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Mate Selection in *Tetranychus urticae* Koch (Acarina: Tetranychidae): A Test of Six Hypotheses

by

Peter R. Everson

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Mate Selection in *Tetranychus urticae* Koch (Acarina: Tetranychidae): A Test of Six Hypotheses submitted by Peter R. Everson in partial fulfilment of the requirements for the degree of Master of Science.

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Abstract

Males of *Tetranychus urticae* Koch search for and tend quiescent female deutonymphs. In this study I examined six hypotheses for how males select quiescent females. These hypotheses can be divided in two groups: those that assume that male behavior is genetically fixed (random mate selection, age dependent mate selection and mate selection based on a fixed time threshold) and those that assume that males vary their choice of females in response to extrinsic variables (mate selection to minimize the time invested in each copulation, mate selection to minimize the likelihood of being forced to accept a cotender, and mate selection based on energetic constraints). The latter three hypotheses predicted that male choice would be influenced by one of the following variables: number of males, number of females or leaf condition.

The six hypotheses were tested with observational data which were analysed using multidimensional contingency tables. Five of the six hypotheses were rejected as primary explanations of male behavior. I concluded that males use a behavioral strategy based primarily on minimization of the time invested in each copulation. This conclusion was corroborated by the fit of a time minimization model to the observed male behavior.

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I. Introduction

Competition among males for females has been hypothesized to be a strong selective force affecting male sexual behavior (Trivers 1972, Halliday 1978, Borgia 1979, Parker 1979, Thornhill 1980c), but this hypothesis has seldom been tested. Part of the difficulty of making such a test is that male sexual behavior can be affected not only by intrasexual selection but by intersexual selection as well. The goal of the present work is to examine some factors affecting male sexual behavior in a system in which there is no intersexual selection.

Intrasexual selection, which is competition within one sex for an individual of the opposite sex, and intersexual selection, which is preferential choice of mates by one sex, are the two components of sexual selection (Thornhill 1980b). Males are thought to compete for females while females discriminate between males (Bateman 1948, Trivers 1972, Halliday 1978, Thornhill 1979, 1980a,b). Typically, a female's reproductive success is limited by her ability to successfully rear her offspring, whereas a male's success is limited by his ability to search for and mate with as many females as possible (Bateman 1948; Trivers 1972; Halliday 1978; Parker 1978a,b; Alexander and Borgia 1979; Davies and Halliday 1979; Thornhill 1979; Alcock 1980).

Alexander and Borgia (1979) divided the reproductive effort of males and females into 2 classes, parental effort and mating effort. Parental effort involves the provisioning of resources into either gametes or offspring. Mating effort has a number of components: competitive interactions with other individuals of the same sex; the transfer of benefits to members of the other sex as part of securing matings; and evidence for a commitment to parental effort directed at offspring resulting from the mating. In general, females have a large parental effort and relatively small mating effort. However, males vary immensely in both mating and parental effort depending on the mating system. In monogamous systems males are similar to females in their distribution of reproductive effort. In promiscuous, polygamous systems, most of the male's reproductive effort is directed at male-male competition (intrasexual competition).

Where male-male competition predominates, males should adopt behavioral strategies that reflect this form of sexual selection (Halliday 1978, Parker 1978b). It is usually assumed that the behavioral strategy adopted will maximize reproductive success (Lewontin 1979). In most studies, this assumption is the working hypothesis, and a mathematical model is constructed that maximizes or minimizes some correlate of reproductive success, such as where to search for mates, copulation frequency, or parental investment (Parker 1978a,b,1979; Davies and Halliday 1979; Lewontin

1979; Thornhill 1979). The difficulty with this approach arises because male behavior is often a compromise, reflecting the relative intensities of intrasexual and intersexual selection (Thornhill 1979). Therefore, the predicted and observed behaviors are likely to deviate from one another. Most deviations are explained by *ad hoc* arguments that invoke important yet unidentified selective forces, or by the failure to correctly identify which correlates selection was acting upon (Parker 1978b, Davies and Halliday 1979). These problems are not unique to studies of male reproductive behavior. Optimal foraging theory has been criticised for identical reasons (Pyke *et al.* 1977, Krebs 1978, Maynard Smith 1978, Dawkins 1979, Lewontin 1979, Strobeck pers. com.).

Lewontin (1979) argued that there is no theoretical or empirical reason to expect optimization in nature. He stated that optimality models were too simplistic because they emphasised only one "problem" for solution while assuming the appropriate genetic mechanisms and genetic variation exist for its solution. He felt that optimality arguments were dangerous and that their price was eternal vigilance.

However, Maynard Smith (1978) has argued that

> "...in testing a model we are *not* testing the general proposition that nature optimizes, but the specific hypotheses about the constraints, optimization criteria and heredity."

Rejection of the predictions of a model only indicates that one or more of the assumptions is incorrect. The decision to increase the complexity of the model is subjective, to be based on the qualitative agreement of the model and "biological intuition" (Maynard Smith 1978, Dawkins 1979). Optimality models will be most successful in simple systems, where the "problem" can be readily identified, and the proposed "mechanism" of solution can be easily "quantified".

For these reasons, I am examining the proposition that in the absence of female discrimination, males will adopt behavioral strategies that maximize their frequency of copulation (the "problem"), which is a major correlate of reproductive success. The absence of female discrimination will increase the likelihood that simple optimality models can be applied, since male behavior will then most strongly reflect male-male competition.

Mating systems in which intense male-male competition occurs, but female discrimination is absent, are relatively rare. However, in certain flies (*Arachnocampa luminosa*) (Richards 1960), butterflies (*Heliconius* spp.)(Turner 1973), mites (*Tetranychus urticae* Koch) (Potter *et al*. 1976b), some solitary bees (Alcock 1980), and beetles (*Leptothea galbula*)(Richards 1980), males search for pre-adult, quiescent females and wait for the female to emerge as a sexually receptive adult. Mating occurs soon after emergence. Male selection of pre-emergent females effectively precludes females from discriminating between males. In these systems, males must invest time searching for and tending each female. Clearly, the frequency of copulation will tend to be a simple function of the time invested in each female.

In Parker's (1974a) theoretical paper on male time investment strategies, he indicated that if some males spent longer than others to complete a given activity they would be at a selective disadvantage. The disadvantage would be greatest if the time investment was directly tied to reproductive success. Parker examined the male behavior of courtship persistence; and, pre- and postcopulatory female guarding. His models predicted that if males minimized their searching and guarding times per female, they would achieve greater reproductive success than males that did not. These conclusions should also apply to pre-emergent tending.

My study attempts a rigorous test of the hypothesis that males will maximize their frequency of copulation by minimizing the time invested per copulation. This hypothesis could be tested in many different systems (Parker 1970b, 1974a), however, the best chance to achieve definitive results would be in simple systems where males tend pre-emergent females. In these systems the "problem" is maximization of copulation frequency, the "mechanism" is minimization of the time invested per copulation, and the "quantification" is that all behaviors involve time. From the five known examples of pre-emergent tending (Richards 1960, 1980; Turner 1973; Potter *et al*. 1976a,b; Alcock 1980), I have selected the tetranychid mite, *Tetranychus urticae* Koch as the model system. *T. urticae* offers several advantages: it is readily available, easily reared in the laboratory, and its life history and mating behavior are well known.

II. Mating Behavior of *Tetranychus urticae* Koch

Tetranychid mites, or spider mites as they are commonly known, are serious phytophagous pests of all major food crops(van de Vrie *et al*. 1972). Their importance as pests has encouraged a great deal of scientific and technical research. That literature was reviewed by Huffaker *et al*. (1969), McMurtry *et al*. (1969) and van de Vrie *et al*. (1972).

The life cycle has 5 stadia: egg, larva, protonymph, deutonymph, and adult. The 3 immature stages are each divided into an active and quiescent period. Males mature earlier than females, seek out quiescent female deutonymphs and remain with them until they emerge (van de Vrie *et al*. 1972). This quiescent period lasts approximately 40 hours at 19 °C. Copulation with the female occurs immediately after emergence. Tetranychid mites are haplodiploid; males develop from unfertilized eggs. Mated females produce both sexes, because not every egg receives a spermatozoan.

Males of *Tetranychus urticae* Koch (=*T. cinnabarinus*, see Dupont 1979) search out and actively defend quiescent female deutonymphs. Although this behavior was first observed over 80 years ago (Perkins 1897), it is only recently that the functional significance of this behavior has been investigated (Potter *et al*. 1976a,b; Potter 1978,1979; Potter and Wrensch 1978). Once a male encounters a quiescent female, he begins a "tending" behavior, remaining motionless beside her or climbing on top and assuming a resting position with his palps and forelegs in contact with her dorsum (Potter 1979).

Non-tending males may contest the tending male's ownership of a female. These contests may be violent, resulting in death of one of the combatants, but most are pushing and shoving matches. Usually the interloping male is repelled; occasionally the defender is displaced or forced to accept the interloper as a cotender. Both cotenders are equally likely to inseminate the female (Potter *et al.* 1976a,b). Potter (1978,1979) identified three factors which influenced a male's mating success: size, age, and mating experience.

My observations suggest that death or displacement occurs very rarely. I observed only one death, that could be attributed to a contest between males. Displacement was observed on several ocassions, but I doubt that more than 1% or 2% of the tending males are displaced. Cotending was much more frequent, usually 10% to 20% of the females were cotended at eclosion.

Potter (1978,1979) suggested that pre-ecdysial tending has evolved because the number of quiescent female deutonymphs is small relative to the density of males. The functional ratio of males to quiescent females may approach 6 to 1. Dispersal by teneral females and the absence of dispersal by teneral males results in males accumulating on the leaf resulting in this skewed sex ratio (Mitchell 1970, 1972, 1973).

Although males are capable of multiple matings (Helle 1967, Beavers and Hampton 1971), females need to mate only once to realize maximum fecundity (Helle 1967, Overmeer 1972). In laboratory studies, it appears that females are no longer attractive to males or are refractory after the first mating (Helle 1967, Beavers and Hampton 1971, Overmeer 1972, Potter and Wrensch 1978). Where multiple matings have been observed, only the sperm from the first mating fertilizes the eggs (Overmeer 1972, Potter and Wrensch 1978). This may be due to changes in the wall of the seminal receptacle preventing the passage of sperm from other than the first copulation to the ovaries (Bordreaux 1963, Helle 1967, Pijnacker and Drenth-Diephus 1973, Potter and Wrensch 1978).

It appears that pre-ecdysial tending has evolved as a way in which males can assure themselves of exposure to virgin teneral females. Potter *et al.* (1976a,b) have demonstrated that intense intrasexual competition occurs among males as a result of this tending behavior.

Despite the competition for females, not all quiescent females on a particular leaf are tended. Potter (1979) hypothesized that:

> "...males should discriminate between females that only recently became quiescent and those on the verge of ecdysis ... since such behavior would enable a male to

> avoid waiting many hours before each opportunity to mate..." and

> "...the most successful males will be those whose behavior maximized the frequency of matings - either by finding and guarding or coguarding females near ecdysis..."

These 2 statements are consistent with the predictions of mate selection theory; however, only ancedotal evidence exists to support them. Potter *et al.* (1976b) stated that males usually tended older females. Cone *et al.* (1971a,b) indicated that attractiveness of females increased as they approached eclosion.

Attractiveness of females to males appears to be mediated by a short range pheromone released by the female during the quiescent period (Cone *et al.* 1971a,b; Penman and Cone 1972). The pheromone seems to function primarily in arresting male searching behavior once a female has been contacted (Penman and Cone 1974). Regev and Cone (1975,1976,1980) identified three terpenoid alcohols (farnesol, nerolidol, citronellol) as being constituents of the pheromone. They stated that the pheromone represents an adaptation on the part of the female to ensure mating.

The characteristics of this system ideally suit it to elucidating the kinds of behavioral strategies males might use when intrasexual competition predominates. The fact that females only use the sperm from the first mating facilitates investigation of this problem. This precludes the possibility of sperm competition between males (Parker 1970a), and ensures that males will not adopt strategies that involve mating with older post-emergent females.

III. Theoretical Considerations

The purpose of this study is to test the hypothesis that male *T. urticae* exhibit behaviors that minimize the time they invest in each copulation. This strategy has been predicted on theoretical grounds (Parker 1974a) and corroborated by ancedotal observations (Potter 1979). Despite the intuitive appeal of this one hypothesis, it is desirable to propose a number of alternative hypotheses, based upon a number of different assumptions, which in turn might lead to different expectations for male behavior (Platt 1964). The test of several hypotheses means that any conclusion can be stated with greater confidence, than if only one hypothesis had been tested. The support of a hypothesis, now rests on the rejection of several alternatives, rather than the simple agreement of that hypothesis with the observed male behavior.

I suggest six alternative hypotheses for explaining the mate selection behavior by male *T. urticae*: random mate selection, age dependent mate selection, mate selection based on a fixed time threshold, mate selection to minimize the time invested per copulation, mate selection to minimize the likelihood of being forced to accept a cotender, and mate selection dependent on energetic constraints. I will also develop mathematical extensions of four of these hypotheses.

A. Hypotheses of Mate Choice

All of the following hypotheses, with the exception of the random choice hypothesis, assume that a female's age determines whether or not she is accepted by a male. Males are assumed not to respond to any other differences among females, even though these might influence a male's reproductive success.

In particular, I assume that female size does not influence male choice. However, in many species of insects, egg production is directly proportional to female size (Parker 1970a,b). For example, in *Scatophaga stercoraria*, large females produce twice as many eggs as small females (Parker 1970b). Therefore, a male could increase his reproductive success, if he were to select larger females. However, there is no evidence that egg production in tetranychid mites is influenced by their size; only nutrition, temperature, humidity, and photoperiod are known to have an effect (van de Vrie 1972).

If female size influences male choice in *T. urticae*, I believe that its effect is small, since the potential gain in reproductive success by searching for large females would be considerably less than that gained by seeking females almost ready to emerge. The difference in egg production may be as much as twice, whereas, the difference in female ages may be forty times. In any case, ignoring female size will only increase the random error in any particular analysis.

Increasing the random error is equivalent to decreasing the sensitivity of a statistical test, since the test is less likely to detect effects of particular variables. Conclusions drawn from a less sensitive test are conservative, since variables must have larger effects to be detectable. Therefore my conclusions would not be affected, if it was later shown that female age was not the sole determiner of male choice.

Hypothesis 1: Random choice

Males select females at random with respect to time remaining before eclosion.

Hypothesis 2: Age dependence

The likelihood that a male may select a female is some function of the female's age. Females very close to eclosion should have a higher probability of being accepted than younger females.

Hypothesis 3: Fixed time threshold

Males may have a fixed time threshold of acceptance such that females older than this threshold are accepted while younger females are rejected.

Hypotheses 1, 2, and 3 assume that a male's mate selection behavior is fixed; either, they do not perceive female age (Hypothesis 1) or they respond only to female age.

Janetos (1980) in a general paper on female mate selection proposed models or hypotheses for mate choice similar to Hypotheses 1 and 2. His models assume that males vary in fitness and that females attempt to pick the "most fit" male according to some fixed set of decision rules. However, this will cause strong directional selection which eventually results in reduced genetic variability among the males. In this situation, phenotypic variation will not reflect underlying genetic variation in fitness (Williams 1975, Halliday 1978, Thornhill 1980a). In addition, his models are cost free. There is no constraint on the amount of time or energy a female can invest in selecting a mate (Janetos 1980).

Models of fixed thresholds have been discussed by Dawkins (1979), Cade (1980), and Janetos (1980); these are models of conditional strategies where the male's behavior is genetically fixed and does not require environmental input (Dawkins 1979, Cade 1980). An example of conditional behavior is given by Howard (1978), who found that male bullfrogs (*Rana catesbeiana*) could be territorial, opportunistic or satellites depending on their size and age.

Hypotheses 4, 5, and 6 propose that males vary their choice of females in response to various extrinsic stimuli. Therefore, males will select females of a certain age to solve a particular "problem", e.g., minimizing the time invested in each copulation. Each of the following hypotheses stresses a different "problem" for solution.

Hypothesis 4: Time minimization

Males minimize the time invested per copulation which will include both tending and searching time.

This hypothesis invokes a time investment strategy which is simply the optimum allocation of time spent on given activities so as to achieve maximum reproductive success (Parker 1974a). The time spent searching depends on female availability, and males are expected to vary their choice of females in response to female availability. If females are abundant, males should select females closer to emergence than when females are rare, since the time spent searching would be less.

Hypothesis 5: Copulation maximization

Males may vary their choice of females in response to the likelihood of being forced to cotend.

Unlike Hypothesis 4, this hypothesis assumes that the likelihood of being forced to accept a cotender increases with the amount of time spent tending. Tending males interact with non-tending males, obviously the longer the male tends, the greater the likelihood he will be discovered by a "stronger" male. His probability of mating once forced to cotend is 0.5 (Potter *et al*. 1976a,b). Therefore selection would act against males that tend so long that they are forced to accept a cotender (Parker 1974a,b). Males are expected to vary their choice of females in response to the number of males. If males are abundant, males should select females closer to emergence than when males are rare, since the likelihood of being discovered by a "strong" male is greater.

Hypothesis 6: Differential costs

If tending a female is energetically expensive, males may vary their choice of females in response to probable energetic demand (Parker 1974a).

Hypotheses 4 and 5 have assumed that the energetic costs of searching and tending are the same. This may not be true. Food is readily available to searching males, and tending males may be at a disadvantage with respect to energy expenditure (Parker 1974a). This asymmetry between searching and tending may cause males to allocate more time to searching for females close to eclosion (Parker 1974a,b) in response to low food availability.

Food availability is related to leaf condition. Heavy feeding by tetranychid mites induces yellowing or chlorosis in the leaves of host plants, because of damage to the leaf mesophyll (van de Vrie 1972). Heavily chlorotic leaves are unsuitable food sources (van de Vrie 1972). This hypothesis predicts that males on very chlorotic leaves should select females closer to eclosion, than males on only slightly chlorotic leave

The six preceding hypotheses make different predictions, at least under some conditions. Hence, a particular set of hypotheses can be rejected if conditions can be found under which they provide a unique prediction which can be proved untenable.

These hypotheses are not an exhaustive list of possible explanations for male behavior. For this particular problem, there is probably an unlimited number of explanations. I have presented these hypotheses because they were suggested by mate selection theory (4, 5, and 6) or could be deduced from *T. urticae*'s mating behavior (1, 2, and 3). However, it is possible that male behavior might be explained by some combination of Hypotheses 4, 5, and 6. Males may minimize the time invested in each copulation (Hypothesis 4) when the number of males is low, but as the number of males increases, they may switch and vary their choice of females in response to the likelihood of being forced to cotend (Hypothesis 5). Each "combination" hypothesis makes predictions that differ from either of its components. If male choice depends on female abundance, then Hypothesis 4 is correct; if choice depends on male abundance, then Hypothesis 5 is correct; however, the "combination" hypothesis requires that choice be dependent on both male and female abundance.

The preceding discussion indicates that males may simultaneously use several different strategies. It is not the purpose of this study to examine every detail of male behavior. My goal is to examine the six primary explanations, and attempt to elucidate some of the general patterns which govern male behavior.

B. Models of Mate Choice

I will only develop Hypotheses 1, 3, 4 and 5 mathematically because of the unspecified nature of certain relationships in Hypotheses 2 and 6. This approach allows me to investigate the predictions of these hypotheses in greater detail. A group of hypotheses may, under certain conditions, give very similar qualitative predictions, so that, the predictions of their corresponding mathematical models may be the only way of distinguishing among them.

The models and equations presented here make use of elementary theorems in mathematical statistics (see, Mendenhall and Scheaffer 1973).

Assume that in any group of quiescent females some proportion p are untended and some proportion q are tended where $p + q = 1$. If the quiescent period lasts for T time units and the rate at which females enter the quiescent period is constant, then it follows that the probability of a male encountering a female of a particular age is $1/T$. This is the same as the probability density function for the uniform distribution. Therefore we can assume the distribution of female ages is that of a uniform random variable with expectation $T/2$.

Assume that females are randomly distributed on the leaf and that males search randomly for them. Under this assumption, the time for a male to encounter a female at any fixed density of females is an exponentially distributed random variable with expectation b (Pulliam 1974). The number of females encountered, until the first untended one is found, will be distributed as a geometric random variable with expectation $1/p$.

Hypothesis 1: Random choice

Let the time investment per female of a male that selects untended females at random be **Ir(untended)**. This has two components: search time and tending time. The expected search time can be derived as follows. If the expected time to find a single female is **b** and the number of females encountered until an untended one is found is **1/p**, the expected search time is the product **b*1/p** or **b/p** because the expectation of a product is the product of expectations for independent variables. Males are assumed to exhibit no preference for any particular age class of females, therefore a male is equally likely to encounter every age class. Hence, the expected tending time will be T/2. The expected investment time, **Ir(untended)**, is the sum of these expectations:

$$Ir(untended) = b/p + T/2 \tag{1}$$

Similarly, the expected investment time for males selecting only tended females is

$$Ir(tended) = b/q + T/2 \tag{2}$$

Hypothesis 3: Fixed time threshold

If males accept females whose time remaining before eclosion is less than a fixed time threshold, **t**, then the proportion accepted is t/T, since we have assumed an uniform distribution of female ages. Therefore, the expected search time will be b/(p*(t/T)) or (T*b)/(t*p). Males accepting untended females older than some time t will have an expected investment, **It(untended)**:

$$It(untended) = (T*b)/(t*p) + t/2 \tag{3}$$

The expected investment for males selecting only tended females is

$$It(tended) = (T*b)/(t*q) + t/2 \tag{4}$$

Hypothesis 4: Time minimization

The two preceding models have assumed that the male's mate selection behavior is fixed. Such models will not result in a minimum investment per female, **Im**, under all conditions. The following model assumes males vary their behavior in response to the proportion of untended or tended females available to them. If we take the derivative of equation (3) with respect to t and set it equal to 0, we can solve for a relative extremum. The extremum is **t'** =

sqrt((2*T*b)/p) and since the second derivative of equation (3) is positive, t′ is a relative minimum. If we substitute t′ into equation (3) then **Im(untended)**= t′.

The **Im(tended)** can be derived as follows. Males deciding to cotend can only choose females with t′ remaining before eclosion or less. Therefore, we substitute t′ for T in equation (4) and take the derivative with respect to t and set it equal to 0 we get another relative minimum t" = sqrt((2*t′*b)/q). If we substitute t" into equation (4) then **Im(tended)**=t".

Hypothesis 5: Copulation maximization

The models of Hypotheses 1 and 3 are not easily tested. They were derived because they provided the foundation for the model of Hypothesis 4, which could be easily tested. The model of Hypothesis 5 expands on the model of Hypothesis 4 examining the effects of the constraint that the probability of mating is dependent on the time spent tending. I will assume that the probability of mating at any time t is an exponential function, **exp(-c*t)**, where c is a constant. The constraints on c are discussed below. I have selected this function because it is mathematically tractable, and its decreasing monotonicity will be characteristic of the relationship between the probability of mating and the time spent tending. The expected investment (**Ip**) for males selecting only untended females is

Ip(untended) = (**exp(c*t)***T*b)/(t*p)+(**exp(c*t)***t)/2 (5)

If we take the derivative of equation (5) with respect to t and set it equal to 0 we can solve for a relative minimum. This can only be simplified to

$$(2*T*b)/p = -((t*c+1)*t^2)/((t*c)-1) \tag{6}$$

For all values of T, p, and b, t must be solved iteratively. Under all conditions t*c must be < 1. When c = 0 the minimum described by equation (6) is the same as t′. If c > 0 then the value of t from equation (6) will be < t′. Therefore, if the probability of mating is dependent on the time spent tending (0 < t*c < 1), then males will select females closer to emergence than t′.

The purpose of this model was to illustrate the effect of having the probability of mating dependent on the time spent tending. It does not provide an easily tested prediction, since c is unknown. However, the observation that males should select females closer to emergence than t′ may prove useful for interpreting deviations between observational data and the predictions of Hypothesis 4.

IV. Methods

A. General Study Methods

Tetranychus urticae Koch were maintained on bush bean plants (*Phaseolus vulgaris* L. cv. Tendergreen) and were cultured using the methods of Theaker and Tonks (1977).

Most experiments with mites use small arenas excised from the leaves of host plants (e.g., Potter *et al*. 1976a,b). My observations indicated that bean leaves deteriorated rapidly after excision. Marked yellowing or chlorosis was observed within 36 to 48 h. Necrosis began after 48 h. Chlorosis was probably preceded by the breakdown and loss of proteins, chlorophylls, and inorganic ions within the excised leaf (Bidwell 1974). Leaching of photosynthates was very likely because of the damage caused by excision. For these reasons, observations of male behavior were only recorded from arenas ≤ 24 h old.

Unless otherwise noted, all experiments were run at 19 ± 1 °C on 1 cm^2 arenas of excised bean leaf. These arenas were placed on water-saturated absorbent cotton in 1.5 cm X 10.0 cm petri dishes. Prequiescent deutonymph females were placed on the arena with a sable hair brush (size 0). When all the females on the arena became quiescent, males were transferred to it and observations began. If all the females on an arena were not quiescent after 24 h, (about 5% of all arenas) then the arena was discarded. All observations were made with a Wild M3 stereomicroscope at x16 magnification.

Continuous observation of each arena was not practical because of the duration of the female's quiescent period (40 to 50 h). Each observation period was 4 h, and 3 to 5 periods were completed every 24 h. To increase the number of replicates, several arenas were run simultaneously during each observation period and observations were made sequentially. To prevent biasing a set of observations, the order of observing arenas was randomized between each set of observations. The total number of arenas run at any one time was 5 to 10. The interval between two observations of the same arena was ≤ 5 min. If the eclosion time of any female was missed, which happened on 10% to 50% of the arenas, then data from that arena were not used.

Not only were different arenas observed sequentially, but each arena was used for a sequence of trials; once a male had completed the behavior of interest, he was removed and another male was introduced on to the same arena. The objection to this design is the possibility that the behavior of the second male is not independent of the first. However, this design substantially reduces the number of arenas necessary, and the assumption of independence can be tested.

The three variables, number of males, number of females, and leaf condition, were classified dichotomously. Leaf condition was classified as good or poor, depending on the degree of mite induced chlorosis. The category good corresponded to a rating of 1 or 2 (little or no chlorosis) on a scale developed by the Glasshouse Crops Research Institute; whereas poor corresponded to a rating of 3 or 4 (moderate or heavy chlorosis)(Anonymous 1972). The number of males and the number of females were classified as high or low. The category low corresponded to the ≤ 0.75 males or females / cm². This cutoff point (median density) was found by classifying 25 leaves, and then counting all the males and females on each leaf.

B. Statistical Methods

This study presents several statistical problems. Male choices may be quantal or they may be categorical. In addition, each variable was classified dichotomously. Discrete data in these forms can not be analysed using traditional statistical methods such as multiple linear regression or analysis of variance. These data sets are best analysed as multidimensional contingency tables (Bishop *et al*. 1975).

Since 1900, contingency tables have been used to analyse categorical or quantal data (Bishop *et al*. 1975). However, the ability to analyse tables with more than two dimensions or variables had to await the general availability of high speed computers. Formerly, many such tables were analysed by examining all possible two dimensional tables. This method of analysis may not provide an undistorted view of the underlying relationships and interactions between the variables.

The following discussion relies heavily on Bishop *et al.* (1975) notably chapters 2, 3, 4, 9, 11, 12, and 14. Other discussions of this technique may be found in Fienberg (1970), Schoener (1970), Jenkins (1975), Brown (1976), Addicott (1979), and Dixon and Brown (1979).

Tables are analysed for two purposes, to describe the structure of the table (the underlying relationship between variables), or to test if a particular relationship exists. A table's structure is elucidated by comparing the fit of successive proposed structures or models, to the observed values in the table. A log-likelihood chi-square goodness of fit statistic is used to evaluate this fit. If the expected values generated by a model are close to the observed values, then the resulting chi-square will be small. Small chi-squares are associated with large probability values, therefore, models with probability values > 0.05 are considered to adequately fit the data.

Finding an adequate model may require the use of several systematic search procedures such as stepwise search; forward selection; backwards elimination or a screening procedure developed by Brown (1976). These procedures attempt to find those individual relationships (terms) between variables that contribute most to explaining the structure in the table. There usually are several models that adequately describe any particular table. The best model not only adequately describes the data, but does so with the fewest number of terms, or with only those terms which are easy to interpret.

A model expresses the pattern of dependence within the table. For example, suppose we have a data set with five variables: A, B, C, D, and E, and suppose that the best model is A*B*C, D, E. The second order interaction term A*B*C implies that A, B, and C are mutually dependent, whereas the terms D and E are independent of one another and independent of A, B, and C. The preceding model could have been written as: A*B*C, A*B, A*C, B*C, A, B, C, D, and E. However, A*B*C implies mathematically that the terms A*B, A*C, B*C, A, B, and C are necessary to explain the structure in the table because models formed by this analysis are hierarchical.

A hierarchical model is one where the absence of a single lower order term from the model requires that all the higher order terms that include this term be absent as well. The absence of all second order interactions, with the exception of A*B*C, implies that no third order interaction (e.g., A*B*C*D) is required to explain the structure of our example.

The hierarchical properties of this analysis are extremely useful. If a "combination" hypothesis is suggested (e.g., Hypotheses 4 and 5), then the only acceptable model must include a second order interaction (CHOICE*MALE*FEMALE). If any primary term (e.g., CHOICE) or first order interaction term (e.g., CHOICE*MALE) is absent, then that hypothesis is untenable.

A model that includes independent terms may be collapsed, ignoring these terms without affecting the table's structure. This allows the reduction of an unwieldly table to one of smaller dimensions for subsequent analysis. Unlike first order interactions (e.g., A*B), there is no single coefficent of association that expresses the directionalities of higher order interactions. Unless a table can be collapsed to two dimensions, the directionalities of any high order interaction must be explained verbally.

Multidimensional contingency table analysis can be used to determine if a particular term makes a significant contribution to explaining the structure of the table. A term is tested by subtracting the chi-squares and degrees of freedom (df) of models with and without that term. For example, subtracting the chi-square for the model A*B,C from the chi-square for the model A*B tests the contribution of the term C. If the difference between these two chi-squares is significant ($p < 0.05$), then the contribution of the term C is also significant.

This method of analysis depends heavily on iterative maximum likelihood estimation and asymptotic approximations for the calculation of various table values. The accuracy is dependent on the sample size. Marascuilo and McSweeney (1977) have suggested that the sample size should be adjusted so that the expected value of each table cell is > 5; however, this criterion tends to be overly conservative

(Cochran 1952, 1954). In addition, it is known that too large a sample size can produce a table that is almost impossible to analyse (Bishop *et al*. 1975, Chap. 9). As a result, there are no accepted rules to determine the sample size of a table.

The computations necessary to analyse any particular table are exceedingly complex; therefore, the program 3F of the BMDP statistical package (Dixon and Brown 1979) was used for this study.

Other types of standard statistical analyses are from Neter and Wasserman (1974) or Marascuilo and McSweeney (1977).

V. Results

Independence of trials

Physical and logistic limitations required that each experimental arena be used more than once, thereby introducing the potential for lack of independence between observations from the same arena.

To examine whether or not the choice of one male influenced the choice of a subsequent male on the same arena, two males were placed sequentially on each arena with two quiescent females and their choices were recorded. This procedure was repeated on 126 separate arenas. The two females were arbitrarily labeled "female 1" and "female 2". If the first male influences the choice of the second male, then the frequency with which the second male selects "female 1 or 2" will be dependent on the choice of the first male. This can be detected with a two way contingency table.

The results indicated that the first male did not influence the choice of the second male (Table 1). The choice of each male may be considered statistically independent, and therefore each arena can be used more than once.

Male discriminatory ability

All of the hypotheses proposed to explain mate selection by male *T. urticae*, with the exception of the random choice hypothesis, assume males select females based

Table 1. A test for independence between the choice of the first male and the choice of the second male.

First male's choice	Second male's choice female 1	 female 2
female 1	46	37
female 2	20	23

Pearson's chi-square = 0.902 with 1 df, p = 0.342

on the time the females have remaining before eclosion. Males could detect time differences between females in two ways. They may compare females and determine which is closer to eclosion (relative time difference), or they may perceive directly the time remaining before each female emerges (absolute time difference). However, male response to relative time differences may depend on absolute time differences. For example, a relative time difference of 4 h may not be important if the females have 40 and 44 h remaining before eclosion, whereas it may be very important if they have 1 and 5 h remaining before eclosion.

An individual male was placed on each arena with two quiescent females, and the time he initiated tending and the female selected were recorded. A total of 379 choices were observed. The difference between the eclosion times of the two females was used as the relative time difference. The time between initiation of tending and eclosion was used as the absolute time difference. These data were analysed as a multidimensional contingency table consisting of 3 variables: time remaining before eclosion (absolute time difference)(both females < 20 h or > 20 h, denoted as TIME), relative time difference between the females (< 1, 1-2, 2-3, 5-8, or > 10 h, denoted as RELATIVE) and male choice (whether the male had selected the first or second female to emerge, denoted as CHOICE).

This experiment cannot test if the absolute time difference influenced male choice, since both females had either < 20 h or > 20 h remaining before eclosion. However, it can test whether or not the absolute time difference altered any influence of the relative time difference on male choice. This is the hypothesis of interest. The best model for the data in Table 2 was (CHOICE*RELATIVE). This model states that the variables, male choice and relative time difference, are dependent. The absolute time difference did not influence this relationship. Therefore, Hypothesis 1 (random choice) may be rejected as a plausible explanation of mate selection by male *T. urticae*.

To determine how male choice varied with the relative time difference, Table 2 was collapsed, ignoring the variable TIME, and analysed using Scheffe-type contrasts (Marascuilo and McSweeney 1977). This analysis separated the data into only 2 groups: 0-2 h (includes: < 1 h and 1-2 h) and ≥ 2 h (includes: 2-3 h, 5-8 h, and > 10 h)($p = 0.05$). The pooled proportion of males picking the first female to emerge in the 0-2 h class was 0.510 ± 0.112 (95 % confidence limit), and in the ≥ 2 h class it was 0.702 ± 0.023. The confidence limit of the 0[illegible] h class includes 0.5, therefore we can infer that males were non-selective. When the age difference was ≥ 2 h males were selective, since the confidence limit does not include 0.5.

This experiment demonstrated that males respond to relative time differences between females. How males determine female age is unknown. Males may be able to use pheromone production as an index of female age. Cone *et al.*

Table 2. A 3 way contingency table testing for an interaction between the male's choice (females ranked in order of eclosion), relative time difference between females, and the time remaining before eclosion for both females.

TIME remaining before eclosion for both females	RELATIVE time difference between females (h)	Male's CHOICE First female	 Second female
< 20 h	< 1	14	12
	1-2	17	19
	2-3	15	7
	5-8	30	10
	>10	32	18
> 20 h	< 1	20	17
	1-2	12	13
	2-3	29	11
	5-8	45	15
	>10	28	15

Best model	df	log-likelihood chi square	p
CHOICE*RELATIVE	10	13.99	0.176

(1971b) suggested that production of a sex pheromone may be linked to formation of oocytes. They indicated that attractiveness of single females increases as they near eclosion. This suggests that males estimate absolute time differences. In addition, as a female nears eclosion, her green integument becomes wrinkled and silvery as air becomes trapped between the old and new cuticles (Laing 1969). Males, when they palpitate the female's cuticle, may be able to detect surface changes which indicate the time remaining before she emerges.

Past history

The results of the preceding experiment rejected Hypothesis 1 (random choice), but do not distinguish among the other five hypotheses. The next experiment was designed to differentiate between those hypotheses that assume that males have fixed mate selection strategies (2,3), and those that assume that males vary their choice of female in response to extrinsic stimuli (4,5,6).

These hypotheses could be tested by experimental manipulation of the relevant variables (number of males, number of females and leaf condition), or by the analysis of observations made on male behavior in the natural system. The former is the most desirable method to test hypotheses (Platt 1964). Experimental manipulation establishes the causality between a variable and its proposed effect, whereas analysis of observational data can only test for dependence between variables.

In this study, attempts to manipulate the variables were not successful. Arenas were only useable for 24 h, too short a period to establish both males and females on the arena. Attempts to use whole leaves were not successful. These arenas were so large, that sufficient numbers of males and females could not be collected.

In view of these and other formidable logistic problems of the experimental method, an observational approach was used in this study. This sacrifices the precision of direct manipulative experiments. However, if the expected dependence between variables can be deduced from each hypothesis, then it is possible to reject hypotheses based on the analysis of observational data.

This experiment involves the transfer of males to an arena with four females. It was assumed that a male's past history (i.e., number of females, number of males, and leaf condition on the leaf he was collected from) would influence his choice of females on the arena. This approach depends on the following: that males were not affected by the transfer to the arena, and that males were not adjusting their behavior to conditions on the arena.

Individual males were placed on each arena with four females. The following observations were recorded: whether or not the male had made a choice within 90 minutes; the time at which the female was selected; which female was selected; the order of female eclosion; and the time of eclosion. In addition, number of males, number of females, and leaf condition were recorded from the leaf from which the male was collected. A total of 288 choices were observed. Each choice was classified accordingly: number of males and females (denoted as FEMALES and MALES); leaf condition (denoted as CONDITION); and male choice (females were ranked in order of eclosion and separated into 2 groups: "female 1 or 2" and "female 3 or 4", denoted as CHOICE).

If males have fixed mate selection strategies (Hypotheses 2 and 3), then the variables suggested by Hypotheses 4, 5, and 6 (number of males, number of females, and leaf condition) would not influence which female was selected. The term CHOICE is predicted to be significant ($p < 0.05$) and independent of number of MALES, number of FEMALES, or leaf CONDITION. Hypothesis 2 (age dependence) predicts that the proportion of males selecting "female 1 or 2" should be greater than the proportion selecting "female 3 or 4", since females close to eclosion will be more likely to be accepted than younger females. Hypothesis 3 (fixed time threshold) predicts that females older than some fixed threshold should be accepted while younger females should be rejected. Of the four females on the arena, it was more likely that "female 1 or 2" would be acceptable to males. In this experiment, the predictions of Hypothesis 3 were the same as Hypothesis 2.

Hypothesis 4 (time minimization) predicts that males should trade off searching and tending times to minimize the time they invest in each copulation. When the number of available females has been high then males should accept females closer to eclosion than when the number of females has been low. Hypothesis 4 would be supported, if there were an interaction between male choice and number of females (CHOICE*FEMALES). The proportion of males selecting "female 1 or 2" should be high when the number of females has been high and should be low when it has been low.

Hypothesis 5 (copulation maximization) predicts that males should maximize the likelihood that they will successfully mate with the female they select. When the number of males has been high, then the likelihood of mating should be low and males should accept females closer to eclosion than when the number of males has been low. Hypothesis 5 would be supported, if there were an interaction between male choice and the number of males (CHOICE*MALES). The proportion of males selecting "female 1 or 2" should be low when the number of males has been low and should be high when it has been high.

Hypothesis 6 (differential costs) predicts that the female selected would depend upon the energetic constraints acting on the male. Males from chlorotic leaves should select females closer to eclosion than males from nonchlorotic leaves. Hypothesis 6 would be supported, if there was an interaction between male choice and leaf condition (CHOICE*CONDITION). The proportion of males selecting "female 1 or 2" should be low when the leaf condition has been good and should be high when it has been poor.

The multidimensional contingency table analysis of the influence of past history on male choice is presented in Table 3. The best model is (CHOICE, FEMALES*CONDITION*MALES) which is interpreted as male CHOICE independent of the number of MALES and FEMALES and leaf CONDITION, which in turn are mutually dependent. The predicted term CHOICE was significant because the proportion of males choosing "female 1 or 2" (0.677 ± 0.031) was significantly greater than the proportion choosing "female 3 or 4" (0.323 ± 0.031). These results are consistent with the predictions of Hypotheses 2 and 3. None of predicted terms involving CHOICE and one of MALES, FEMALES, or CONDITION were significant, suggesting that Hypotheses 4, 5, 6 and potential "combination" hypotheses may be rejected.

Other observations of male behavior can be used to test the predictions of Hypotheses 2 and 3. Both hypotheses predict that the proportion of males choosing a female should increase as the females available to them near eclosion, since both hypotheses predict that females close to eclosion should be accepted. Hypothesis 2 predicts a continuous increase in this proportion. Hypothesis 3 predicts a discontinuous increase, since males are assumed to reject females younger than a certain threshold.

Data on the proportion of males selecting a female within 90 min versus the time remaining to eclosion were analysed. Both hypotheses predicted a trend between the time to eclosion and the proportion of males making a choice, hence Maxwell's trend test was used (Marascuilo and McSweeney 1977). This test is sensitive to trends within contingency tables, whereas the commonly used Pearson's chi-square test is not (Marascuilo and McSweeney 1977).

The range in time remaining before eclosion for the four females was used; instead of the mean time before eclosion. If means had been used, then would be likely that at least one female on each arena would have been acceptable. However, using a narrow range of eclosion times should provide some arenas where all of the females would be unacceptable, sint the time to eclosion for each female would be within this range.

The time remaining to eclosion did not influence the proportion of males making a choice (Table 4). This is contrary to the predictions of Hypotheses 2 and 3 and suggests that both should be rejected.

This experiment is equivocal. Statistical analysis indicated that past history did not influence male choice which suggested that males had a fixed mate selection strategy. However, subsequent analysis showed that neither Hypothesis 2 or 3 were adequate explanations of male behavior. Any potential explanation of male behavior must either be a fixed strategy, or one where males vary their choice of females in response to extrinsic stimuli. The rejection of both these alternatives suggests that one of

Table 3. A 4 way contingency table testing for interaction between male choice (females ranked in order of eclosion), number of females, number of males, and leaf condition.

CONDITION	MALES	FEMALES	CHOICE female 1 or 2	 female 3 or 4
poor	low	low	9	6
		high	20	10
	high	low	68	24
		high	6	7
good	low	low	9	4
		high	35	14
	high	low	7	3
		high	43	23

Models or Terms	df	log-likelihood chi square	p
Best Model			
CHOICE,FEMALE*MALE*CONDITION	7	5.14	0.643
Terms			
CHOICE	1	39.94	<0.001
CHOICE*FEMALE	1	1.09	0.296
CHOICE*MALE	1	0.01	0.920
CHOICE*CONDITION	1	0.01	0.920

Table 4. A test for independence between the time remaining before eclosion for the four females and whether a male had made a choice within 90 min.

Time to eclosion (h)	Percentage of males choosing within 90 min	Sample size
0-10	72.4	29
10-15	53.9	26
15-20	90.0	46
20-25	77.3	44
25-35	57.8	33
35-40	74.1	27
40-45	55.6	9

Maxwell's trend chi-square = 0.395 with 1 df, p = 0.530

the assumptions of this experiment has been violated. Continuous observation of male behavior did not indicate that males were disturbed by transfer from the leaf to the arena. Therefore, I suggest that males adjusted their behavior in response to conditions on the arena, thus violating the second assumption of this experiment.

The conditions on the arena were the following: low number of males, high number of females, and good leaf condition. Under this combination of variables Hypothesis 4 predicts that the proportion of males selecting "female 1 or 2" would be high, and Hypotheses 5 and 6 predict that it would be low. The proportion of males selecting "female 1 or 2" was significantly greater than the proportion selecting "female 3 or 4" (0.667 > 0.323). This is consistent with the predictions of Hypothesis 4, but it is not consistent with Hypotheses 5 or 6.

Model testing

The results of the preceding experiment suggested that mal[illegible]sponded to conditions on the arena. Their response was consistent with the predictions of Hypothesis 4. This experiment re-examined the suggestion that males would vary their choice of females in response to the following variables: number of males, number of females, and leaf condition.

In this experiment, instead of using arenas, leaves were collected and the proportion of tended females that emerged within a fixed time period was analysed. Males from different leaves would have experienced a unique combination of these variables. If the male's choice of females was influenced by these variables, then the proportion of tended females that emerged in a fixed time period should reflect this influence.

Leaves were collected randomly and number of males, number of females, leaf condition, and which females were tended were recorded. After 20 h these leaves were re-examined, and the number of tended females that had emerged was recorded. A total of 409 tended females were observed. These data were classified to form a 4 way contingency table. The following categories were used: number of males and females (denoted as MALES and FEMALES), leaf condition (denoted as CONDITION), and emerged (whether the female emerged in < 20 h or > 20 h, denoted as EMERGED).

Hypothesis 4 (time minimization) predicts that whether the female emerged < 20 h or > 20 h, and number of females on the leaf would be dependent. This prediction is denoted by the interaction term (EMERGED*FEMALES). The proportion of females emerging in < 20 h should be high when the number of females has been high, since high numbers of females decreases the search time, and that allows males to be more selective in their choice of females.

Hypothesis 5 (copulation maximization) predicts that whether the female emerged in < 20 h or > 20 h, and the number of males on the leaf would be dependent. This prediction is denoted by the interaction term

(EMERGED*MALE). The proportion of females emerging in < 20 h should be high when the number of males has been high, since high numbers of males decreases the likelihood of mating, and males should be more selective in their choice of females.

Hypothesis 6 (differential costs) predicts that whether females emerge in < 20 h or > 20 h, and leaf condition would be dependent. This prediction is denoted by the interaction term (EMERGED*CONDITION). The proportion of females emerging in < 20 h on good leaves should be less than the proportion emerging on poor leaves, because males should only be selective when food is scarce.

Any "combination" hypothesis (e.g., both 4 and 5) requires a second order interaction between the relevant variables (e.g., EMERGED*FEMALES*MALES). The absence of any first order interaction (e.g., EMERGED*MALES) included in the second order interaction means that the "combination" hypothesis must be rejected.

The contingency table was analysed and the best model was (EMERGED*FEMALES,CONDITION)(Table 5). This model states that the variables EMERGED and FEMALES were dependent, and that the variable CONDITION was independent. The only significant predicted term was (EMERGED*FEMALES). This term was predicted by Hypothesis 4. Table 5 was collapsed, ignoring the variables MALES and CONDITION, to investigate the dependence between EMERGED and FEMALES. When the number of females was high, the proportion of females emerging in <

Table 5. A 4 way contingency table testing for interaction between the time for a female to emerge, number of males, number of females and leaf condition.

CONDITION	FEMALE	MALE	EMERGED < 20 hours	EMERGED > 20 hours
poor	low	low	15	13
		high	17	12
	high	low	31	10
		high	42	12
good	low	low	21	23
		high	24	22
	high	low	57	21
		high	62	27

Models or Terms	df	log-likelihood chi square	p
Best model			
EMERGED*FEMALE,CONDITION	11	4.96	0.933
Terms.			
EMERGED*FEMALE	3	92.17	<0.001
EMERGED*MALE	2	1.90	0.387
EMERGED*CONDITION	2	1.19	0.549

20 h (0.733 ± 0.055) was significantly greater than when the number of females was low (0.524 ± 0.082). These results support Hypothesis 4 and suggest that Hypotheses 5, 6, and potential "combination" hypotheses may be rejected.

The results of the preceding experiment supported Hypothesis 4 (time minimization) and rejected several other potential explanations of male behavior. However, that experiment only provides qualitative support for Hypothesis 4; to gain quantitative support, the predictions of the time minimization model for Hypothesis 4 were tested.

Mathematical models are engimas because they are both strong and weak tests of a hypothesis. They are strong tests because good agreement between observed and predicted values eliminates most alternative hypotheses, and weak tests because it is difficult to define "good" agreement, and interpret deviations between observed and predicted values (Caswell 1976). This experiment tests the time minimization model and attempts to deal with the problems of agreement and interpretation of deviations.

The time minimization model predicts what age of female a male should select to tend (t') or cotend (t") in order to minimize the time invested in each copulation. To test these predictions it is necessary to have estimates of search time, b and the quiescent period, T (t' = sqrt(2*T*b/p), t" = sqrt(2*t'*b/q), page 21).

The length of the quiescent period (T) was estimated by observing how long it took quiescent females to emerge. This period was 41.9 ± 1.4 h (n=127) at 19 ± 1 °C. This value is similar to that obtained by Cone *et al*. (1971b) of 36 h at 24 °C. The difference between these estimates probably reflects the different experimental temperatures, since development in mites is sensitive to temperature (Tanigoshi *et al*. 1975).

The time it takes a male to encounter a female (b) depends on the density of females on the leaf. Density is a function of the number of females present and the area of the leaf. To estimate b we need the relationship between female density and search time, and a simple method to calculate leaf area.

The relationship between leaf area and leaf length was Area(cm^2) = 10.5 + 3.78*Length(cm) ($R^2 = 0.958$; $F = 750.6$ with 1 and 33 df; $p < 0.001$). This relationship was used to determine the density of females on individual leaves (number of females/leaf area = female density).

Search time was estimated by placing a male on an arena (excised from infested leaves) with a single female and timing how long he took to find her. Different densities of females were simulated by varying arena size. The *a priori* assumption, that search time was exponentially distributed, was tested using Kolmogorov's goodness of fit test (Marascuilo and McSweeney 1977).

The relationship between search time and female density was determined at 3 densities: 0.20, 1.0 and 3.0 females / cm^2 (Table 6). The *a priori* assumption of exponentially distributed search times was accepted. The use of 3 points is sufficient to describe the slope and curvature of the response curve (regression line)(Neter and Wasserman 1974). One hundred observations were taken at 2 densities, 0.20 and 3.0, and 10 observations at 1.0. This placement of observations minimizes the variance of the slope (Neter and Wasserman 1974). This relationship was used to determine the search time of males for individual females at known densities.

It is desirable to test the predictions of a mathematical model against observed data. Most attempts are reduced to stating that the predictions of the model are consistent with observed data. This is weak support for any model. This problem arises because the parameters of a model are often difficult to measure, or because the underlying probability distribution of the model is unknown, preventing the use of common statistical tests.

Parameters of the time minimization model are easy to measure (T, b, and p). To test the fit of the time minimization model to observed male behavior it is only necessary to have a knowledge of the probability distributions of t′ and t″. Both t′ and t″ are products of several asymmetric probability distributions. The resulting probability distribution will also be asymmetric, and the mean and median will not overlap. This asymmetry precludes the use of parametric statistics to test the fit of the model. The following outlines a novel statistical method for

Table 6. The relationship between male search time and female density.

Female density (cm^2)	Search time (min)	Standard deviation	Kolmogorov " K "	p
0.20	163.0	165.0	0.06	>0.20
1.0	113.8	83.9		
3.0	61.9	83.3	0.09	>0.20

Regression function

Time′ = 4.88 - 0.367*Density

$R^2 = 0.216$
F = 47.01 with 1 and 208 df, $p < 0.001$

Based on the following statistical model:

Y′ = B0 + B1X + E′ where,

Y′ = ln Y(time) B0 = intercept (4.88) B1 = slope (-0.367)
X = density E′ = ln e (error term)

dealing with this problem.

If we determine the predicted medians of t′ and t", we would expect the observed values of t′ and t" to be symmetrically distributed about them, if the time minimization model was an adequate explanation of male behavior. If the distribution of observed values is asymmetric, then we would infer that the time minimization model did not adequately fit the data. However, simply rejecting this model would not identify the cause of any asymmetry. If the observed values were also classified according to other variables hypothesised to influence male behavior (number of males and leaf condition), it should simplify detection and analysis of any asymmetry.

Leaves were selected at random and the length of the leaf, its condition, number of males and the number of tended and untended females were recorded. These leaves were then observed (≤ 24 h), and the instances of an untended female becoming tended (n=158) or a tended female becoming cotended (n=86) and the eclosion time of each female were recorded. The time between initiation of tending and emergence was the observed t′, and t" was the time between the initiation of cotending and emergence. The time to encounter a female, b, was estimated by using leaf length to calculate female density, and subsituting this value into the equation in Table 6.

The statistical distributions of t′ and t" were simulated for each leaf. Since t′ and t" were products of several distributions, it was necessary to simulate each of the constituent distributions. The quiescent period, T, was normally distributed with mean = 41.9 and standard deviation = 7.9 (page 48). Search time, **b**, was exponentially distributed (Table 6). The expected number of females encountered, **1/p**, was geometrically distributed, and was approximated by the exponential distribution (Woodroofe 1975). In each simulation of **t′** (**t″** was similar), 100 observations were generated for each leaf using its observed values of **b** and **p**. The predicted median was calculated, and this procedure was repeated 10 times to give an average value for the median. The observed values of **t′** and **t″** for each leaf were classified according to the number of observations above and below each predicted median (denoted as MEDIAN), number of males, and leaf condition. These data were analysed as a 3 way contingency table.

Hypothesis 4 predicts that the term MEDIAN would *not* be included in the contingency model because the distribution of the observed values was predicted to be symmetric. I have argued that the expected **t′** for Hypothesis 5 is less than that of Hypothesis 4 (page 23). If Hypothesis 5 was correct then the distributions of observations should be asymmetric about the predicted medians of **t′** and **t″**, the variables MEDIAN and number of males would be dependent, and the predicted interaction term was (MEDIAN*MALES). Hypothesis 6 predicts that the variables MEDIAN and leaf condition would be dependent. The predicted interaction term was

(MEDIAN*CONDITION).

The analysis of the medians for t′ and t″ is presented in Tables 7 and 8, respectively. For both t′ and t″ the model which best described the data was, (MALE). The term MEDIAN was not significant (Tables 7 and 8). This agrees with the predictions of Hypothesis 4 and rejects Hypotheses 5, 6, and potential "combination" hypotheses as explanations of male behavior in *T. urticae*.

Table 7. A test for interaction between the median of t', number of males, and leaf condition.

CONDITION	MALES	MEDIAN	
		Above	Below
poor	low	4	5
	high	39	37
good	low	3	2
	high	35	33

Models or Terms	df	log-likelihood chi square	p
Best Model			
MALE	6	2.03	0.917
Terms			
MEDIAN	1	0.07	0.792
MEDIAN*CONDITION	3	1.05	0.789
MEDIAN*MALE	2	0.11	0.946

Table 8. A test for interaction between the median of t", number of males, and leaf condition.

CONDITION	MALES	MEDIAN Above	MEDIAN Below
poor	low	6	4
	high	14	17
good	low	7	5
	high	16	17

Model or Terms	df	log-likelihood chi square	p
Best Models			
MALE	6	1.30	0.972
Terms			
MEDIAN	1	0.01	0.920
MEDIAN*CONDITION	3	0.32	0.956
MEDIAN*MALE	2	0.98	0.806

VI. Discussion

Tetranychus urticae Koch has a promiscuous, polygamous mating system in which males search for and tend pre-emergent quiescent female deutonymphs. Males appear to use a behavioral strategy that minimizes the time invested in each copulation to determine their choice of females. Parker (1974a) predicted that this strategy would occur in those systems where males could allocate searching and tending times to maximize reproductive success. By minimizing the time invested in each copulation, copulation frequency is maximized, which in turn maximizes reproductive success. Whether a female is selected depends on the amount of time she has remaining before eclosion. When female *T. urticae* are abundant, males spend less time searching, which allows males to select females closer to eclosion. Analysis of both observational data and the fit of a model incorporating this time minimization strategy support this interpretation for male behavior.

Observational data revealed patterns of dependence that were consistent with a time minimization strategy (Hypothesis 4). Males were predicted to select females close to eclosion when females were abundant, and to be less selective when females were rare. Male choices on arenas (Table 3) and whole leaves (Table 5) were consistent with this prediction.

A time minimization model model was derived using elementary statistics and calculus, and predicted when a male should begin tending and cotending females. Observations of males initiating tending or cotending were consistent with the predictions of this model (Table 7 and 8).

Each line of evidence supports the hypothesis that males use a time minimization strategy in their selection of females. In addition, five alternative hypotheses were rejected as possible explanations for the behavior of male *T. urticae*. These alternative hypotheses were suggested by the mating behavior of *T. urticae* (1, 2, and 3), or by mate selection theory (4, 5, and 6). Therefore my conclusion rests not only on the ability of a time minimization strategy to explain male behavior, but also on the rejection of five other plausible explanations.

Many other studies have described male and female mate selection strategies which appear to maximize reproductive success. Parker (1978b) showed that male dung flies (*Scatophaga stercoraria*) adopted searching strategies that maximized their likelihood of encountering a sexually receptive female. Manning (1975) provided good evidence for male preference for larger, more fecund females in *Asellus* isopods (*A. aquatics* and *A. meridianus*). Downhower and Brown (1980) showed that female mottled sculpins (*Cottus bairdi*) preferentially selected larger males. They indicated that hatching success was positively correlated to male size.

Maynard Smith (1956) found that female *Drosophila subobscura* selected outbred males as mates, and, in doing so, had greater fertility than those females mating with inbred males. Searcy (1979) provided evidence to show that female red-winged blackbirds (*Agelaius phoeniceus*) selected males based on territory quality, and that brood survival was positively correlated with territory quality. Thornhill (1979,1980c) has established that female scorpionflies (*Panorpa* spp. and *Hylobittacus apicalis*) accept as mates only those males presenting large nuptial gifts. As a result, these females are more fecund and are spared having to hunt for their own prey; reducing the likelihood they will fall prey to web building spiders. Finally, Davies and Halliday (1979) showed that male common toads (*Bufo bufo*), like dung flies, appeared to adopt a search strategy which maximized the likelihood of encountering a receptive female.

These studies suggest that Lewontin's (1979) criticism that there is no empirical reason to expect an animal to maximize reproductive success may be wrong. This does not answer the question of just how useful optimality approaches are to the study of behavior; it may be that their usefulness is strictly heuristic. Formulation of a model requires clear statements about what correlate of reproductive success is important, how this correlate is minimized or maximized, and what constraints are acting on an organism's behavior. The cycle of testing, rejecting and modifying the model should lead to better understanding of the system, provided every addition to the model is shown experimentally to be necessary, and is not added simply to improve the model's fit. Ignoring the experimental verification of new constraints would change an explanatory model into a strictly predictive model.

Nor is it necessary to apply an optimality approach to the study of reproductive success in all organisms. Of the preceding studies, only Parker (1978b) and Davies and Halliday (1979) found it necessary to derive behavioral models. This approach is valuable technique in those systems where individuals can not be identified, however; where the reproductive success of individuals

My model assumes that males perceive female age and female availability. My results (Table 2) demonstrate that males readily distinguish relative time differences between females. The ability of males to determine female availability can only be inferred by agreement of the model with observed male behavior.

Ability of an organism to assess a particular resource is commonly postulated by optimality models (Schoener 1971, Pyke *et al.* 1977, Parker 1978b). Optimal foraging studies assume that predators recognize the expected value of the encountered prey and monitor their average energetic yield over time (Krebs *et al.* 1977, Pyke *et al.* 1977, Elner and Hughes 1978, Palmer 1980). Support for these assumptions is based entirely on the agreement between expected and observed foraging behaviors. The assessment mechanisms animals use are generally unknown, although it is widely accepted that they measure the resource directly, or use cues which are tightly correlated to it (Emlen and Emlen 1975, Krebs *et al*. 1977, Houston *et al*. 1980). Some foragers may assess their habitat while they search for food (Schoener 1971, Pulliam 1974, Pyke *et al*. 1977). Others, such as bumblebees, appear to engage in resource sampling at the beginning of their foraging careers (Oster and Heinrich 1976).

My model assumes that male recognition of female age is instantaneous. This is a simplification. Among non-visual foragers, a small proportion of the total handling time is usually devoted to prey recognition (Elner and Hughes 1978, Hughes 1979). Males must invest many hours in each copulation, therefore I believe I am justified in ignoring the time males spend in determining female age.

The potential relationship between different models of foraging behavior and my model of time minimization is an interesting one. Many of these models can be shown to be formally identical with one another (Pyke *et al*. 1977, Hassell and Southwood 1978, Palmer 1980). Each model attempted to describe the same behavior, the maximization of net energy intake, therefore it is not surprising that this led to formally identical models. The model developed in this study may or may not be formally identical to foraging models proposed to date. Despite repeated attempts I have been unable to prove whether or not it is identical.

VII. Bibliography

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