy with a probabilistic decision rule, ESS may stand for evolutionary stable strategy. But in that case calling and satellite behaviour, fighting and sneaking, or whatever they are, should not be called two “strategies” but two stochastic outcomes of one mixed strategy. In this paper we follow the current convention of using the word strategy for each of two behavioural paths to the same end, although the example we analyse turns out to be closer to a single mixed strategy than to a true polymorphism. But we are uneasily conscious that ESS theorists are soon going to have to standardize their terminology. As a contribution to this, we try the experiment of substituting the less ambiguous term *decision*, to be defined below.

We shall report two behavioural paths to the same end, two “strategies”, coexisting in a population of great golden digger wasps (*Sphex ichneumoneus* L.; Hymenoptera, Sphecidae). We demonstrate, using field data, that the two alternatives are equally successful at observed frequencies in a population in New Hampshire, and we develop and test a model of the stabilizing selection which maintains the equilibrium. A more detailed account of the behaviour and a discussion of the model’s relevance to the evolution of eusociality will be found in a companion paper (Brockmann & Dawkins, in prep.). The companion paper also gives the statistical justification for many of the facts quoted in the present paper.

2. Biological Background

The normal nesting behaviour of *Sphex ichneumoneus* begins with the female digging a burrow at the bottom of which is a side tunnel ending in an oval brood chamber. She then goes out to fields and hedgerows where she hunts katydids (Orthoptera, Tettigoniidae), paralyses them by stinging, and brings them back to the burrow (Brockmann, 1976). Having accumulated a cache of from one to six katydids, a process which takes from one to ten days, she lays a single egg on the food store, fills in the brood chamber with soil, and begins the cycle again. At this point she may either fill in the whole burrow and dig a new one, or she may dig a new side tunnel and brood chamber higher up in the same main shaft. Meanwhile the larva hatches in its chamber, feeds on the katydids until the food is gone, spins a cocoon in which it remains throughout the winter, pupates the following spring, and emerges as an adult in the early summer. The adults all die at the end of the summer.

Little is known of the males, but the females usually dig their own nests in

the same general area as they themselves hatched. In this way "traditional" breeding aggregations develop where several dozen females can be reliably found nesting year after year. The wasps are conventionally regarded as solitary, but occasionally two individuals co-occupy the same nest: while the wasp who dug the burrow is out hunting katydids, a second wasp moves in. This is not a case of "communal" nesting, in which the individuals provision different brood chambers leading off one main burrow shaft (Wilson, 1971; Michener, 1974); our wasps share not only the same burrow but usually the same brood chamber as well (Brockmann & Dawkins, in prep.). They work at provisioning the chamber simultaneously. The two do not often meet because both spend most of their time out hunting. But if they do meet they fight, and the loser usually leaves the burrow for good. The final upshot is that only one of the two wasps ever lays an egg on the jointly provided cache of katydids. It was this appearance of a "winner take all" game that first suggested to us the applicability of ESS theory. The theory of evolutionarily stable strategies was rich in cunning speculation but poor in hard data, and the first author's comprehensive records of individual wasp behaviour and economics seemed capable of filling an important gap.

3. The Data

Brockmann (1976) studied colour-marked individuals in the field. At a site in Exeter, New Hampshire, referred to as NH, all the 30 females in the area were watched continuously through the daylight hours. With a few inevitable breaks of only minutes at a time, the moment by moment actions of all the wasps while at their nests were recorded from 24 July to 22 August 1975, most of their adult life. Similarly comprehensive observations were made for three populations at a site in Dearborn, Michigan, referred to as MI. In 1973 18 MI wasps were observed, in 1974 12 wasps, and in 1975 eight (with the help of an assistant, T. Manning). In all, this represents over 1500 h of observation, and is a nearly complete record of the histories of 410 burrows and of all the nest-related activities of 68 wasp lifetimes. We know when each one of the wasps in the area dug a burrow, when she left on each hunting trip, when she was joined by a second wasp and which wasp it was who joined her, when she temporarily filled in the burrow for the night, and when she brought in the last katydid, permanently filled in the nest and began a new cycle.

Excavation of a sample of burrows established that a wasp almost never went through the highly characteristic motions of permanently filling a nest unless she had just laid an egg in it. We therefore use permanent filling as an indicator of egg-laying. We also know the approximate size of each katydid caught. Every time a female returned with a prey she left it outside the burrow

while she went in for a quick inspection. Before she re-emerged the katydid was swiftly measured and replaced.

We shall use these data to test two models. Model 1 will be rejected, but its development and rejection are instructive and pave the way for Model 2 which is supported by the NH data. The MI data do not support either model, and we postpone consideration of them until the end of the paper. Because Model 1 is simpler it will be used for the explanation of various general points which are equally applicable to both models. We begin with one of these, the use of the decision concept.

4. Decisions in Model 1

Model 1 postulates two alternative behavioural routes to the same functional end—the laying of a properly provisioned egg in a secure underground chamber. The two alternatives are called “founding” and “joining”. Joiners do not dig a burrow in the manner described. Instead they short-circuit the labour of digging by attempting to move into the burrow of another wasp—a founder—and take it over.

We know that we are not dealing with a polymorphism. Any given individual sometimes founds and sometimes joins. Throughout her life she takes a series of decisions, or choices between founding and joining. A decision is defined as a commitment of a period of future time (Dawkins & Dawkins, 1973). In the present case each decision commits the wasp concerned to a period of association with a particular burrow. When she takes a joining decision she begins her period of association with a burrow by joining an already established foundress. All wasp/burrow associations which do not begin with a joining decision must begin with a founding decision. A founding wasp begins her association with the burrow alone; she may or may not subsequently be joined. A temporary foray into another wasp's nest is not considered to be a true joining decision. To qualify as having committed herself to joining, a wasp has to return to the burrow after leaving it for the first time.

An individual female typically packs a dozen or so decisions into her brief life. ESS theory predicts that the overall frequency of joining decisions in the population is adjusted by natural selection to the level at which a typical joining decision is exactly as successful as a typical founding decision. How are we going to measure “success” in order to test this prediction?

5. Measuring Success Rate

The first thing to note is that, since there is not a polymorphism, we are not interested in measuring the lifetime success of particular individuals. We want

to measure the success of a type of decision, averaged over all individuals who make it and across all occasions on which it is made. What would a successful decision be? It would at least have to result in the wasp concerned laying a properly provisioned and securely housed egg. We have no information on subsequent hatching success, and can only record whether or not an egg was laid (strictly whether the wasp showed permanent filling behaviour), and how much food it was laid upon.

This gives us two practical measures of B , the benefit resulting from a particular decision. When the burrow concerned has only one chamber, the calculations are straightforward. The "egg score" is simply 1 if the wasp succeeded in laying an egg (i.e. showed permanent filling behaviour) on that occasion, 0 otherwise. The "food score" is also 0 if the wasp failed to lay an egg. If she succeeded, the food score is the volume of food upon which the egg sits (the volume of a katydid is regarded as the cube of its length). But things were not always so simple. A decision is a commitment to one burrow, but this may involve association with a succession of brood chambers within that burrow. In this case the egg score of a decision is the total number of eggs which the wasp concerned laid in the whole burrow, and the food score is the sum of the food scores for the separate chambers in which she laid an egg. These success scores are always credited to the decision which originally initiated her period of association with the burrow.

The rationale for using the food score as well as the plain egg score is this. A wasp who consistently skimped on katydids might run up an impressive egg score but each egg would have low subsequent success because the larva would be inadequately nourished. But just as the egg score probably underestimates the role of food in determining true reproductive success, the simple length-cubed food score probably overestimates it: obviously more means better only up to a point. Fortunately, as far as the predictions of our two models are concerned, the two measures of benefit give almost identical results. We shall quote both sets of results, but for purposes of explaining we shall normally use the egg score because it is simpler.

In any case, as the "optimal foraging" theorists have taught us (e.g. Pyke, Pulliam & Charnov, 1977), a vital quantity has so far been left out of the reckoning—time. It takes time to dig a burrow, time to catch a katydid, precious, limited time, for all the wasps die at the end of the six summer weeks of the nesting season. The appropriate measure of success is a *rate*, B/T , the benefit accrued divided by the time taken to accrue it. The time taken over each burrow is measured from the moment at which the wasp left her previous burrow for the last time. Every minute of her adult life is accounted as spent on one burrow or another. Transit time between one burrow and the next is debited to the second of the two: it is "searching time" or "preparing time"

(Larkin & McFarland, 1978). The success rate of a type of decision is the total benefit B accrued on all occasions when that type of decision was made, divided by the total time, T , spent by wasps on burrows with which they began their association by making that type of decision.

An example may make this clear. At 1330 on 9 August, wasp red/red/yellow (RRY) abandoned her burrow when it was invaded by ants. At this moment we restart our accounting clock, although the decision which is running up the time debt is still in the future. She wandered around the nesting area for the rest of the afternoon, looking furtively into other wasps' nests and occasionally making tentative digging movements. The next morning at 1000 she entered a burrow already occupied by green/green/green (GGG). She returned later that day and is now definitely identified as having made a joining decision. The time "debt" of the joining decision is "back-dated" to the moment at which she left her previous burrow. Both wasps continued to provision the nest regularly, and brought five katydids between them. Then on 13 August at 0800 they both happened to return at the same moment. A fierce fight ensued and GGG ("founder") chased RRY ("joiner") from the nest. RRY never returned to the nest, and her association with it was clocked-off from this moment. She had spent 90.5 h in association with the burrow, and she received no benefit from it since she was driven off before she had a chance to lay an egg. GGG eventually did lay an egg in the joint chamber, and went on to lay another in a new chamber. When she finally left, her association with the burrow had lasted 299 h. She gained a benefit of two eggs. When it comes to computing the food score, GGG is credited with the benefit of all the katydids that her defeated rival caught, as well as her own catches.

We could compute the lifetime benefit and time scores of RRY, GGG, and all the other individual wasps. But this is not the object of the present exercise. RRY joined on this occasion but she sometimes founded; GGG founded, but she sometimes joined. In all, of 136 wasp decisions in NH, 23 were joining decisions and 113 founding decisions. The total number of eggs laid by wasps who, on that occasion, joined, was 8, or 0.348 per decision. The time they spent on joining episodes, whether or not they succeeded in laying an egg, was, in total, 1683.9 h, or 73.2 h per decision. The average B/T score for joining decisions was therefore $8/1683.9$ or 0.48 eggs per 100 h.

Notice that we do not calculate the rate B/T separately for each burrow and then average the rates. This would be like computing the average speed of a car on a journey by looking at the speedometer. Our method is equivalent to working out the car's average speed by dividing total distance by total time. The "speedometer method" is appropriate for measuring variance in success rate, and we do use it for purposes of statistical comparison (Brockmann & Dawkins, in prep.).

Our usage of average success rate is based upon some assumptions. The longevity of a wasp is assumed to be unaffected by the strategic decisions she makes. If joining decisions, for instance, shortened the wasp's life expectation, T would not be a suitable denominator for the success rate. "Joining time" would have to be reckoned in a costlier currency than "founding time". A related assumption is that a wasp ends each episode of one type in the same state as she ends each episode of the other: the slate is wiped clean when the clock is restarted for the new nesting episode, and there is no carry-over of influence from one decision to the next. And, indeed, it is true that decisions are not made in runs (Brockmann & Dawkins, in prep.).

6. Outcomes of Model 1

So far, all we have said of Model 1 is that it postulates two types of decision called "found" and "join". Before we can test it we need to express the model in more detail. It is illustrated in Fig. 1. The basic decision is represented by the bifurcation of arrows on the left. In addition to this decision, which is under the wasp's control, we can also distinguish three possible *outcomes*, which are not necessarily under the wasp's control. If a wasp takes the decision to found, she may be subsequently joined, represented by the box labelled "is joined". Or she may not be joined, in which case the outcome is the one labelled "is alone". The outcome "joins" always results from the decision to join. Which of the two possible outcomes befalls a wasp who has founded her own nest is

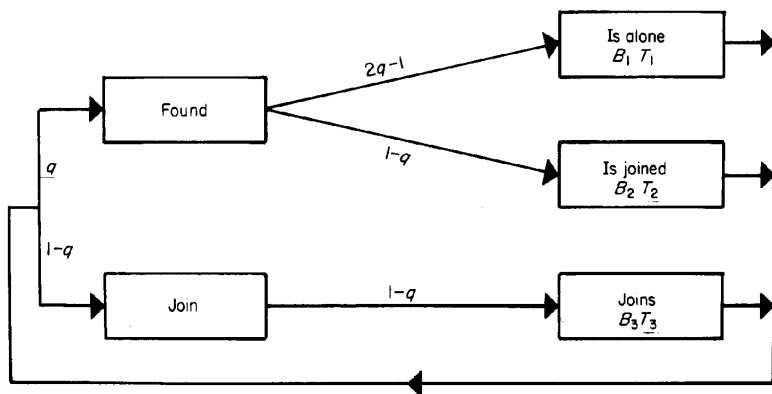


FIG. 1. Model 1: There are two alternative kinds of nesting decisions a wasp can make—a proportion q of the decisions are to "found" a nest and a proportion $1-q$ are to "join" another wasp in her burrow. The "found" decision has two possible outcomes: the wasp either nests alone or she is later joined by another wasp. B_1 , B_2 and B_3 are the average benefits associated with each of the outcomes and T_1 , T_2 and T_3 are the average times spent in each outcome.

determined by the relative frequencies of founding and joining in the whole population. If the proportion of decisions per unit time which are founding decisions is q , the proportion which are joining decisions is $1 - q$. Since for every "joins" outcome there must be one "is joined", the proportion of all decisions per unit time which end up in the "is joined" outcome must also be $1 - q$. (Strictly, this statement should be amended. It is theoretically possible for a founding wasp to be joined in the same nest by two different joiners.) Finally, the proportion of all decisions per unit time whose outcome is "is alone" must, by subtraction, be $q - (1 - q) = 2q - 1$.

A wasp who founds has no control over whether she is subsequently joined, but this does not stop us calculating whether she would be better off joined or not. B_1 , the average egg score for the "is alone" outcome, is the number of eggs laid, per decision, by all wasps who, on that occasion, made the founding decision and were not subsequently joined. Similarly, B_2 and B_3 are the average egg scores for the "is joined" and the "joins" outcomes, and T_1 , T_2 and T_3 are the average times taken, per decision, over nesting episodes for each of the three outcomes. A wasp who decides to join can therefore expect a benefit of B_3 eggs at a cost of T_3 h. For a wasp who decides to found, we must make a more complicated calculation. If she happens to be joined she can expect B_2 eggs, but if she is not joined she can expect B_1 eggs. We know the odds of each of these two outcomes: they are $1 - q$ and $2q - 1$ respectively. So the net expectation is that a wasp who founds will lay, on average $(2q - 1)B_1 + (1 - q)B_2$ eggs per $(2q - 1)T_1 + (1 - q)T_2$ hours. We now apply the central dogma of this paper: at evolutionary stability the average success rate of founding decisions must equal the average success rate of joining decisions, B_3/T_3 . This gives the simple equation

$$\frac{(2q - 1)B_1 + (1 - q)B_2}{(2q - 1)T_1 + (1 - q)T_2} = \frac{B_3}{T_3}. \quad (1)$$

Solving for q , we obtain the testable prediction

$$q = \frac{T_3(B_1 - B_2) - B_3(T_1 - T_2)}{T_3(2B_1 - B_2) - B_3(2T_1 - T_2)}. \quad (2)$$

This equation is the condition for equilibrium, but an equilibrium is not necessarily stable. In order for this one to be stable it is necessary that small perturbations of q away from its equilibrium value should be automatically corrected by natural selection: if founding decisions become more common, joining must receive a higher payoff and vice versa. The condition for stability

in Model 1 can be deduced algebraically from the equation above, and is as follows:

$$\frac{B_2}{T_2} > \frac{B_3}{T_3} > \frac{B_1}{T_1}. \quad (3)$$

In words, independently of frequencies of occurrence, a decision ending in the "is joined" outcome has to be more successful than a joining decision, and both have to be more successful than a decision ending in the "is alone" outcome. (There is an intuitive rationale for this. If the proportion of joining decisions goes up it is obvious that the number of "is joined" outcomes goes up too. For there to be stabilizing selection, when the rate of joining goes up the average success of founding as a whole must go up; the only way this can happen is if the founding outcome that has automatically increased in frequency, namely the "is joined" outcome, is the generally more prosperous of the two. So "is joined" must be more prosperous than "is alone" in order for the equilibrium to be stable. "Joins" has to be intermediate in payoff between the two outcomes of founding: if it was either better or worse than both of them it could not possibly be equal to their average, and we could never have equilibrium.)

Model 1, therefore, is in spirit an amicable, sharing model. Wasps alone do worse than both partners in a shared nest. This would have to mean that the advantages of sharing—presumably getting help in speedy provisioning, and in keeping fly parasites out of the nest (Brockmann & Dawkins, in prep.)—are so great that they compensate for the fact that only one of the two ends up by laying the egg. Intuitively this seems like a heavy gamble for a wasp. The best thing of all, according to Model 1, is to found a nest and then be joined by a second wasp. Next best is not to found, but to join an incumbent. The worst outcome, according to Model 1, is to be left alone after founding a burrow, for either partner in a sharing menage does better than a lone wasp.

This is all very interesting for the theory of the origins of eusociality, and there could be species to which Model 1 is applicable, but the next section suggests that *Sphex ichneumoneus* is not one of them.

7. Testing Model 1 on the New Hampshire Data

The basic assumption of the model is that the average success rate for founding decisions should equal that for joining decisions. Table 1 shows, on the contrary, that founding decisions are approximately twice as successful. The difference is statistically reliable (Brockmann & Dawkins, in prep.). The inequality conditions for stability are also violated by the NH data. Far from

the two sharing outcomes being most successful, the real order of success rates is "is alone" > "is joined" > "joins". As we should expect, the predicted q proportion is also completely wrong.

Model 1, the amicable, sharing model, is decisively rejected. We need a new model, a model in which a wasp does better when alone than when sharing. We go back to the drawing board, and the first thing to do is to look more carefully at the biology of the wasps.

8. Decisions in Model 2

The rationale for Model 1 ignored a vital fact about the wasps. Founders sometimes spontaneously abandon burrows even when no joiner is present. Sometimes there seemed no obvious reason for this. One other occasions the abandoning seemed to be provoked by some catastrophe, invasion by ants, say, or a centipede. The marauder usually left after a while, and the empty burrow was none the worse for it. The original owner had fled, and the burrow was left untenanted and available for easy occupation by another. There was a good surplus of five to ten empty burrows available in the nesting area at any time. Wasp did quite often enter and use burrows which had been abandoned by their original owners.

Perhaps Model 1 postulated the wrong fundamental decision. Maybe there are indeed two alternatives, but they are not found and join, but "dig" and "enter". This is the basis of Model 2. It makes good sense in the light of the actual opportunities available to a wasp. The strategies "founding" and "joining" leap naturally to the mind of a biologist interested in the phylogenetic origins of eusociality. But the decision which actually faces an individual wasp in practice must surely be: shall I enter this hole here, or shall I dig a new one? A wasp who enters a burrow may have no opportunity to even find out whether the original owner is still in occupation until several hours or even days later. Model 2 uses the same 136 wasp decisions as Model 1, but it re-allocates them. In 80 cases the wasp began her association with the burrow by digging it. In 56 cases she began her association with it by entering and adopting it after it had been dug by somebody else. From now on we shall use the word "enter" only in its technical sense as the name of a decision. Once again, we are not talking about a polymorphism. We know that any given individual sometimes dug and sometimes entered, with an overall bias towards digging but not an individually specific bias, and we know that the decisions did not occur in runs (Brockmann & Dawkins, in prep.). When we loosely speak of, for instance, a "digger", we merely mean an individual who on that occasion began her association with the burrow in question by digging it.

TABLE 1

The average success rate of found and join decisions and their outcomes in the New Hampshire population of wasps

Decision	Frequency in pop.	Average success rate B_e/T	Average success rate B_e/T	Outcome	Benefit: B = volume prey provisioned	Benefit: B = number eggs laid	Time T associated with nest	Average success rate B_e/T
Found	0.83 (113)	32.42	0.96	is alone is joined	39.85 33.98	1.18 1.06	116.17 142.96	1.01 0.74
Join	0.17 (23)	13.68	0.48	joins	10.02	0.35	73.21	0.48

B_e/T is the average rate of accruing benefit based on the volume of prey provisioned per 100 h for all decisions or outcomes of this type.
 B_e/T is the average rate of accruing benefit based on the number of eggs laid per 100 h for all decisions or outcomes of this type.

TABLE 2

The success rates of dig and enter decisions and their outcomes in the New Hampshire population of wasps

Decision	Frequency in pop.	Average success rate B_e/T	Average success rate B_e/T	Outcome	Benefit: B = volume prey	Benefit: B = number eggs	Time T associated with nest	Average success rate B_e/T
Dig	0.59 (80)	33.16	0.96	abandons is alone is joined	1.79† 67.04 33.98	0.11† 1.93 1.06	38.97 170.48 142.96	0.28 1.13 0.74
Enter	0.41 (56)	26.81	0.84	joins	10.02	0.35	73.21	0.48

† There is some benefit associated with the abandons outcome because a few burrows are not abandoned until after one chamber has already been completed.

Enterers exploit the available surplus of empty burrows. Sometimes they have the misfortune to enter a burrow which is still occupied by its former owner. In this case they fall into the "joins" outcome which we formerly identified with a strategic decision. But according to Model 2 this is an accident, the worst thing that can happen to an enterer. If she is lucky the burrow she adopts will turn out to have been abandoned by its original owner. Unlike Model 1, then, Model 2 has nothing to do with amicable sharing. Sharing is an unfortunate byproduct of entering. The best outcome for a wasp is to end up alone. She is most likely to achieve this desirable end if she takes the digging decision, but this carries with it the risk that she may have to abandon her burrow after spending time on digging it. If she refrains from digging, and looks for a burrow to enter, she may save time but she runs the risk of finding herself joining an incumbent. If she is fortunate enough to find herself alone, she runs the same risk as a digger of being subsequently joined by a second enterer (Fisher Exact Test $P = 0.46$; Brockmann & Dawkins, in prep.).

Model 2 is more complex than Model 1, and before developing it in detail we should satisfy ourselves that it is going to be worthwhile: is the basic equilibrium assumption upheld? At evolutionary stability Model 2 expects the average success rate for digging decisions to equal that for entering decisions. The total number of eggs laid by wasps who, on that occasion, had begun their association with the burrow by digging it was 82. The total time spent by wasps in association with burrows that they had dug was 8518.7 h. The success rate, B/T for digging decisions is therefore 0.96 eggs per 100 h. For entering decisions the corresponding figures were 57 eggs in 6747.4 h, which gives an average success rate of 0.84 eggs per 100 h. These figures are not identical but they are similar and, together with the comparable figures when benefit is represented by the food score (Table 2), they are encouraging. A one-way analysis of variance of the B/T scores for the separate decisions ("speedometer readings"—see above) suggests no significant difference between the success rates of digging and entering decisions (egg scores, F ratio = 0.0 for 1 and 134 d.f., $P > 0.5$; food scores similar, Brockmann & Dawkins, in prep.). It is therefore believable that digging and entering could coexist in the same population without one of them being removed by natural selection.

So, we seem to have an equilibrium. But is it stable; what keeps it so? Qualitatively the outlines of a model of the necessary stabilizing selection seem clear enough. If too many wasps enter, they will tend to saturate available abandoned burrows, and the risk of an entering decision leading to the undesirable outcome of sharing will become too high. If very few wasps enter, the risk of an enterer finding her chosen burrow already occupied is relatively low. About 41% of all decisions in NH are entering decisions. It is easy to

imagine this as an equilibrium, maintained by selection in favour of entering whenever the percentage drops below 41 % and in favour of digging whenever the entering percentage rises above 41 %. We now proceed to develop a more formal model along these lines.

9. Assumptions and Outcomes of Model 2

An important assumption of Model 2—indeed this is one of its essential differences from Model 1—is that an enterer enters empty versus occupied burrows in proportion to their availability. Intuitively this may seem odd, since it implies that a wasp cannot sense the presence of another, and the model surely predicts selection in favour of such discrimination (see below). Yet there is some empirical evidence for it ($\chi^2 = 2.7$ for 1 d.f., $P > 0.1$; Brockmann and Dawkins, in prep.). It seems less surprising when we reflect that a wasp spends 80–95 % of her time away from her burrow, so the chance of the incumbent being at home at the moment when the new enterer makes her decision is fairly low. Like Model 1, Model 2 assumes that longevity is independent of decision, and that successive decisions are independent of each other. Evidence on the latter point, including a demonstration that the wasps are not deciding in runs, nor using a conditional strategy of the “win-stay-lose-shift” variety, is given in Brockmann & Dawkins (in prep.).

We make two additional assumptions. The first is that the probability that a wasp who has dug a burrow will abandon it is a constant. All this really means is that the likelihood of a given burrow being abandoned is independent of the frequency of digging relative to entering decisions in the population. It seems a reasonable assumption: ants and centipedes are hazards which can assail any burrow at any time. The second assumption is that at equilibrium the rate at which burrows are used up by enterers is equal to the rate at which they are abandoned by diggers. The intuitive rationale for this is as follows. Enterers obviously cannot use up burrows at a faster rate than diggers abandon eventually re-usable burrows. If they did so at a much slower rate, on the other hand, the increasing surplus of re-occupiable burrows would make enterers better off than diggers, and we would not have equilibrium. We assumed that the two rates were actually equal, and further that all abandoned burrows eventually become re-usable. The effect of this is that there is a static market economy of burrows, a fixed stock of empty holes which is being added to at the same rate as it is being drawn upon. Any of these assumptions could be wrong. If so, the predictions of the model will probably also be wrong. A good model is one whose predictions are vulnerable to disproof but are not disproved.

Figure 2 illustrates Model 2 in the same way as Fig. 1 did for Model 1. The

bifurcation on the left represents the initial strategic decision, in this case between digging and entering. Once again we distinguish decisions which a wasp makes from outcomes which just happen. In this case there are four outcomes. "Abandons" is one possible outcome of a digging decision, and it is assumed never to result from an entering decision. "Joins" is one possible outcome of entering, and it cannot result from digging. The other two outcomes, "is alone" and "is joined", can result from either digging or entering. As already mentioned we assume, with justification, that neither of the two decisions is more likely than the other to lead to any particular one of these two outcomes. This assumption is represented by the merging of the two arrows in the centre of the figure; diggers who do not abandon, and enterers who do not join, merge into a single sub-population of "foundresses". Of these foundresses, a proportion r are subsequently joined, and a proportion $1 - r$ remain alone.

Of all the decisions which occur in a given time, a proportion w lead to the "abandons" outcome, a proportion x are digging decisions that do not lead to the "abandons" outcome; a proportion z lead to the "joins" outcome, and

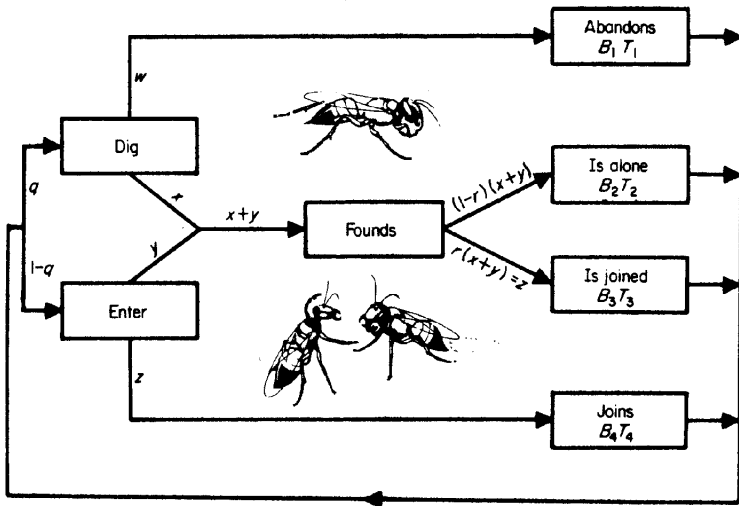


FIG. 2. Model 2: There are two alternative kinds of nesting decisions a wasp can make: dig and enter. A digging decision may result in one of three outcomes. The wasp may abandon her burrow, or she may found a nest in which case she may remain alone or she may be joined by another wasp. An entering decision may also result in one of three outcomes. A wasp may join another in her nest or she may found a nest of her own in which case she may end up nesting alone or in company with another wasp. B_1 , B_2 , B_3 and B_4 are the average benefits associated with each outcome and T_1 , T_2 , T_3 and T_4 are the average times spent in each outcome.

a proportion y are entering decisions that do not lead to the "joins" outcome. $w + x + y + z = 1$. $w + x = q$, the proportion of all decisions which are digging decisions. $y + z = 1 - q$. $x + y$ is the proportion of all decisions which result in the wasp becoming one of the sub-population called foundresses. $r(x + y)$ is the proportion of all decisions which lead to the outcome "is joined". This must equal z , since for every "is joined" outcome there has to be one "joins" outcome (with the same reservation as mentioned earlier).

As in the case of Model 1, we measure average benefit scores and time scores for each of the four outcomes. T_1 is the time per decision spent on burrows which are eventually abandoned. T_2 is the corresponding time spent on burrows which are occupied alone, and T_3 is the time per decision spent by wasps who, on that occasion "founded" (whether they began by digging or entering) but were later joined. T_4 is the corresponding time spent by wasps who found themselves in the "joins" outcome. B_1 , B_2 , B_3 and B_4 are the corresponding benefit scores, either egg scores or food scores.

A wasp who decides to dig can expect to lay a number of eggs which is a weighted average of B_1 , B_2 and B_3 . A wasp who decides to enter can expect a corresponding weighted average of B_2 , B_3 and B_4 . The times they spend will be homologously weighted averages of the corresponding T scores. The weighting factors are the frequencies with which the various outcomes occur. These are variables in the model, where the B and T scores are parameters. We can read them off Fig. 2 as w for the abandoning outcome, z for the joins outcome, $r(x + y)$ for the "is joined" outcome and $(1 - r)(x + y)$ for the "is alone" outcome (where r , it will be remembered, is a short-hand symbol for the proportion of foundresses who are joined, i.e. $z/(x + y)$). The average expectation for a wasp who enters is, therefore $(zB_4 + yrB_3 + y(1 - r)B_2)$ eggs per $(zT_4 + yrT_3 + y(1 - r)T_2)$ h. The corresponding expected success rate for a wasp who takes the digging decision is $(wB_1 + xrB_3 + x(1 - r)B_2)$ eggs per $(wT_1 + xrT_3 + x(1 - r)T_2)$ h.

At evolutionary stability these two success rates must be equal. Therefore we may set up the simple equation

$$\frac{wB_1 + xrB_3 + x(1 - r)B_2}{wT_1 + xrT_3 + x(1 - r)T_2} = \frac{zB_4 + yrB_3 + y(1 - r)B_2}{zT_4 + yrT_3 + y(1 - r)T_2}. \quad (4)$$

The four B and four T scores are measured parameters, in terms of which any one of the variables might be expressed. At first sight there appear to be too many unknowns in the equation, namely w , x , y , z and r , but we dispose of all but one as follows. r , as we have seen, is simply a short-hand expression for $z/(x + y)$. By definition, $w = 1 - x - y - z$. Our economic assumption that the

rate of recruitment to the pool of available burrows equals the rate at which burrows are used up may be written in the form $y = w$, therefore $y = 1 - x - y - z = (1 - x - z)/2$. Finally, we use our assumption that the probability of a burrow being abandoned is constant. If this constant is K , then $K = w/(w + x) = y/(y + x)$. K is used as a parameter like the B and T scores, and is measured from the NH field data as 0.4625. By means of these supplementary simultaneous equations we can solve our main equilibrium equation, treating any one of the variables as the unknown. We arbitrarily chose to solve for z . z as an algebraic function of the B , T and K parameters is very complicated so we do not give it here, but simply give the predicted value of z from the nine measured parameters. Having obtained the predicted value of z , we can then easily deduce the predicted values of w , x , y and q from it.

The stability condition is also complicated, and so not presented here. It is readily calculated once the rates of benefit of the two decisions are expressed as functions of q ; it is only necessary to check that the rate for enterers increases faster than the rate for diggers as q increases. The stability condition is met by the NH data.

10. Testing Model 2 on the New Hampshire Data

Table 3 summarizes the terms and equations of Model 2. Table 4 gives the tests of the predictions. Separate sets of predictions of the four proportions, w , x , y and z are given, one deduced using egg scores for benefit, the other deduced using food scores. Since the four predicted values are proportions which necessarily add up to 1, we really only have three predictions.

The fit of observed to predicted proportions is very close, so close that we should clearly state again which measured parameters were used in making the predictions. In addition to the four B scores and the four T scores we also used the measured value of K , the proportion of dug burrows which were abandoned. K determines that the ratio between the predicted w and x necessarily agrees with the observed ratio. It does not determine the actual magnitudes of w and x .

It is important to stress that this is very much *not* the kind of model where one fits parameters to observed results so comprehensively that the "predictions" almost cannot help being right. Our predictions really were genuine predictions, and they could very easily have come out wrong. In particular, the fact that we estimated the parameter K did not make the predictions trivial. This can be demonstrated by the following rough randomization test.

Suppose we recalculated our predictions using, not the observed mean value of T_1 , but a smaller value, or a larger value. How much difference would it have made to the predictions? Might the fit of predicted to observed z

TABLE 3
Summary of variables and equations for Model 2

Definitions

- w* Proportion of all decisions which are followed by the digger abandoning her nest
x Proportion of all decisions which are followed by the digger occupying the nest she dug, i.e. founding
y Proportion of all decisions which are followed by the entering wasp occupying a nest, i.e. founding
z Proportion of all decisions which are followed by the entering wasp occupying an already occupied burrow, i.e. where the enterer joins another wasp
r Proportion of all foundings which are followed by the founder being joined by another wasp
-

Equations

$$w + x + y + z = 1 \quad (\text{by definition})$$

$$\frac{w}{w+x} = K \quad (\text{by assumption})$$

$$z = r(x+y) \quad (\text{by assumption})$$

$$w = y \quad (\text{by assumption})$$

$$\frac{wB_1 + x(1-r)B_2 + xrB_3}{wT_1 + x(1-r)T_2 + xrT_3} = \frac{zB_4 + y(1-r)B_2 + yrB_3}{zT_4 + y(1-r)T_2 + yrT_3} \quad (\text{equilibrium assumption})$$

have come out even better? If so, we would not be so impressed by the goodness of fit we actually obtained.

Rather than play around, piecemeal, with artificially distorted values of our eight parameters, we adopted a systematic randomization procedure. For each of the four *B* (egg scores) and four *T* parameters we made the computer choose a random number from a normally distributed population having a mean and standard deviation equal to the appropriate observed mean and standard deviation (the distributions were truncated to avoid negative values). We then recalculated our model prediction of *z* using these randomized parameters instead of the real ones. If the goodness of fit of the computer prediction to the observed *z* had been better than the one in Table 4, this would have weakened our confidence in the model's power to explain the real world. In fact this happened in only 9 out of 1000 separate runs of the simulation, less than 1%. On the remaining 991 occasions, the simulated prediction gave a less good fit to the observed value of *z* than our own real prediction. We conclude that Model 2 is highly sensitive to the data which are fed into it, and that it would be remarkably difficult to obtain, by chance, as good a result as the wasps actually gave.

TABLE 4

A comparison between the predicted rates of various outcomes and the observed rates in the New Hampshire population

Proportion that		Observed	Predicted <i>B</i> = eggs	Predicted <i>B</i> = food volume
<i>w</i>	dig then abandon	0.272	0.257	0.260
<i>x</i>	dig and do not abandon	0.316	0.298	0.303
<i>y</i>	enter and do not join	0.243	0.257	0.260
<i>z</i>	enter and join	0.169	0.188	0.176

This conclusion is ironically borne out by the total failure of the model to predict the results in the other study area, in Michigan.

11. Testing the Models on the Michigan Data

The Michigan data disprove the predictions of Model 1 as decisively as the New Hampshire data did, but in a different way. Joiners do far better than they did in NH. Indeed they do about as well as founders do (Table 5). But although this might look like an equilibrium, the conditions are not met for it to be stable. The "joins" outcome and "is alone" outcome both have a higher success rate than the "is joined" outcome. Model 1 cannot give a stable equilibrium under these conditions. We must reject the amicable, sharing model here, as in the New Hampshire population, but in this case because joiners are doing so much better than those they join.

But whereas Model 2 successfully accounted for the New Hampshire data, the Michigan data seem irreconcilable with it. Table 6 shows that entering decisions are more successful than digging decisions. One-way analysis of variance shows that enterers lay more eggs than diggers ($F = 5.85$, for 1 and 272 d.f., $P < 0.05$) and bring more food ($F = 5.17$, $P < 0.05$) and they take no longer over it ($F = 3.0$, $P > 0.05$). Selection, then, should be severely penalizing digging decisions and increasing the frequency of entering decisions.

Is Model 2, perhaps, basically applicable to the Michigan population, but the relative frequency of enterers happens to be below equilibrium at present? If this were so, we should be able to solve the equation of Model 2 to predict how far the swing back toward entering should go: what is the predicted equilibrium frequency? The equation is a quadratic. For the particular values of the nine parameters which were measured at the Michigan site, there are no real roots to the equation: there is no equilibrium frequency at which the two strategies would have equal success rates. Computer simulation shows that,

TABLE 5

The success rates of found and join decisions and their outcomes in the Michigan population of wasps (1973-1975 combined)

Decision	Frequency in pop.	Average success rate B_e/T	Average success rate B_e/T	Outcome	Benefit: $B =$ volume prey	Benefit: $B =$ eggs laid	Time T associated with nest	Average success rate B_e/T
Found	0.95 (259)	48.18	1.69	is alone is joined	32.13 35.99	1.12 1.42	63.56 139.11	1.76 1.02
Join	0.05 (15)	53.54	1.86	joins	19.23	0.67	35.92	1.86

TABLE 6

The success rate of dig and enter decisions and their outcomes in the Michigan population of wasps (1973-1975 combined)

Decision	Frequency in pop.	Average success rate B_e/T	Average success rate B_e/T	Outcome	Benefit: $B =$ volume prey	Benefit: $B =$ eggs laid	Time T associated with nest	Average success rate B_e/T
Dig	0.84 (230)	46.28	1.64	abandons is alone is joined	0.89 64.10 35.99	0.08 2.17 1.42	16.38 110.56 139.11	0.50 1.96 1.02
Enter	0.16 (44)	56.49	1.91	joins	19.23	0.67	538.8	1.86

according to the model, enterers would have the advantage over diggers at all frequencies. Diggers should not exist! This is biologically absurd, since there would be no burrows to enter unless the species was an interspecific parasite, which it is not. We cannot, then, salvage Model 2 in Michigan by saying that the population is temporarily away from equilibrium, and is in the process of returning there. We do not understand why the model does not work there, and can only make guesses.

12. What Might We Learn from Model 2's Failure in Michigan?

The failure of a model can be illuminating if it leads us to re-examine our assumptions constructively. Certain of Model 2's assumptions are so basic that to tinker with them would amount to setting up a whole new model. For instance we assumed that the expected benefit and time scores of the four "outcomes" are constant parameters. What would happen if they were frequency-dependent, or density dependent? Is there, perhaps, a Model 3 which replaces "dig" and "enter" by some completely new set of "strategies"? "Join a burrow only if it has at least three katydids in it" should be far more successful than Model 1's "join" and Model 2's "enter". The evidence goes against the wasps having the necessary powers of discrimination (indeed they appear to commit the "Concorde Fallacy" of valuing a nest in proportion to their own prior investment in it, Dawkins & Brockmann, in prep.). But we must not rule out some kind of radical redefinition of the decision options.

Other assumptions of Model 2 seem less fundamental. For instance the "static burrow economy" assumption, $y = w$, might be replaced by $y = uw$, where u is a constant representing the probability that an abandoned burrow can be re-used. In effect the Model 2 which we tested was the special case with $u = 1$. As a matter of fact it is true that u is close to 1 in NH ($u \geq 0.83$, since 0.83 of the abandoned burrows were actually re-used) whereas in MI only 0.27 of the abandoned burrows were re-used. Such a gross violation of an assumption might help to account for Model 2's failure in MI. Out of curiosity, we did try the experiment of plugging the observed minimum value of u into Model 2: the fit to the NH data became even more impressive, but still no stable solution could be found for the MI data. Indeed we showed that *no* value of u exists such that Model 2 even comes close to making realistic predictions for the MI economic data: the violation of the assumption that $y = w$ is therefore not sufficient to explain the failure of Model 2 in MI. This is an instructive result in itself. Incidentally, the low value of u in MI could just as well be an inevitable *consequence* of there being fewer enterers than expected, rather than the cause of Model 2's failure.

Setting aside the strong likelihood that Model 2 is fundamentally wrong in

MI, we now turn to the second potentially instructive possibility. This is that Model 2 is right but that something is wrong with our data. For instance our assumption that egg-laying success is a good estimator of fitness may be approximately true in NH but false in MI. This could arise if there is a larval or pupal disease in MI which differentially infects shared nests. The important point is that the B scores which we measured may not be the ones which truly apply in MI, and that the overestimate is greatest for shared nests. The latter proviso is needed, since to divide all the B scores by a common mortality constant would leave the predictions unchanged.

Another interesting possibility is that the MI wasps are really adapted to some environment other than the one in which they were studied. If MI conditions have recently changed, the wasps could simply be "out of date". Or there might be continual gene flow into the study area from outlying populations in which digging is more strongly favoured. Incidental observations, and reports from local amateur entomologists, did indeed suggest that the MI aggregation, but not the NH one, was surrounded by outlying lone wasps for whom entering would presumably be bad policy. It is not implausible, then, that the MI study site is subject to a continuous inflow of digger genes which maintain the study site population away from its equilibrium point, thereby inducing continuous selection in favour of entering at the study site itself.

In all this, it should be remembered that the MI population is not behaving as though in accordance with Model 2 but away from the equilibrium point. Something more fundamental is wrong with Model 2 in the Michigan population. The suggestions arising out of this failure should be regarded as stimulation to further work. Meanwhile we return to New Hampshire.

13. What Might We Learn from Model 2's Success in New Hampshire?

If a model's predictions are successful we are entitled to regard this as evidence that its assumptions represent truth about the real world, not overwhelming evidence, but still evidence. We can, therefore, list the assumptions of Model 2, not merely as assumptions but as putative facts about the New Hampshire population of wasps for which we have provided some indirect evidence. They are:

(1) There exist two alternative nesting "strategies" called "dig" and "enter" in the population. This is not a polymorphism in which individuals are consistent specialists. Rather each individual intersperses through her adult life a sequence of choices between the two alternative behaviour patterns. This could be regarded as a simple *mixed* strategy.

(2) The wasps cannot distinguish an empty abandoned burrow from one

that is still occupied by an incumbent. This is a surprising result since the model also predicts selection in favour of such discrimination.

(3) Burrows are re-occupied by enterers at approximately the same rate as they are abandoned by diggers. There is a static market economy of burrows.

(4) The two strategies enjoy equal success rate in the population. There is an equilibrium such that selection does not favour either one of them over the other at observed frequencies.

(5) The equilibrium is stable. It is maintained by frequency-dependent advantage whose nature is as follows. Enterers do relatively well when they are rare, because the chance that they will find themselves sharing is relatively low. Enterers do relatively poorly when they are common, because they run a substantial risk of finding themselves joining an incumbent. The equilibrium frequency in the New Hampshire population is about 41% enterers.

Students of Hymenoptera are inevitably awed by the heights of adaptive achievement of the social species, and they tend to see solitary species as the bottom of a kind of entomological "great chain of being". We too began by regarding the nest-sharing of *Sphex ichneumoneus* as a tentative groping toward the brave new world of eusociality. This is why we talked about founding and joining, why we used the word sharing at all. We were prepared to reverse the sign of social benefit, and contemplated regarding joiners as parasites. The one thing we never considered in the early stages was that nest "sharing" might be neither mutualistic nor parasitic but simply *incidental*. This seems obvious now, but it was the decisive failure of Model 1 and the need to think of a radical alternative to the "sharing" assumption which it made, that raised our doubts. And it was the fact that Model 1 had been formulated as a series of precise assumptions that enabled us to question these assumptions systematically and pinpoint the one whose change gave rise to Model 2. "Joining" just does not seem to be an option open to the wasps. It is an incidental consequence of selection in favour of entering and adopting abandoned nests.

As such it is a potential *pre-adaptation* to the evolution of social life. Suppose the parameters of Model 2 were to shift over evolutionary time. Could selection ever begin to favour entering *because* sharing is an outcome of it, rather than in spite of the fact? If it is a pre-adaptation, it is surely the more promising for being an evolutionarily stable minority habit, rather than a freakish mistake. The relevance of Model 2 to the evolution of social life is the main theme of the companion paper (Brockmann & Dawkins, in prep.).

The great deficiency of our data is the lack of information on post-egg-laying success. It would theoretically be possible to watch the young adults emerging from the ground the following year, but it seems impossible to know

which of last year's females should get the credit. This is why the first author intends to switch to mud-daubing wasps (*Sceliphron* and *Trypoxylon*). Instead of digging chambers underground they build mud nests on walls like swallows. It will be possible to trap emerging adults of the next generation, and so award posthumous but all important credit to the successful mothers of a summer ago. Otherwise the essential features of their biology are similar to *Sphex ichneumoneus*, with whom they are closely related. In particular it seems likely that, whatever improvements can be made in the numerator of the success score, the denominator will still be the same—time. Time is a currency which an animal spends. Decisions are the moments at which the down payments are made.

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