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DIVERSITY IN THE NESTING BEHAVIOR
OF MUD-DAUBERS
(*TRYPOXYLON POLITUM* SAY; SPHECIDAE)*

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The pipe-organ mud-dauber, *Trypoxylon politum* Say (Sphecidae: Larrinae), constructs long tubular mud nests under bridges and in tree holes. The female provisions each cell of her nest with paralyzed spiders, lays an egg and seals the cell with a plug of mud (Cross et al. 1975). Building a new mud nest is the commonest method of acquiring one, but there are at least 4 other ways. A female may abandon her nest at any stage in the nesting sequence and another female may take it over. Sometimes a wasp moves into a nest that is occupied by another, and the 2 then jointly provision the same brood cell. Occasionally a wasp parasitizes a conspecific by

breaking open the mud partition, removing the egg and replacing it with 1 of her own. Finally, Barber and Matthews (1979) have shown that pipe-organ mud-daubers also use trap-nests, hollow twigs, or other existing cavities. Whenever animals are found to have more than 1 way of achieving the same functional end, we are presented with a most intriguing biological problem: How are these differences in behavior of individuals maintained in the population? It is very unlikely that all patterns would be equally success-ful. Why is the inferior one not eliminated through the action of natural selection?

I observed similar variation in the nesting behavior of the golden digger wasp, *Sphex ichneumoneus* (L.) (Sphecidae; Sphecinae). The principles developed during the *Sphex* study may shed some light on mud-dauber behavior. At least superficially the nesting of the 2 species is similar. Golden digger wasps dig burrows (frequently abandoning newly dug holes), provision them with several paralyzed prey, lay an egg and seal the burrow with soil (Brockmann and Dawkins 1979). As in mud-daubers, these wasps are usually solitary, but occasionally 2 females jointly provision the same brood cell. They viciously defend their nests from the intrusion of con-specific females and in both species joint nesting usually ends in a fight with only 1 of the 2 wasps laying an egg on the jointly-provided cache of food. Golden digger wasps also nest in the abandoned nests of conspecifics (but never in trap-nests).

Richard Dawkins, Alan Grafen, and I (Brockmann et al. 1979, Brockmann and Dawkins 1979) tried to develop a model that would explain the diversity of nesting behavior in *S. ichneumoneus*.[1] If joint nesting were a functional alternative to nesting alone, then joining and founding (starting a new nest alone) behavior should be, on average, equally successful. Using the rates of laying eggs as a measure of reproductive success, we found that when a wasp joined another (or was joined) she was much less successful than when she nested alone. This result suggests that joining behavior is being selected against in our populations of digger wasps. Why, then, is joining so com-mon?[2]

We found a possible explanation when we discovered that wasps who nested in existing burrows utilized occupied and unoccupied nests in proportion to their availability in the nesting area. This suggests that the wasps were not distinguishing between occupied and unoccupied burrows, and were simply using any suitable existing burrow they could find. We define, then, 2 ap-parent nesting strategies: in 1, called "digging", wasps dig new nests and in the other, called "entering", wasps use already existing burrows. After entering there are 2 possible outcomes: sometimes the wasps end up in an abandoned burrow by themselves, and sometimes the wasps end up in a nest with another. Joint nesting, then, is not really a nesting strategy at all, but rather a by-product of using already existing nests (since they do not tell the difference between occupied and unoccupied burrows). We also found that apparently the wasps dig or use existing burrows independently of previous decisions, past success or searching difficulty, and that the 2 strategies do not show individual or seasonal variation or biases. It is as though the animals are programmed with a decision rule that says, "dig

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[1]This and subsequent superscript numbers refer to comments recorded in an Appendix, p. 62.

with probability p, enter with probability $1\text{-}p$". If the wasps are in fact programmed with such a stochastic rule (called a "mixed" strategy by ESS theorists), then we expect on the theoretical grounds given by Maynard Smith (1974) that the frequencies of digging and entering decisions will be set by natural selection at a value such that the 2 are equally successful. This, in fact, appears to be the case in 1 well-studied population of golden digger wasps. The success of individuals (number of eggs laid divided by the time spent on that nesting strategy) on the occasions when they dig (including searching time) is approximately equal to the success of individuals on the occasions when they enter already existing burrows (including occupied and unoccupied). It appears that digging and entering may be 2 functionally alternative nesting strategies.

But is equal success sufficient to maintain 2 such alternatives in a population? It would be, only if the 2 strategies remain equally successful through evolutionary time—which would seem most unlikely. There is another feature to the model we developed which makes the long-term maintenance of alternative strategies more likely, namely frequency-dependence. Digging a burrow is a costly, time-consuming undertaking. When a wasp chooses to enter, she avoids the cost of digging but she may pay another cost: she risks finding another wasp in possession and we have seen that joint nesting is relatively unsuccessful. Whether she digs or enters, she may be joined by another wasp. This is also less desirable than nesting alone. When there are many wasps choosing to dig, there are many burrows being made available for wasps that choose to enter. This means that as digging increases in frequency, entering becomes more profitable. On the other hand, as entering becomes more common, empty available burrows are correspondingly less abundant, and the entering wasps increasingly run the risk of joining another wasp. This has the effect of reducing the profitability of entering when it is common. The frequency of digging relative to entering, then, is held in balance by the kind of frequency-dependent advantage just described. The mixed strategy, "dig with probability p enter with probability $1\text{-}p$", is said to be evolutionarily stable, and the population exists at an evolutionarily stable state with respect to these 2 forms of nesting.

Whenever there are alternative behavioral patterns being followed by an animal, decisions or choices are being made. By decision I do not mean any conscious action, but only that the animals are programmed to follow a particular course of action; at a decision point an animal may change to a different behavior. These programmed rules of behavior are the result of natural selection just as surely as are the rules that govern morphological development. Although there are 4 kinds of nesting activities in the digger wasp, these apparently result from only 1 decision, whether to dig or enter. Similarly, although wasps occasionally "usurp" the nests of other females, this results from a decision to enter nests which might have been abandoned, not from a positive decision to usurp (Brockmann and Dawkins 1979).

The dig/enter *mixed strategy* may be unusual. What appear to be 2 alternative strategies may turn out to be the outcomes of 1 *conditional strategy*. A conditional strategy is a programmed rule of behavior which is followed only in particular circumstances. For example, in some bees large males pursue 1 highly profitable mating pattern and small males pursue other less successful ones (Alcock 1979, Alcock et al. 1976, 1977, 1978, Bar-

rows 1976). All individuals may be said to be programmed with the same conditional rule, "if large, guard emergence sites; if small, patrol the area looking for unmated females." There is no particular reason to expect that 2 behavioral patterns of 1 conditional strategy will be equally successful (Dawkins 1980). In order to explain the presence of diverse patterns of behavior, the biologist must determine (1) the nature of the decisions that the animals are making, (2) the outcomes of those decisions and (3) whether or not the decisions are conditional on some particular circumstance. If, as in the case of the digger wasps, we are unable to find any conditional strategy (based on past success, searching difficulty, time of year, etc.), and if we can find, as we did, a possible frequency-dependent advantage, then it is plausible to hypothesize that the behavior is maintained as a part of a mixed evolutionarily stable strategy in the population.[3]

I do not yet know whether the diverse nesting behavior found in pipe-organ mud-daubers is an evolutionarily stable mixture or not, but I believe that the concept may apply to some of the nesting patterns. Before going into this, it is necessary to give more background on the wasps, their nesting behavior and the manner in which I observed them.

I observed the behavior of pipe-organ mud-daubers under a bridge over Hatchet Creek, Alachua County, FL.[4] We individually marked 128 female and 152 male wasps.[5] Many were never seen again or appeared under the bridge only briefly and then disappeared. We observed 83 females as they built 103 mud nests for a total of 319 brood cells (mean 3.4 cells per mud tube). We have complete records on all activities associated with 132 of these cells. Running commentary notes were taken from about 0900 to 1700 each day of the study. Since all wasps were individually marked, we knew when more than 1 female was using a nest, when the female that had built a nest was (or was not) using it and when a female was marauding the nest of another. We also more casually observed the behavior of other species of wasps which were nesting under the bridge.

At the beginning of a nesting sequence, a female flies about the nesting area, presumably looking for a suitable place to build. She frequently sticks her head into or briefly enters the nests of other wasps, and is often repelled by a lunge and bite from the resident male (see below). She may walk repeatedly along 1 side of or on top of an active or old nest. After a sequence of searching which lasts from an hour to most of a day, the female begins to build, normally next to or on top of a new or old nest, rarely (4% of 103 nests) extending an old nest. Building a nest is a time-consuming process: it may take 1 to 2 days to complete the outside of a 7 cm nest and line the inside with a layer of mud. The female may abandon the nest after she has completed the outside or after completing the entire nest.[6] She may then start another nest under the bridge or she may disappear altogether. Sometimes a female completes 1 or more cells before abandoning the nest. These partially built or partially provisioned nests are readily adopted by other females who repair them if damaged or line them with more mud if necessary (Fig. 1).

The mud-dauber provisions her nest with any of a number of species of locally available spiders (Muma and Jeffers 1945, Dorris 1970, Cross et al. 1975). After accumulating from 3 to 12 prey, she lays a large egg and then immediately builds a mud partition. The partitioning takes only a few
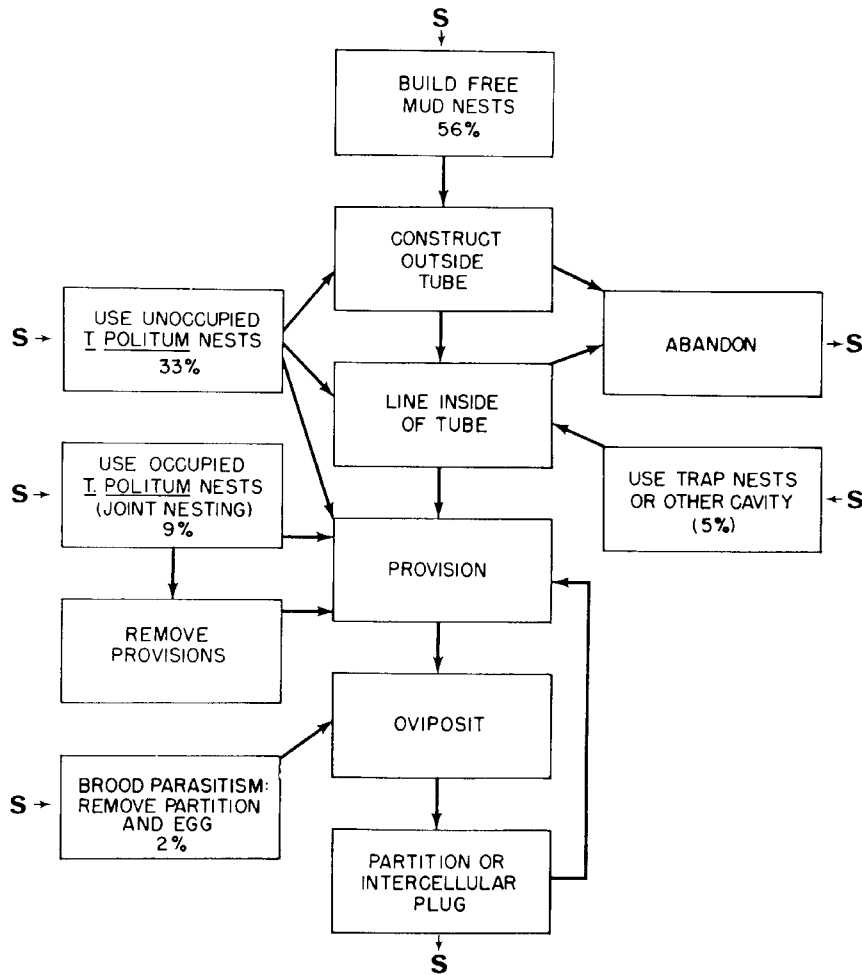
Fig. 1. A flow diagram of the nesting behavior of *Trypoxylon politum.*
"S" refers to the searching behavior that precedes a nesting sequence. The
observed percent of brood cells (N = 132) completed using each nesting pat-
tern is given (except for trap-nesting which is estimated for another popula-
tion by Barber and Matthews 1979).

minutes, although she may continue to add mud for half an hour or more,
particularly if it is the last cell in the nest. In 2 or 3 days the egg hatches
into a larva which consumes the provided food and then spins a cocoon in
which it remains until the following spring when it pupates and emerges as
an adult (Cross et al. 1975).

In *T. politum* and other species in this subgenus (*Trypargilum*), males
show a most un-hymenopteran-like pattern. They remain in a female's nest
near the entrance and guard it from the intrusions of parasites, other males,
and females. A male may join a female's nest at any stage during the nest-
ing process and he may even help her: if he joins a nest while she is still
building it, he may smooth the wet mud on the inside walls of the tube with
his mandibles, just as a female does; if he is present while she is provision-

ing the nest with spiders, he may push the spiders to the top of the tube with his mandibles, as females do. He may make copulation attempts or copulate with her briefly at any time, including while she is constructing the mud tube, provisioning or building a partition.[7] However, if he is present just before oviposition, there is a long sequence of courtship and multiple, long copulations.[8] The resident male defends the nest from intruders such as parasitic cuckoo wasps and miltogrammine flies (Cross et al. 1975). He also staunchly, although not always successfully, defends the nest from intruding males, and he appears to deter some intrusions by conspecific females. In another sphecid wasp in which the male guards the nest, Peckham (1977) has demonstrated that the presence of a guarding male significantly increases the survival of the brood. I suspect that the nests of *T. politum* are similarly protected by the guarding behavior of the male.

As already mentioned, in addition to building new mud nests and taking over abandoned nests, females show at least 3 other nesting patterns (Fig. 1). Occasionally a mud-dauber occupies and provisions a nest which is being provisioned by another female, a pattern reminiscent of the joint nesting described in golden digger wasps. Since females spend most of their time away from the nest, 2 jointly nesting wasps may not meet for several days. When they do a vicious fight ensues which may last up to 14 min (mean 2.8 min, N = 28). The 2 bite and grapple, often falling from the nest onto the sand or into the water below. At the end of a fight, 1 of the females re-enters the nest and successfully prevents the other's attempts to return. Again, as in *S. ichneumoneus*, only 1 of the 2 wasps lays an egg on the (joint) provisions. This individual is as likely to be the original owner as the intruder (X^2 Test, p = 0.76; N = 13). It seems at least plausible that something like the *S. ichneumoneus* dig/enter mixed strategy model may apply to mud-daubers ("build/enter"; also, individual females mix building and entering). If this is true, we expect to find that mud-daubers will not be distinguishing between occupied and unoccupied nests when they "enter". Another prediction of the model is that the success rates of females on the occasions when they choose to build or enter should be equal. When I have collected these data (spring 1980), I will have hatching success rather than rates of laying eggs as I did for the digger wasps. This was an important weakness in the digger wasp study, since we had to ignore larval and pupal mortality.

Intraspecific brood parasitism is a fourth form of nesting in these mud-daubers. On 3 occasions I saw a female (which had no nest and appeared to be searching for a place to build) enter a nest which had just been partitioned by another wasp, chew a hole in the soft mud and remove *just the egg* (observed twice) or the egg and the spider to which it was attached (observed once). She then oviposited and rebuilt the partition with fresh mud. Brood parasitism occurs only on the rare occasions when a wasp encounters a mud partition that has not yet hardened (less than 30 min old). It seems unlikely that this could be a functional alternative to other forms of nesting and it is probably an example of a conditional strategy.

Barber and Matthews (1979) observed a fifth nesting pattern in *T. politum*, the provisioning of bamboo trap-nests. Unlike other members of the subgenus, *T. politum* line the cavity with mud. Barber and Matthews also observed the wasps building mud nests in the same area and estimated that

only about 5% of the nesting was in existing cavities. They suggested that where mud or appropriate nesting sites are scarce, *T. politum* may choose these rather than building free nests of their own. Before man-made structures were so common, sites for free mud-nests might have been rare and selection might have favored individuals utilizing existing cavities. At my study site, wasps frequently nested under the bridge for a week or 2, left for a week or 2 and then returned. It is likely that while they were gone, they were nesting in the surrounding woodlands, either building free mud-nests in cavities or using natural trap-nests such as hollow stems and beetle galleries. It is even possible that there is a "cavity-nest/mud-nest" mixed evolutionarily stable strategy. Evidence on this will be more difficult to obtain than for the hypothesized "build/enter" mixed strategy.

In a sense a bridge is an optimal spot for a mud-dauber, with mud and spiders close at hand and a good surface on which to build a nest. On the other hand, the presence of conspecifics and other species may reduce the quality of this location to the point where it may be more profitable for the wasp to nest in an area that was previously considered sub-optimal (Brockmann 1979). At my study site, at least 3 species of sphecid wasps frequently destroyed *T. politum* nests. *Trypoxylon texense* Saussure and *Chalybion californicum* (Saussure) (Sphecinae) chewed open completed *T. politum* nests [as well as those of *Sceliphron caementarium* (Drury); Sphecinae], removed the contents, including spiders, larva or prepupa, and then reprovisioned it themselves. *Trypoxylon texense, T. johannis* Richards, *C. californicum* and particularly *T. striatum* Provancher stole mud from the outside of *T. politum* and *S. caementarium* nests often damaging them severely and increasing their susceptibility to parasitism and desiccation. *Trypoxylon striatum* was a champion at this. These wasps did not nest under the bridge very often, and when they did they took over abandoned *T. politum* nests. Many *T. striatum* came to the bridge from the surrounding woods (where they were probably nesting in twig-nests) to gather mud from active and inactive *T. politum* nests. Sometimes this chewing actually caused the *T. politum* cocoon to fall to the ground, although the silk laid down on the inside of the nest by the larva usually held the cocoon in place, even when virtually all the mud was removed. *Trypoxylon texense* and *T. striatum* occasionally gathered mud on their own, but they usually stole it from *T. politum* nests. A chemical analysis has been made on the mud nests of *S. caementarium* by Qureshi and Ahmad (1978). Interestingly, they found that the mud of the nests contained organic compounds including paraffins and ketones, which were thought to be used for waterproofing. The already-worked mud on *S. caementarium* and perhaps *T. politum* nests, then, may be superior to freshly-procured mud, and may be an important resource for mud-stealing species.

Trypoxylon politum also, almost spitefully, damage the nests of conspecifics. I have observed females entering a nest without a male and removing the provisioned spiders. They did not use the spiders but simply let them drop to the ground (14% of cells have 1 spider removed by a conspecific female). Females even force their way in past guard males and remove provisioned spiders. When this happens, males usually try to copulate with the intruding female. I have also observed a female gnawing holes in the newly-built nest of a conspecific, allowing the mud to drop into the water

below the nest. In addition to the extensive marauding of nests by various species, there is also a high incidence of interspecific nest parasitism (Cross et al. 1975, Johnson 1974, Rau and Rau 1916). Bombyliid and sarcophagid flies, cuckoo wasps and *Melittobia* destroy the provisions or larvae of a significant number of *T. politum* nests (Table 1).

On theoretical grounds we would expect that as bridge nesting became less profitable due to parasitism and intraspecific marauding, as space became limiting or when mud was difficult to find, it would be more profitable for females to search for and nest in twig-nests and other existing cavities. As the success of twig-nesting (relative to bridge-nesting) decisions increased, the frequency of twig nesting would rise in the population. This

TABLE 1. INCIDENCE OF MARAUDING AND PARASITISM IN A POPULATION OF *Trypoxylon politum* FROM ALACHUA CO., FL.

Percent of *Trypoxylon politum* cells disturbed by:

Marauding*	
Conspecific (N = 132)	0.8%
chewing on nests	
brood parasitism	2.0%
removal of 1 spider	14.0%
Interspecific (N = 319)	
Trypoxylon texense	
chewing on nests	3.5%
brood parasitism	1.9%
Trypoxylon striatum	
chewing on nests	5.0%
brood parasitism	0%
Chalybion californicum	
chewing on nests	3.4%
brood parasitism	1.3%
Parasitism**	
Bombyliid flies (*Anthrax limatulus*)	12.6%
Unknown pupae (probably sarcophagid)	1.2%
Cuckoo wasps (Chrysididae)	4.0%
Melittobia sp.	0.9%
Trypoxylon johannis	0.3%
Trypoxylon striatum	0.3%
Total loss from parasitism	19.4%
Unknown Causes**	
Nothing in cell	0.6%
No larva, spiders only	0.6%
Dead larva	10.8%
Live larva, no metamorphosis	11.1%
Dead pupating wasp	1.5%
Total loss from unknown causes	24.7%

*From direct observation at Hatchet Creek in 1979 as described in text.
**From cells collected at Lochloosa Creek in 1978 and reared in the laboratory (N = 324); 55.8% of cells resulted in hatched adult wasps.

would continue until twig nesting became so common that it was increasingly difficult for wasps to find appropriate cavities and then selection would begin to favor building. Thus, it is conceivable that mud nesting and twig nesting may be mixed in an evolutionarily stable state such that the success of each is on average equal, maintained by a frequency-dependent advantage. Of course this is speculative and it needs the kind of hard evidence we provided for *S. ichneumoneus*.

Finally we can apply the theory to 1 of the mysteries of sphecid wasp evolution: How have such extremely diverse nesting patterns evolved within very closely related groups? Among the Sphecinae, for example, there are burrow diggers (*Sphex, Stangeella, Prionyx, Palmodes, Podalonia* and *Ammophila*), species that use burrows dug by other species (*Chlorion aerarium* Patton) including their prey *Chlorion maxillosum* (Poiret) and *C. lobatum* (Fabricius), twig and cavity nesters (*Podium, Isodontia* and *Hoplammophila*), mud-daubers (*Sceliphron* and *Trigonopsis*), brood parasites (*Chalybion*) and primitively social species (*Trigonopsis*) (Bohart and Menke 1976, Eberhard 1974, Peckham and Kurczewski 1978). Within the Trypoxylini there are mud-daubers (*Pison* and *Trypoxylon*), species that use the pre-existing mud-nests of other wasps (*Pison* and *Trypoxylon*) twig and cavity nesters (*Pisonopsis, Pison* and *Trypoxylon*), wasps that use burrows dug in the ground by other species such as bees (*Pisonopsis clypeata* W. Fox and *Pison nigellum* Krombein) and females of 1 species apparently dig burrows of their own (*Pison chilensis* Spinola) (Rau 1928, Janvier 1928, Krombein 1950, 1967, Evans 1969, Bohart and Menke 1976, Menke and Bohart 1979).

The mystery of these diverse nesting patterns takes on a new perspective when we find nearly as much diversity in the nesting behavior of 1 species. Female *T. politum* build free mud-nests, use existing nests, jointly occupy nests, use trap nests and brood-parasitize conspecifics. Under the same bridge, *Trypoxylon texense* use active and inactive nests and emergence holes (often nesting inside broken pupal cases) of *T. politum, S. caementarium* and *C. californicum*, as well as nesting in pre-existing cavities such as bolt holes and cracks in the cement (see also Rau 1928). Hungerford and Williams (1912) observed this species nesting in burrows dug in a clay bank by bees. *Sphex ichneumoneus* dig burrows, use existing nests and jointly occupy nests with conspecifics. The pattern of using burrows which were dug by conspecifics (entering) may be a preadaptation among fossorial species for using existing cavities (trap-nesting) in general. If this is true then we might expect to find species in which females sometimes dig (and enter) burrows and sometimes nest in existing cavities (trap-nest). The full range of the apparently diverse nesting patterns of Sphecinae and Larrinae may be found in just a few closely-related species. To a large extent the nature of the variation available within a species determines the course of evolution. With such variability present in 1 species, it is easy to imagine how members of 1 tribe or family might have evolved such diverse nesting patterns. The problem of the evolutionary origins of diverse nesting patterns, then, is replaced by the even more puzzling question of how such diversity is maintained in 1 species. The concept of the mixed evolutionarily stable strategy provides us with 1 mechanism by which such variability may be maintained in a population.

APPENDIX NOTES

[1]We used the evolutionarily stable strategy or ESS approach pioneered by Maynard Smith (1974, 1976) and developed by Parker (1978) and Dawkins (1976, 1979). Natural selection is the differential survival of alleles. If a new allele arises and spreads in a population, we can ask what was it about that allele that increased the survival and reproductive abilities of the individuals who carried it? Sometimes the answer to this question is simple, such as it makes all individuals more resistant to parasitism. However, sometimes the answer to the question depends in part on the frequency of that allele relative to others in the population. If the effect of an allele is frequency-dependent, then the population will evolve toward an evolutionarily stable state, an uninvadeable mixture of the 2 alleles (Dawkins 1980). One familiar example of an ESS is Fisher's explanation of the sex ratio. A population tends to evolve toward a 1:1 sex ratio (with equal investment in the 2 sexes) because male-producing is favored when females are common and vice versa.

As long as the average success rates of the alternative strategies remain the same, the population will evolve toward the ESS. However, there is nothing necessarily static about an ESS. If the success rate of a strategy changes (for example if there were an increased rate of parasitism) then the ESS will change and the population will begin to evolve toward the new ESS.

[2]I observed joint nesting by golden digger wasps at all 3 of my study sites, but the frequency of the behavior differed. In Dearborn, MI 5% (observed 1973 to 1975), in Exeter, NH 12% (1975) and in Northfield, MN about 5% (1976) of the brood cells were the result of joint nesting (Brockmann and Dawkins 1980).

[3]Several authors have observed marked differences among populations in the occurrence of certain behavioral patterns (eg. Evans and O'Neill 1978, Alcock 1979). One explanation for such variability might be that the 2 patterns are frequency-dependent and that the success of 1 relative to the other is different in the different locations. Hence the populations may be at different evolutionarily stable states. Another explanation is that the starting conditions for the populations may have been different, a situation that is known to influence the final ESS. In either case these are very different kinds of explanations for the presence of diverse nesting patterns than would have been considered prior to the application of the ESS approach to evolutionary problems (see Dawkins 1980 for further discussion).

[4]Observations were conducted from 28 June to 1 September 1979 with the assistance of Martin Obin.

[5]Wasps were individually marked with dots of Testor's enamel paint after briefly anesthetizing them with a small amount of CO_2, from which they nearly always recovered quickly.

[6]The reasons for these abandonings are not clear. Sometimes a female abandons a nest because she has had a fight with another female or because of the presence of intruders such as centipedes, crickets or ants. Other times the female simply fails to return to the nesting area and I presume that she may have died. But in a number of cases the wasp simply begins another search and builds another nest near the first 1 or she begins to provision another already existing nest.

[7]There are 2 kinds of copulations in *T. politum*, short and long (see below). Short copulations are 3 to 12 sec (mean 6.6, N=54) and occur at any time while the female is at the nest, such as when she is building, bringing in a spider or making a partition.

[8]The pre-oviposition sequence (from the time the last spider was brought in to the time at which the female leaves the nest to gather mud for the partition) lasts 6 to 23 min (mean 12.7 min, N=25) when a male is present.

The male alternately holds the female's head with his prothoracic legs and copulates (3 to 8 copulations during a pre-oviposition sequence, mean 6; N=25). These are long, 5 to 55 sec, copulations (mean 14.4, N=135). If the male is not present the female oviposits after only about 2 to 5 min.

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