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A TEST OF BATEMAN'S HYPOTHESIS IN TERMS OF
MALE AND FEMALE TIME DIVISION STRATEGIES

by

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INTRODUCTION

The two sexes commonly are loosely defined in terms of a difference in initial energetic investment per offspring. Since both sexes contribute genetic information equally to the next generation, average reproductive success for the two sexes must be equal (Fisher, 1930). Bateman (1948) proposed that as a result, female reproductive success will be limited by energy availability and male reproductive success will be limited by mating opportunity. If males are able to divide their energy into smaller amounts and produce more offspring, but achieve on average a reproductive success equal to that of the females, male reproductive success should exhibit a higher variance. The reproductive success of an individual male will therefore be limited by the number of mates he can obtain in competition with other males, while that of a female will be limited way below the maximum level possible for a male by the energy she can collect. The fitnesses of the two sexes are thus limited by different resources. Further food will benefit females but not males, while further mate availability would benefit males but not females. This theory has decided implications for sexual selection which have been developed by Trivers (1972).

Time considerations, such as those offered by Schoener (1971) for foraging theory, alter the conclusions of Bateman's logic. If total time is limited by the eventual certainty of death, time spent foraging limits that available for mating and vice versa. The reproductive success of either sex may then be limited by that resource which requires more time to find in proportion

to the fitness it bestows for that sex. The fitness of either sex may then be limited by either resource depending upon its availability. Hence if mates are highly available, require no guarding and are 100% likely to be 100% receptive, while food is scarce, fitness of males as well as females will be limited by food availability. If on the other hand, densities are very low so that mates are widely spaced while food is highly available, the female as well as the male may be limited by whether or not she finds a mate. Thus the factors limiting the fitness of each sex may vary with the relative availability of the two resources, while the average reproductive success remains equal and the variance unequal for the two sexes.

A corollary of Schoener's suggestion is that to maximize their fitness, animals of each sex must divide their time between foraging and mating activity so as to derive the greatest possible benefit from each. A given energetic investment per offspring, mate availability, and food availability thus dictate a given optimal time division strategy and corresponding fitness. A simple model given below predicts how males and females will divide their time between mating and foraging under varying conditions of resource availability and illustrates the corresponding limitations on fitness. The model shows that under most conditions, when the density of one resource is increased, more time is made available to pursue the other, so that increases in either resource may result in increased fitness for either sex.

A major difference between the system in which Bateman

developed his ideas and the system he extended them to is in the time interval during which fitness must be attained. In his laboratory Drosophila system, neither food nor mates were scarce relative to the time required to obtain them; hence time was not limiting total reproductive success. In this situation, fitness would indeed be limited as one might predict on the basis of energetic investment alone. In the natural system in which these further ideas are to be tested, it is probably safe to assume that both food and mates are sufficiently scarce to require search time, and that total reproductive success may therefore be time-limited. The test animal is the cotton rat, Sigmodon hispidus, observed by telemetry under free-living conditions. It was not possible to measure fitness directly as Bateman did; however, it was possible to determine how the sexes divide their time between mating and foraging, and to manipulate the time necessary to forage for a given amount of energy. Thus we may determine whether an animal's time use coincides with the optimal time division strategy predicted by the model. The optimal strategy in turn entails limitations on fitness that may or may not be consistent with Bateman's predictions.

MODEL

1. Consider an animal foraging for a time t during a time interval p and pursuing mates for $p-t$.
2. Let b_1 = feeding rate = net energy gathered per unit time
 y = amount energy invested per offspring
 b_2 = mating rate = number copulations achieved per unit time
 b_3 = average number of offspring per copulation
3. Let N = number of offspring possible given mating activity during $(p-t) = b_2 b_3 (p-t)$
 Let N^0 = number of offspring possible given foraging activity during $t = (b_1 t)/y$
4. If no time were required for mating, the number of offspring an animal could produce from the energy acquired during t would be a simple function of the amount of energy invested per offspring, y , and the net energy gathered per unit time, b_1 . The latter will be taken to be a simple function of food availability. However, y is a quantity subject to natural selection and hence affected by the outcome of this model. We will use it as an independent constant in accord with the following arguments:

First, the environment presumably affects offspring fitness such that offspring fitness vs. energetic investment is a convex curve. As a result there will be an optimal energetic investment; that is, parents will maximize their own fitness by investing the optimal amount of energy and varying the number of offspring to fit the total amount of energy that they can collect (Smith and

Fretwell,1974). Y may thus be considered a constant dictated by overall environmental conditions which include expected fluctuations of b_1 . Constancy of seed size (Harper, et al.,1970) is often cited in support of this view.

Secondly, however, the optimum energetic investment subject to the above selection in mammals is weaning size, and, as noted hitherto, the two sexes contribute unequally to it. Maynard Smith (1978) provides a good explanation of how this could come about. In a hypothetical isogamous system, both parents would contribute equal amounts, but the system would be liable to invasion by a parent that produced smaller gametes able to fuse at a higher rate. Once this strategy became frequent, then a second strategy producing gametes larger than half optimum zygote size would gain in frequency as it would provide zygotes closer to the optimum size. Thus two strategies will persist, one that invests very little energy in the offspring but achieves fusion quickly, and another that invests energy in proportion to that needed for offspring survival. Throughout the introduction, "initial energetic investment per offspring" thus refers to energy that is invested according to one or the other strategy. Further parental care invested by males is not consistent with their basic strategy and may be considered forced on them by sexual selection. Since we wish to distinguish cause from

effect in our definition of sex, we will not consider cases where sexual selection has operated on males to yield high levels of energetic investment. Hence y is potentially very small for males, and large for females. Strategies in between these two are not expected to persist. Y therefore essentially remains a constant with two and only two possible values.

The number of offspring which an animal can produce given the energy gathered during t is thus equal to that energy, $b_1 t$, divided by y . It is assumed to increase linearly with t for all positive values of b_1 , as illustrated in Fig. 1a. The slope is a function of b_1 in the numerator and y in the denominator. A lower y results in a steeper slope for males.

When plotted vs. the mating time $p-t$, therefore, N^0 decreases with a steepness again dependent on b_1 and y (Fig. 1b). Plotting N^0 vs. $p-t$ enables us to compare it to N , the number of offspring permitted by the mating time.

5. If no time were required to gather the energy required for offspring survival, the number of offspring that a parent could produce from a given time spent mating would simply be a function of the number of successful copulations achieved during that time, and of the expected number of offspring per copulation. Recall, however, that where prior considerations limit the production of the opposite sex to a level below that afforded by mating opportunity, no fitness is gained by mating with the same individual twice. (Presumably either

males or females could be limited by energy if a total time limitation obtains.) Therefore, assuming equal efficiency in mate-finding, etc., both sexes would search for new mates. The latter would then decrease in frequency as more successful copulations were achieved. Hence the number of offspring possible out of a given mating time does not increase linearly with time but levels off progressively until all possible mates have been successfully dealt with and the slope is horizontal (Fig. 1c).

Trivers (1972) explains that since the maximum possible number of offspring is much greater for males than females, while the average reproductive success remains equal, males will compete among themselves to be the one or two individuals that achieve that maximum. Hence b_2 , the number of successful copulations per unit time, will differ for individual males, but will be equal among females. The N curve will thus level off more quickly for the average male than for the alpha male, who more nearly achieves the maximum number possible (Fig. 1d).

In this experiment we used the first large (over 95g.) rats trapped, and so were using dominant members of the population (Summerlin and Wolfe, 1973). The maximum N curve is therefore the one relevant to the males we were using. Females hypothetically have a mating rate dependent only on the number of available mates and therefore a mating-time fitness curve equal in slope to the maximum success achievable

by a male, since females presumably do not compete among themselves for mates (Fig. 1d).

Finally, if actual time spent mating were to be measured, which it will be indirectly, this curve will drop abruptly to zero as it approaches p (Fig. 1e). This is because if 100% of p is spent mating, no time is allowed to obtain the energy for copulation. However, this is not energy invested in the offspring and for our purposes such foraging time is time devoted to mating. We will assume for the purposes of our measurements that the energy required for copulation requires no more search time than is spent anyway in the process of looking for mates. Any searching beyond this will arbitrarily be considered necessary for investment in offspring. Some foraging for offspring investment may thus be measured as mating time, but not the other way around, according to these assumptions.

6. To determine how animals of either sex should divide their time between mating and foraging, we plot both N° and N vs. $p-t$ (Fig. 1f). The optimum mating time $\hat{p}-t$ occurs at the intersection of the N and N° curves. If more of the time interval is spent mating, then insufficient time will remain to feed the offspring resulting from the copulations and fitness will be limited to that permitted by the foraging time. If less time is spent mating, the animal will have plenty of energy to feed offspring but not be able to achieve enough copulations to produce that many, and so will be limited to

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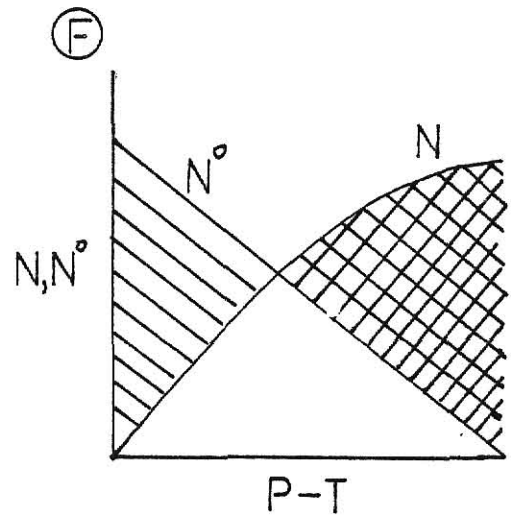
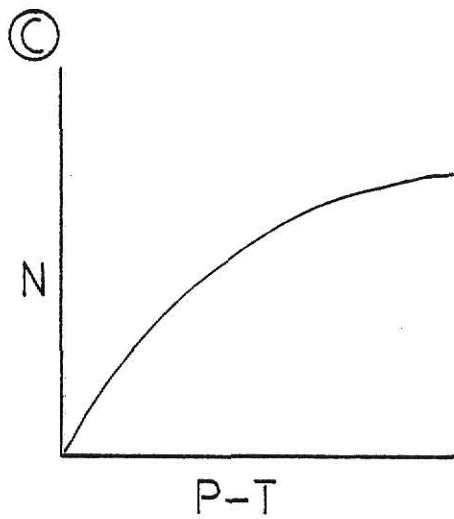
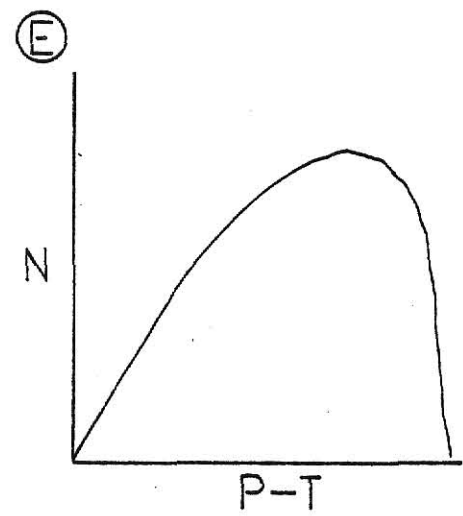
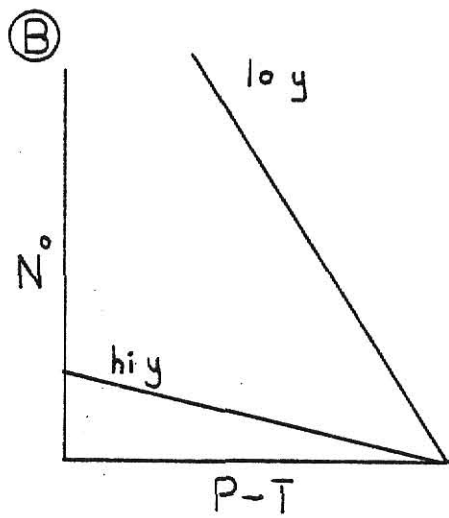
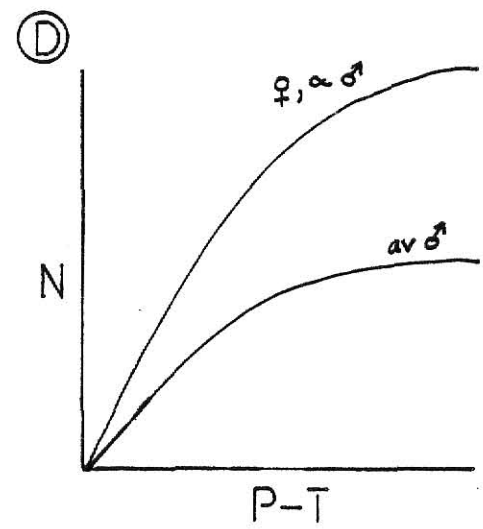
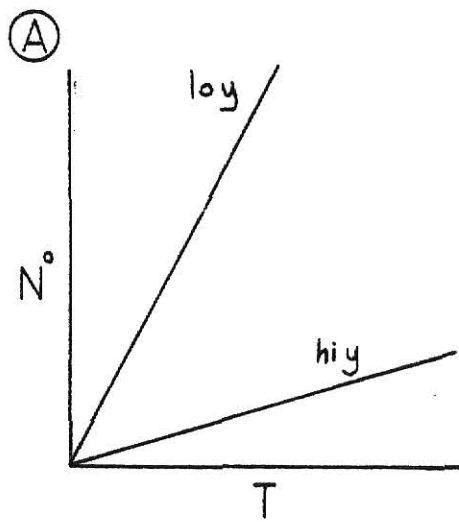


Fig. 1. Illustrations of the number of offspring which may be produced from the resources acquired during a given amount of time spent foraging or mating out of a total time interval p .

Fig. 1 legends, cont.

- a) N^0 , the number of offspring possible for males (low energetic investment per offspring y) and females (high energetic investment per offspring y) having spent t time foraging.
- b) N^0 for males and females plotted versus the remaining mating time $p-t$.
- c) General curve of N , the number of offspring which may be produced out of $p-t$ time spent in mating activity
- d) N for alpha males and females is approximately dependent only on mate availability and rises more steeply than N for the average male whose achievable fitness suffers the effects of competition from other males.
- e) The measured N curve, excluding time spent foraging for copulation energy.
- f) A comparison of the number of offspring possible from either foraging or mating time for determining the optimum time division.

the number permitted by the mating time. At the intersection, neither foraging time nor mating time limits the fitness permitted by the other.

7. The intersection point depends on the slopes of the two curves and therefore on y and on b_1 and b_2 which are positively related to food and mate availability respectively. The intersection determines $\hat{N}$, the maximum fitness, as well as optimal mating time ($\hat{p}-t$). The fitness $\hat{N}$ of both sexes may be limited by either food or mate availability depending on the relative slopes of the N and N^0 curves. Thus the different slopes of the N^0 curves for the two sexes result in different optimal foraging and mating times, but not necessarily different limitations on fitness.

Since b_2 varies below the maximum for males, this will result in a lower N slope and a higher optimum mating time for the average male than for the dominant male (Fig. 2). The fitness achieved by the average male must equal that of the average female.

8. It is helpful to examine the effect of environmental variations in food and mate availability, hence in b_1 and b_2 , in terms of cases.

CASE I. Conditions: high food availability (hence high b_1) relative to mate availability (hence to b_2). Fig. 3a.

If b_1 is high relative to b_2 , then the N^0 lines for both sexes could intersect the flat part of the

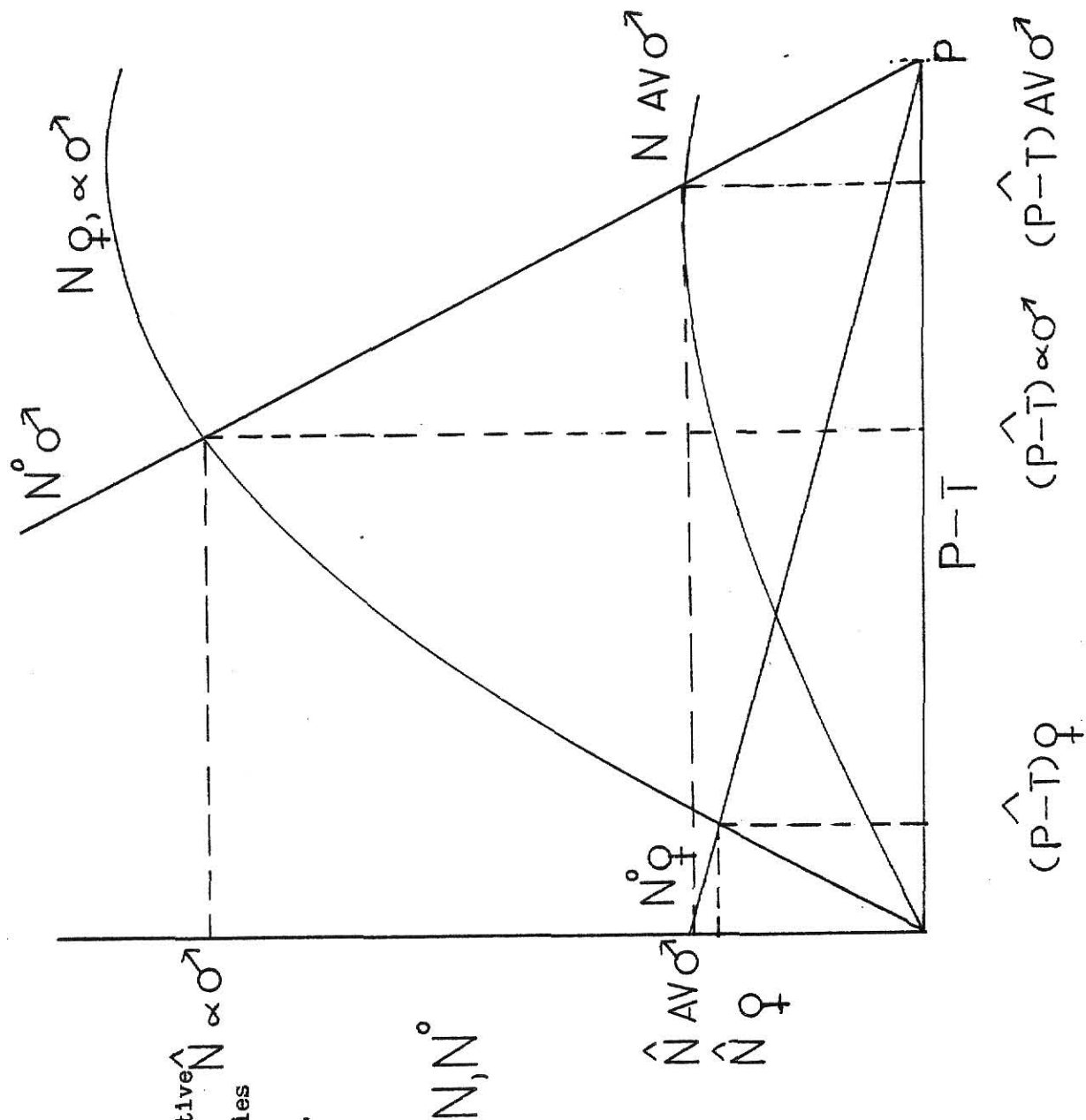


Fig. 2. Predicted $\hat{N}$ from a trade-off between the reproductive benefits of mating and foraging activities for males (alpha and average) and females. Case III of model.

N curve. As a result, little increase in fitness would result from increased food density for either sex, and both could be considered limited by mate availability. Such conditions might occur early in spring before breeding has produced multiple generations so that mate availability is still low inspite of possibly highly available food.

CASE II. Conditions: low food availability (hence low b_1) relative to mate availability (hence to b_2). Fig. 3b

If b_1 is low relative to b_2 , both the male and female N^0 curves could intersect the N curve where it is nearly vertical. Little increase in fitness would result for either sex were mate availability to increase further. An increase in food availability, however, would cause the fitness of both sexes to increase sharply, the male more than the female due to the former's low y value in the denominator of the N^0 slope. Hence the fitness of both sexes would be considered limited by food. This situation may be the case for members of dense populations entering the declining phase. The high density would result in an abundance of mates and a shortage of food. In this situation, high foraging times are predicted for both sexes.

CASE III. At conditions lying between these two extremes (illustrated in Fig. 2), both N^0 curves will intersect at the non-horizontal and non-vertical parts of the N curve. The fitness of both sexes could thus be limited by either factor. An increase in food density and therefore b_1 ,

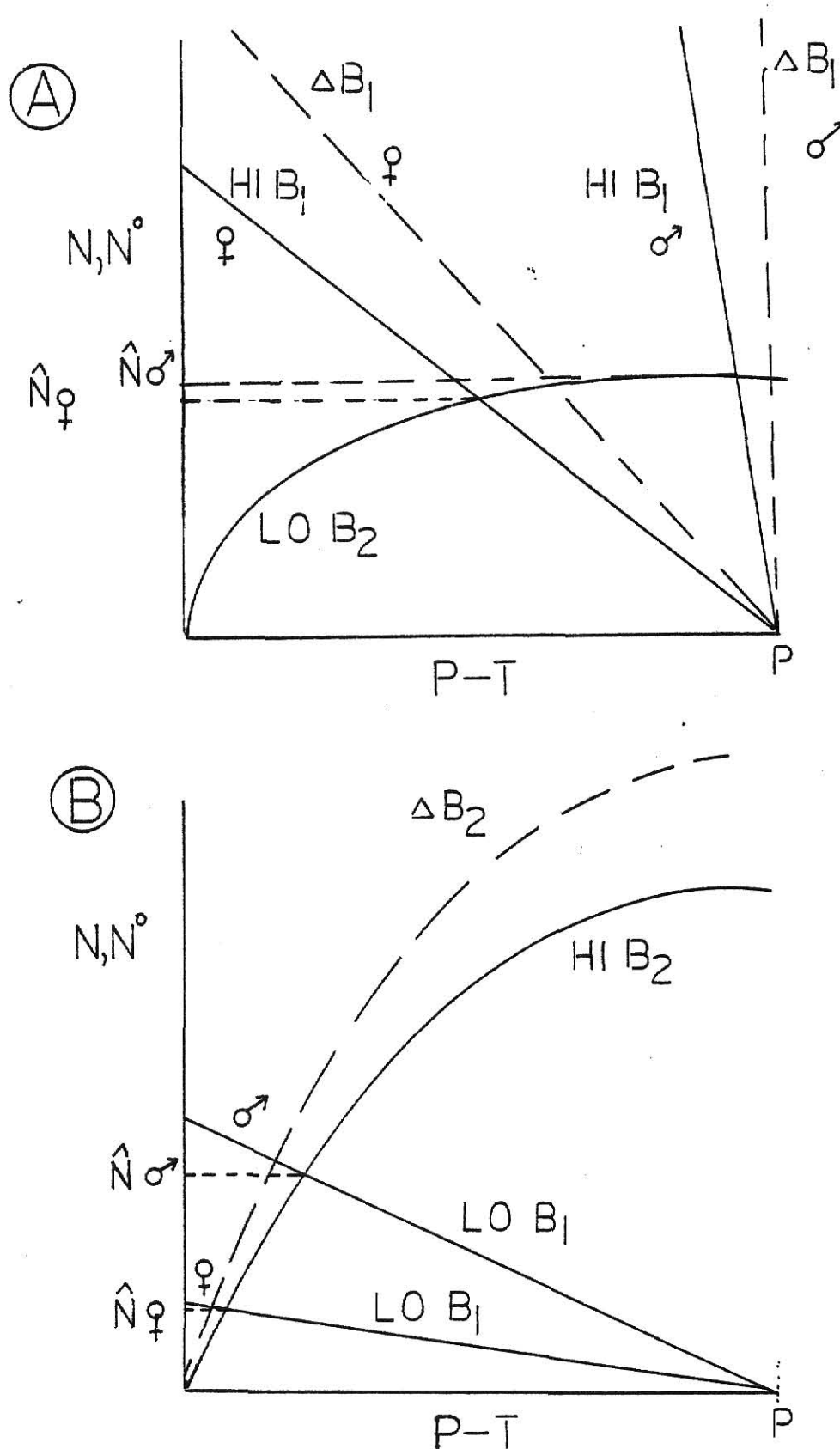


Fig. 3. a) Fitnesses of males and females under conditions of high food availability (b_1), and low mate availability (b_2), showing that increased food availability will not benefit either sex. Case I of model. b). Fitnesses under conditions of low food availability (b_1) and high mate availability (b_2); increased mate availability does not benefit either sex. Case II of model.

increases optimal mating time for both sexes with a corresponding gain in fitness, while an increase in mate availability (hence b_2) increases optimal foraging time for both sexes, again with a corresponding gain in fitness.

Bateman's hypothesis could result from a limiting case of (III) where the female N^0 line intersects N where it is nearly vertical, so that female fitness is limited by food availability only, and the male N^0 line intersects N where it is nearly horizontal, so that male fitness is limited by mate availability only. Bateman's hypothesis may thus obtain where either:

- a. Fitness derived from either foraging or mating activity is essentially independent of the time spent on the activity (complete independence is illustrated graphically in Fig. 4a.) Where mating is concerned, this could occur in the case of a subdominant male, who after losing a few fights (in species that do fight) has very little chance of obtaining further mates by spending much more time at it (Fig. 2). Or it could occur for any male in situations where females are scarce or highly clumped. Energy gain may be independent of the time spent where an animal spends no more time searching for food than it spends anyway in its other activities, especially in searching for mates. Under such conditions, the N and N^0 curves are both

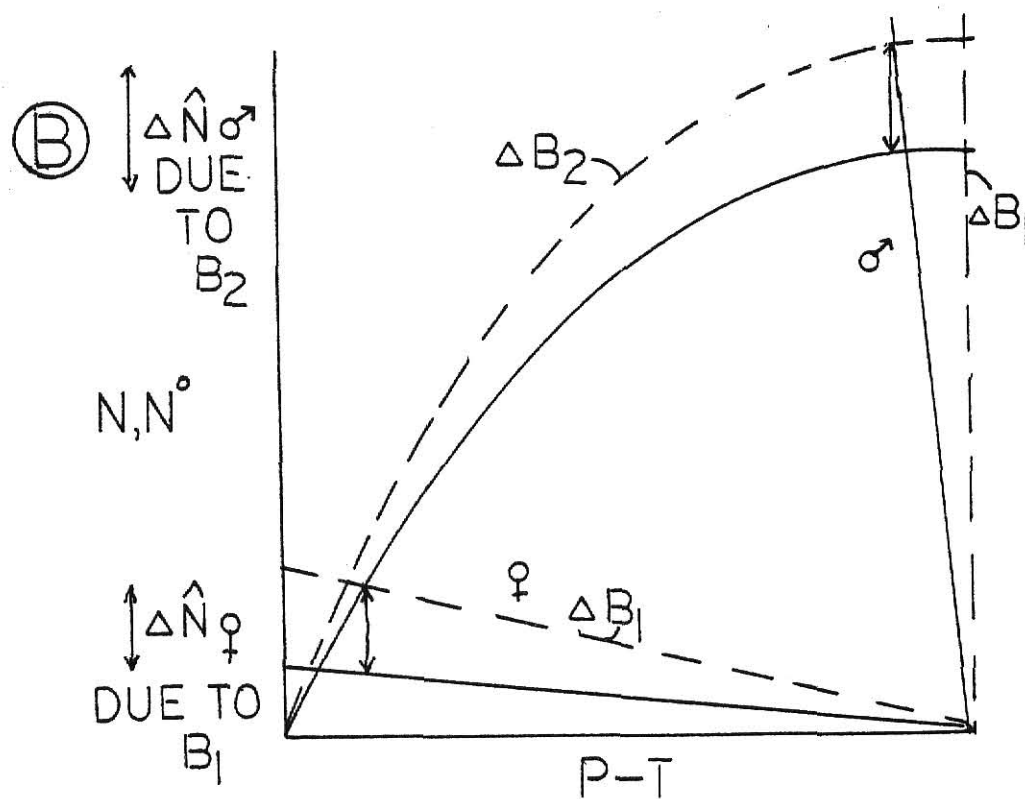
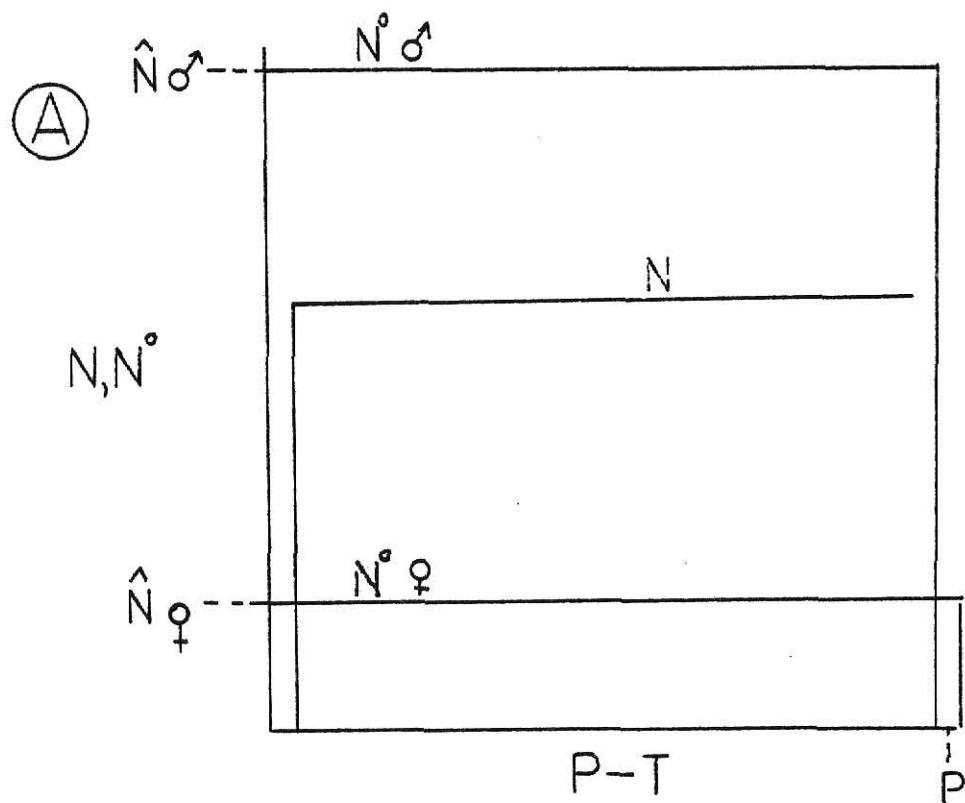


Fig. 4. a) Strict interpretation of Bateman's original predictions illustrated graphically in terms of the time-limited model.
b) A case of the time-limited model which would confirm Bateman's hypothesis.

horizontal lines for most of the time interval, with the N curve out of the female's reach. Males can be benefited only by increasing the number of mates (raising the N line), which will not benefit the females at all. Females can only be benefited by raising the N^0 curve, which will not benefit the males at all. Male fitness is thus limited by mate availability and female fitness by food availability in the strictest sense of the word.

- b. Male energetic investment approaches zero and female energetic investment approaches or exceeds the net energy she could collect by spending the entire time interval foraging (Fig. 4b). In this case nearly 100% of p would be spent in the "limiting" activity (as designated by Bateman), and an increase in the density of the other resource could not contribute enough additional time to substantially improve fitness.

PREDICTIONS

1. The lower slope of the female's N^0 line, resulting from the high value of y in the denominator, causes it to intersect the N curve at a lower $\hat{p-t}$ than for males (see Fig. 2). The model predicts a lower optimum mating time and a greater optimum foraging time for females than for males, for all positive values of b_1 and b_2 . The dominant male is the appropriate standard of comparison as he has the same N curve as the female, but if the average male is used for comparison, the

difference is even greater.

For a test of this prediction in terms of the measurable, hourly movement, consider the following:

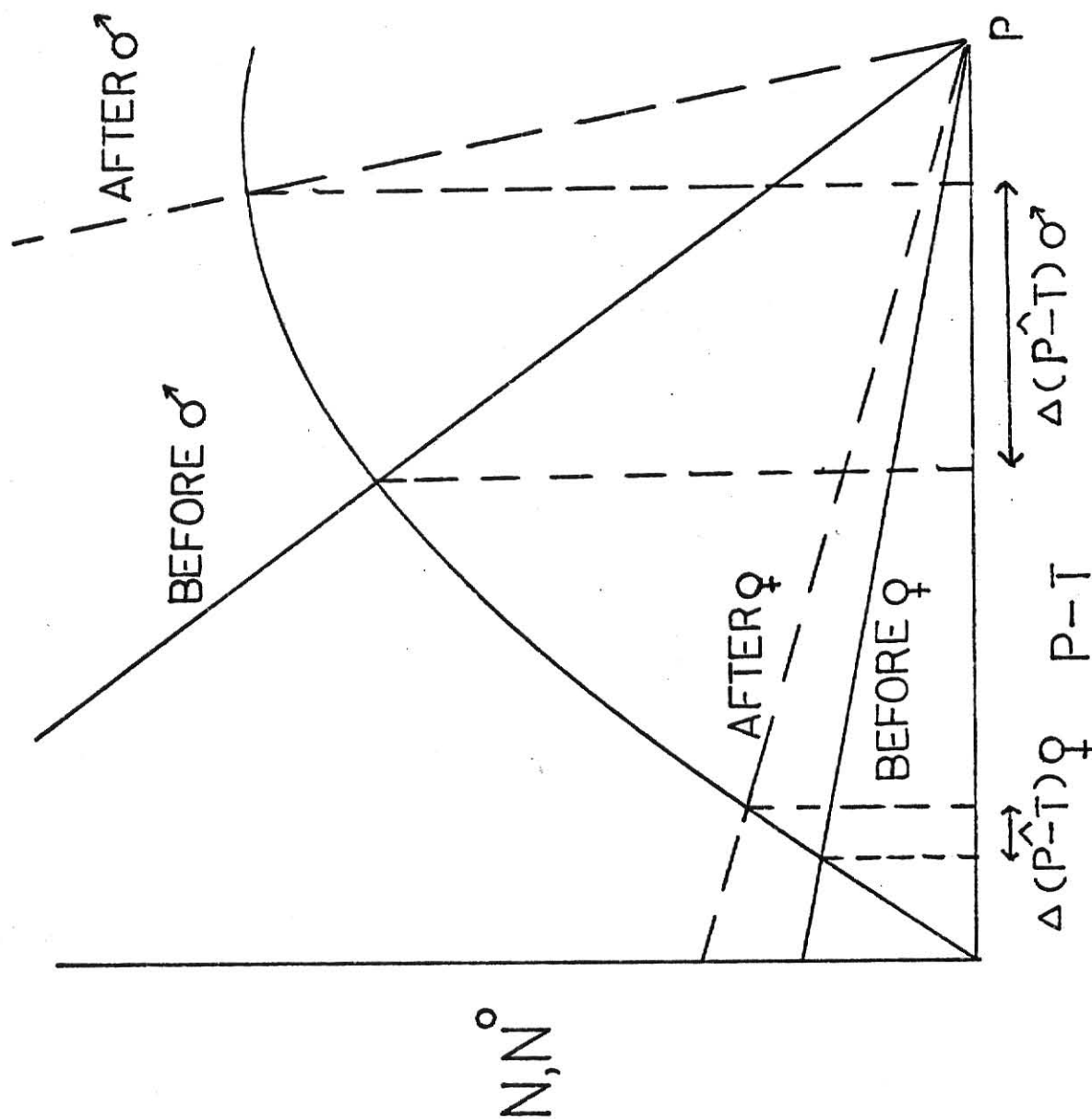
An animal is assumed to move through its home range at a rate which is a function of two speeds: s_1 , which maximizes encounter with food items, and s_2 , which maximizes encounter with mates. Since mates are ordinarily less dense than food items, s_2 is greater than s_1 . So the above rate may be assumed to vary with the following expression:

$$r = s_1 t + s_2 (p - t)$$

Adding a high density of food items approximately evenly should cause the foraging speed, s_1 , to decrease. Therefore the animal with a greater t , that is, the female, will be expected to show more of a decrease in average hourly movement. (The expression should in general increase with food supplementation except in the case of a high value of t . See appendix discussion on dr/db_1 .)

2. When food availability is increased, b_1 should increase, increasing the slopes of the N^0 lines for both sexes. The lower y in the denominator for males should cause a greater absolute increase in optimal mating time (Fig. 5)

Fig. 5. The predicted effects of food supplementation on male and female time division strategies. An increase in food density results in an increased N° slope.



Thus the increased time made available for mating by the food supplementation is not expected to be substantial for females, but it is for males. Whether r will increase or decrease depends ultimately on the ratio of the increase in mating time to the $s_1 t$ term (see Appendix.) This ratio is expected to be greater for males than for females due to the high value of t predicted for the latter.

If males increase their movement in response to food supplementation, they will thereby demonstrate that they have used the extra time made available for mating. However, the increase in mating time may or may not be great enough to counteract the decrease in r due to the decline in s_1 . Therefore negative results will as usual simply indicate a lack of evidence for an improvement in male fitness due to the extra time provided by food supplementation, rather than sound evidence that it did not in fact occur.

MEASURABLE VARIABLES

1. Average hourly movement per day.

The first male and female trapped on each grid that were large enough to carry the transmitter package (over 100g) were equipped with commercial transmitters mounted on collars and released at the site of capture. Including time spent in the trap, rats were held for six hours or less. The data thus pertain to dominant

animals who had presumably not lost their home ranges to aliens. All animals tracked had either scrotal testes or conspicuous mammae.

One male and one female were tracked hourly per grid and four grids, grouped by habitat, were tracked simultaneously. Thus eight rats were tracked at a time. Rats were located using a 7-element Yagi antenna and either a Cedar Creek or AVM receiver as receiving equipment (one receiver was used in the spring and the other in the fall.)

Eight or ten permanent tracking stations composed of seven foot aluminum poles with permanently mounted compass dials were set up on each one ha. grid. Directional readings could thus be taken from the same set of points each time, and the experimenter moved only along certain paths. Average distance between stations was 40 m. To be used for triangulation on a single location point, readings had to be finished within four minutes of each other.

Location error and its variation with angle and distance were measured empirically by means of the set-up illustrated in figure 6. The set-up consists of three direction lines each surveyed at a different angle from the baseline and marked every ten meters by the center of a square. A helper placed transmitters at the corners of the squares while the experimenter was blind-folded, randomizing the position in terms of direction, distance and corner. The use of a corner rather than the center point of each square was to ensure that should the experimenter develop a feel for the direction of the line, he could not successfully guess the side

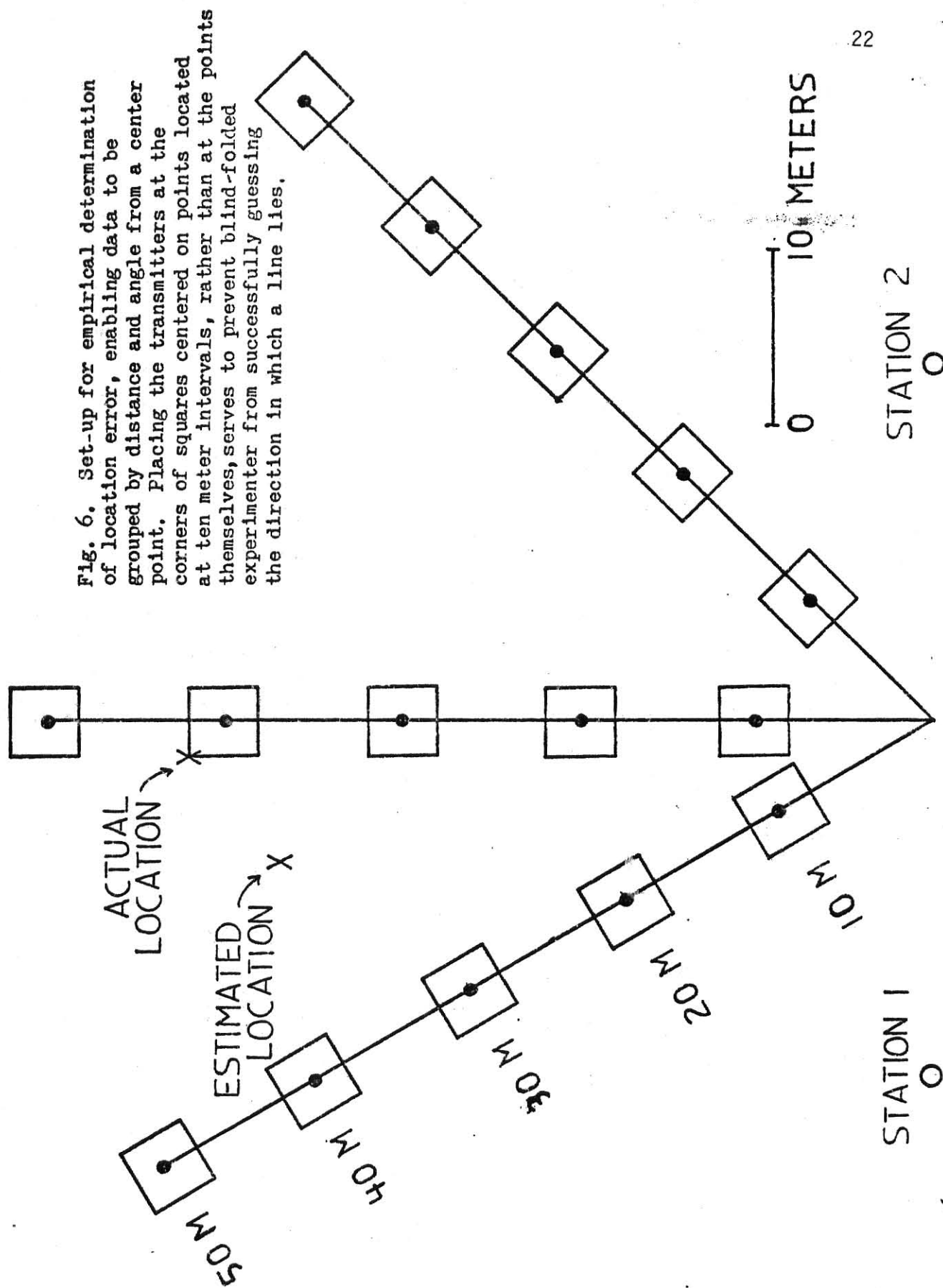


Fig. 6. Set-up for empirical determination of location error, enabling data to be grouped by distance and angle from a center point. Placing the transmitters at the corners of squares centered on points located at ten meter intervals, rather than at the points themselves, serves to prevent blind-folded experimenter from successfully guessing the direction in which a line lies.

to which the transmitter lay. Twenty-nine location points were measured in this manner and yielded an average error of 10.3 m. The average measured hourly movement of a fed female rat in this area was only 12.4 m. These data are therefore not appropriate descriptive data but should be used for comparative purposes only.

Contrary to the usual situation as described by Heezen and Tester (1967), error did not vary with intersection angle as much as it did simply with distance. This is probably due to the noise problems contributed by near-by powerlines and a broad-casting tower that were causing a very low range (under 50m). For this reason, readings were taken from the closest stations (up to 10m) rather than from a 90° angle, although this was attempted where it was possible as well.

Another measurement of location error was made by taking repeated three-cornered observations on a resting rat during the noon hours in the spring, from 11 AM to 2:30 PM. The average length of the side of the triangles thus formed was 5.2 m. The typical area covered by the triangles was thus well below that of a rat's home range.

Location points were plotted on maps and the distance in meters between points measured from the plot. Correction was made for the exact number of minutes elapsed between two location points for the same animal to get distance moved per hour. The technical errors just discussed tend to overestimate the distance moved, since they are bounded at the lower end (i.e., one cannot have a distance less than zero.) Method error, however, underestimates it, since any other path the

rat could have taken would be longer than the linear one assumed. Thus to a certain degree, these two types of error may cancel. It should however be borne in mind that the turning movements of the female will be underestimated by the method, while the ranging movements of the male, which are more nearly linear, will on the other hand be overestimated by the experimental error. The errors involved, to the extent that they do not cancel each other, will thus tend to exaggerate the difference between males and females. However, this should not affect the degree to which the sexes each appear to respond to increased food density.

Activity periods during the fall and spring differed in that a resting period occurred during the middle of the day during the spring. Spring data were therefore taken for an AM and PM period with a three to four hour interval in between. Fall data were generally taken for a continuous 14 hours. In both cases data were taken hourly every day for all of the eight rats that remained. Eight out of the total 16 rats were "lost" due to snake predation and battery failure before the end of the three week session.

2. Body weight.

Each grid was equipped with 66 live-traps in a 1-ha. 6 X 11 square array. All traps were run for two days prior to the experiment and two days afterward. All rats trapped were sexed, toe-clipped, weighed to the nearest gram, and checked for reproductive condition. In the case of rats that were to be transmittered Metofane anaesthesia was used; otherwise it was not.

EXPERIMENT

Eight grids 1 ha. each were set up in two types of habitat in South Carolina. Four were in a densely briar-covered clear-cut, and four in an old field in areas that supported thick growths of Lespedeza or Heterotheca. The briar grids were used in May and the old field grids in November. Seasonal effects listed in the analysis of variance table (Table 1) are thus confounded with habitat effects.

Four grids, two experimental and two control, were tracked simultaneously. All grids were first trapped for two days, and a male and a female radiocollared on each. All eight rats were then tracked hourly for seven days. Food was then distributed on two of the grids by broad-casting 80 kg mixed sunflower seeds and rolled oats (1:2 by weight) on each grid approximately evenly so as to increase food item density and decrease search time. Handfulls thrown to 10 m. were alternated with handfulls thrown forcibly at the ground so as to ensure that some food reached ground level through the leaves.

In order to be sure that the animals' entire home ranges were evenly supplemented, it was necessary to distribute the food on those grids where the animals remained within the grid boundaries. The experimental and control grids thus were not chosen at random, and animal movements on experimental and control grids were significantly different prior to distributing the food (see RESULTS).

Tracking resumed the day following food supplementation and continued for at least seven days thereafter, or until most

of the batteries gave out. Battery failure and snake predation resulted in unequal numbers of days for different rats during the post-feed session. The day following the termination of tracking all grids were again trapped for at least two days, and body weights taken again for all animals.

If females spend more time foraging than males, they are expected to show more of a reduction in hourly movement relative to their controls than males. A comparison of the changes in hourly movement per day due to food supplementation exhibited by males and females therefore indicates whether females spend more time foraging than males, and is tested by the FOOD*SEX*BEFORE interaction, in the analysis of variance (Table 1). The interaction determines whether the relation between the changes (from BEFORE feeding to after feeding) exhibited by control and experimental animals (FOOD supplemented grids vs. non-supplemented grids) is different for the two sexes (SEX).

A comparison of the change in male movements alone relative to their own controls, to determine whether males increased their movements, should indicate whether males made use of the extra time provided by the food supplementation to pursue mates. As the above interaction did prove to be significant, the LSD procedure was used to compare the means of experimental and control males. The weight gains of animals of each sex relative to their controls indicate both whether the food was in fact taken and whether it in fact increased net energy intake, and also whether it did so differently for males and females. Body weight data thus provide an alternative assessment of the

Table 1.
ANALYSIS OF VARIANCE
COMPLETE DATA

SOURCE	DF	TYPE IV SS	F	PR F
SEASON*	1	1148.794	12.50	0.0005
FOOD**	1	1479.607	16.13	0.0001
BEFORE†	1	1.304	0.01	0.9052
SEX	1	329.782	3.59	0.0596
IDNC (SEASON BEFORE FOOD SEX)	16	2995.370	2.04	0.0130
FOOD*BEFORE	1	66.259	0.72	0.3965
FOOD*SEX	1	529.108	5.77	0.0174
SEX*BEFORE	1	45.184	0.49	0.4837
SEASON*BEFORE	1	22.935	0.25	0.6177
SEASON*FOOD	1	264.015	2.88	0.0916
SEASON*SEX	1	571.486	6.23	0.0135
FOOD*SEX*BEFORE	1	309.314	3.37	0.0680
SEASON*FOOD*BEFORE	1	142.536	1.55	0.2142
SEASON*FOOD*SEX	1	1136.871	12.39	0.0005
SEASON*SEX*BEFORE	1	39.755	0.43	0.5112
TOTAL MODEL	30	11977.606	4.35	0.001
ERROR	176	16145.167		

*Fall (data taken in old field) vs. spring (data taken in briars)

**Experimental vs. control grids

†Before feeding day vs. after feeding day

Table 2.

MEAN VALUES OF AVERAGE HOURLY MOVEMENT BY CLASS

CLASS	N	AVE. HOURLY MOVEMENT PER DAY m/hr.
SPRING	97	23.396
FALL	110	16.122
FED	117	16.587
UNFED	90	23.357
BEFORE	107	20.524
AFTER	100	18.468
MALES	96	22.091
FEMALES	111	17.316
FED ANIMALS BEFORE	56	17.863
FED ANIMALS AFTER	61	15.416
UNFED ANIMALS BEFORE	51	23.446
UNFED ANIMALS AFTER	39	23.241
FED MALES BEFORE	26	16.071
FED MALES AFTER	24	17.512
UNFED MALES BEFORE	26	27.718
UNFED MALES AFTER	20	28.097
FED FEMALES BEFORE	30	19.415
FED FEMALES AFTER	37	14.057
UNFED FEMALES BEFORE	25	19.003
UNFED FEMALES AFTER	19	18.129

comparisons made with movement data.

RESULTS

1. Significant heterogeneity of variance resulting from sex and individual rat differences, which were in turn aggravated by the positive relation between location error and distance, made it necessary to analyze the mean hourly movement per day rather than the movements themselves. The analysis of variance is given in Table 1. It shows a highly significant main effect of FOOD (i.e. supplemented vs. non-supplemented grid) with $F=16.13$, $p<.0001$ that must have held both before and after feeding. Thus experimental and control grids must have been different prior to food supplementation. Examination of the table of means (Table 2), indicates that experimental (food supplemented) animals had smaller mean hourly movements per day than control (un-supplemented) animals, 16.587 m/hr ($N=117$) as opposed to 23.357 m/hr ($N=90$). Therefore a given percent reduction due to feeding shown by experimental animals will be smaller in absolute terms than an equal percent reduction shown by control animals. Nevertheless, Table 1 indicates a nearly significant FOOD*SEX*BEFORE interaction ($F=3.37$, $p<.0680$).

It appears from this analysis that since the control grids were not chosen at random, they may be inappropriate comparisons for assessing what happened on the fed experimental

Table 3.

ANALYSIS OF VARIANCE
FED ANIMALS ONLY

SOURCE	DF	TYPE IV SS	F	PR F
SEASON*	1	1598.101	37.32	0.0005
BEFORE†	1	50.006	1.17	0.2824
SEX	1	0.233	0.01	0.9413
IDNO (SEASON SEX BEFORE)	8	358.397	1.05	0.4070
SEX*BEFORE	1	370.811	8.66	0.0040
SEASON*SEX	1	30.514	0.71	0.4006
SEASON*BEFORE	1	136.808	3.19	0.0769
SEASON*SEX*BEFORE	1	63.623	1.49	0.2257
TOTAL MODEL	15	2885.862	4.49	0.0001
ERROR	101	4325.111		

*Fall (data taken in the old field) vs. spring (data taken in briars)

†Before feeding day vs. after feeding day

experimental grids. In order to interpret the above results, the same analysis was performed comparing only experimental animals to themselves before and after feeding (Table 3). The SEX*BEFORE interaction in this case has $F=8.66$, $p<.0040$. Thus it appears that the weak interaction reported above is the result of a strong difference between before and after movements of food-supplemented animals. Examination of the means (Table 2) shows that fed females reduced their movements, from 19.415 m/hr ($N=30$) to 14.057 m/hr ($N=37$), whereas males increased from 16.071 m/hr ($N=26$) to 17.512 m/hr ($N=24$). This indicates that females reduced their movements to a greater degree than males, as predicted by the model.

2. Since the above interaction was significant, comparisons of fed males and fed females to themselves before and after supplementation were then made using Fisher's LSD procedure. The appropriate LSD at $\alpha=.05$ for comparing pre and post-feed movements of experimental females was 3.714, smaller than the 5.36 difference shown. The decrease shown by females was therefore significant. The appropriate LSD to determine whether males increased significantly at $\alpha=.05$ is 4.344 (different due to different sample sizes), greater than the 1.442 increase shown. No increases shown by fed males broken down either by season or by individual were significant either by the LSD procedure. From these data it appears that males in general did not respond to food supplementation by increasing their movements.

Body weight data appear to corroborate these results. Recapture data sufficient for analysis of body weight gains were obtained only in the fall. Only potentially reproductive animals (over 50 g) were analyzed. During the time of the experiment, control males gained an average of 27.14 g (N=7), while control females gained an average of 6.25 g (N=12). These figures may be taken to roughly represent the normal growth of males and females during this time. Fed females gained an average of 33.143 g (N=7), significantly more than their controls ($p < .0025$, one-tailed t test). Fed males on the other hand gained an average of 43.286 g , not significantly greater than their controls even at the 10% level.

DISCUSSION

The FOOD*SEX*BEFORE interaction indicates clearly that females spend more time foraging than males, as predicted by the model. Hence males and females appear to use their time differently and we may conclude that fitness is not independent of the way time is spent. This is a basic assumption of ethology, where fitness is measured per unit time. Furthermore it is the basis for predicting that limitations on the fitness of males and females may be conditional on actual food and mate availability. We have here evidence that time is divided according to energetic investment per offspring. Animals with greater energetic investments per offspring spend more time foraging and less time mating than animals who invest less per offspring.

If this is true, then is the time which a male must spend foraging of significant cost to the fitness which he could derive from a given natural availability of mates? If the time which he must spend foraging is reduced by artificially increasing the food density, will he actually use the extra time to further pursue mates? The answer appears to be no. The evidence is not altogether unambiguous, however. The following points may merit consideration.

Simplifying assumptions adopted in the model may have omitted important factors. For example, if males were to require a strictly dependable increase in food availability in order to take advantage of extra mating time, the artificial food supplementation would not have been adequate. Possibly a male might not venture further in search of mates, even if there were time to do so, if high energy conditions were atypical or unpredictable in his habitat and therefore unlikely to last. In other words, he might not spend energy if he were unlikely to be able to replenish a deficit. This possibility was not allowed for in the model, which a) omitted the energetic costs of mating and b) assumed that the energy gathered per unit time (b_1) would be constant throughout the total time interval p . Our results may stem from the interplay between these two factors. So possibly the simplifying assumptions were too simple. It is the purpose of the test, however, to reveal this and provide a basis for more complicated explanations which merit consideration once simpler ones have failed.

Whether this is the problem and a more advanced model is appropriate could be determined by comparing the movements of males in high and low food availability habitats of comparable density, or in an area where food supplementation had been continuing for some time. Were we to find that males with a reliably greater food supply did move to greater distances we would have reason to include variability in b_1 and probably also the energetic costs of mating in the model.

Body weight data suggest that the energetic costs of mating may not have been an important influence in the comparative questions addressed by the model. Control males gained considerably more weight than control females during the three week experimental period. Since we have concluded that the females spent more time feeding than the males, the males could only have gained more weight by spending less energy. It thus appears that the energetic expenses of copulation may be considered small in comparison to the energy invested in the offspring by females.

Alternatively, it could be that the males have no substantial fitness to gain from moving further. As the model shows, this could be true for two reasons. Either their fitness is limited by the number of females such that all available females are serviced within a short while and no more fitness may be gained from further searching, even when this becomes possible (Fig. 3a), or they may already be spending nearly 100% of their time mating and already moving as far as total time permits (Fig. 4b). The obvious way to distinguish between the two possibilities is to

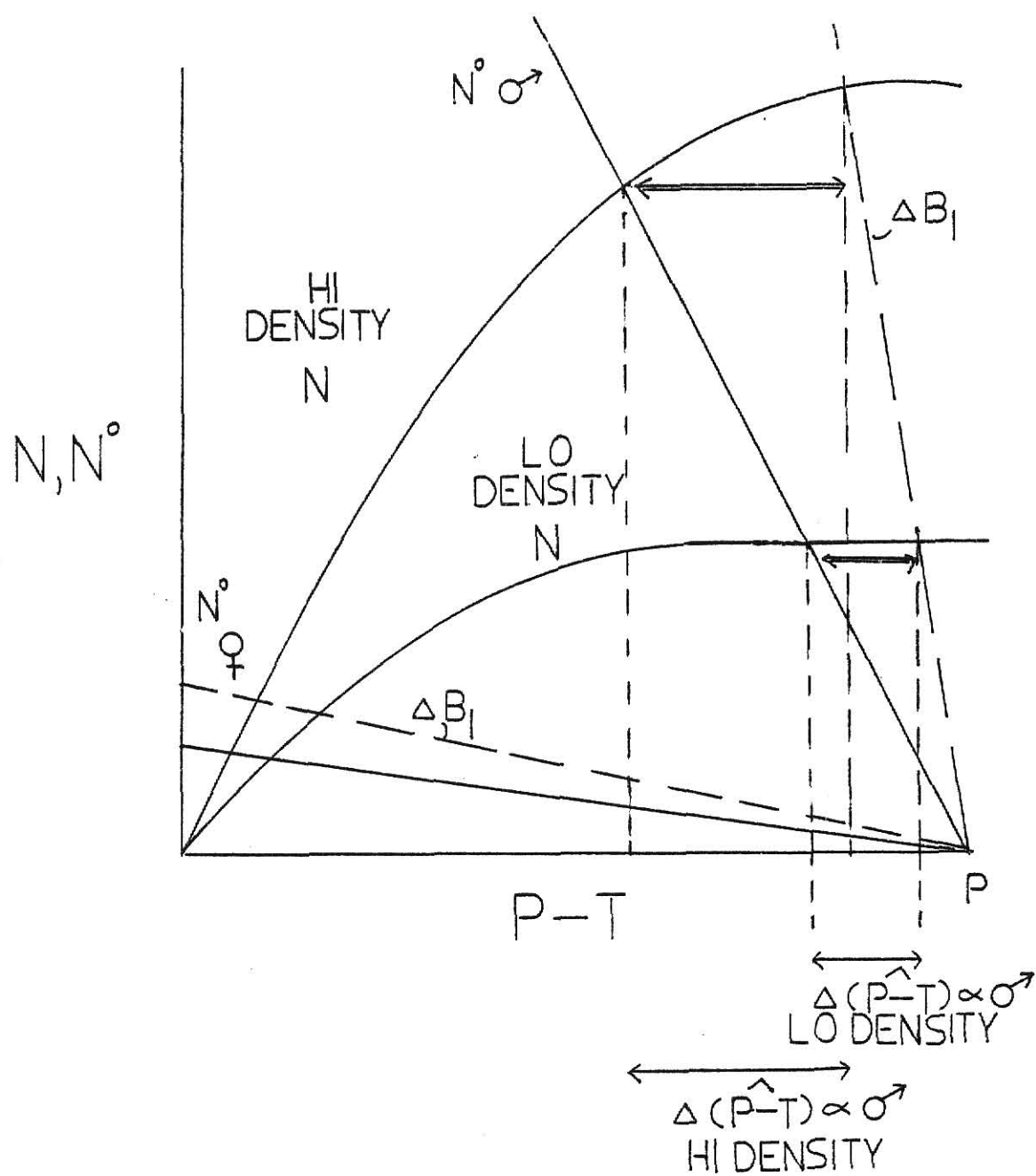


Fig. 7. Predicted increases in optimum mating time ($\hat{p.t}$) for alpha males under conditions of high and low rat density.

compare high to low rat density data. At lower densities, the number of offspring permitted by the mating time rises less steeply because mates require more searching to find; it then levels off earlier because fewer are actually available (see Fig. 7). The predicted increase in optimal mating time for males due to food supplementation is greater at higher densities because the high density N curve intersects the N^0 line at a greater distance from the latter's origin. A change in the slope of N^0 therefore causes a greater increase in (p-t) at high densities than at low densities. Fall pre-feed densities, estimated by the enumeration method (Krebs, 1966), averaged 36.25 animals per ha in the experiment, while spring pre-feed densities averaged 4.0 animals per ha. Thus we may look to see whether males showed any more inclination to increase their movements in the fall than in the spring. They did, in fact, increasing from 11.889 m/hr ($N=12$) to 15.856 m/hr ($N=14$) in the fall, as opposed to 19.655 ($N=14$) to 19.832 m/hr ($N=10$) in the spring. The increase shown by males in the fall relative to themselves prior to feeding, however, is not significant by the LSD procedure at the .05 level. A better test of this matter, involving manipulation of female density, would however be necessary for sound conclusions. It thus appears that at least spring fed males perhaps did not increase their movements because the likelihood of finding another female that had not already been serviced by some other male was exceedingly small.

The evidence would thus appear to lie heavily in

Bateman's favor. There is no evidence for a time-mediated food limitation on male fitness. Male reproductive success appears to be limited by mate availability alone. Although fitness is related to the way time is spent, the time males spend foraging is of no substantial cost to the fitness that could be gained from the actual mate availability. This is either because very little time is spent foraging to begin with, or because no fitness may be gained from spending any further time mating. If the latter case obtains, its implications are interesting. It implies that there may be extra time during an animal's lifetime during which it cannot gain in fitness. This would simply be an instance of resources limiting achievable fitness to a level below that permitted by the total time.

In conclusion, it appears that animals do divide their time according to the fitness accruing from a given activity. However, time considerations do not appear to alter the expected limitations on fitness. Males in nature appear to be effectively limited by mate availability alone, and females probably by food availability alone, as Bateman originally predicted.

Literature Cited

- Bateman, A.J. 1948. Intrasexual selection in Drosophila.
Heredity 2:349-368.
- Fisher, R.A. 1930. The genetical theory of natural selection.
Clarendon Press, Oxford.
- Harper, J.L., P.H. Lovell, and K.G. Moore. 1970. The shapes and
sizes of seeds. Ann. Rev. Ecol. Syst. 1:327-356.
- Heezen, K.L. and J.R. Tester. 1967. Evaluation of radio-tracking
by triangulation with special reference to deer movements.
J. Wildl. Mgmt. 31:124-141.
- Krebs, C.J. 1966. Demographic changes in fluctuating populations
of Microtus californicus. Ecol. Monogr. 36:239-273.
- Maynard Smith, J. 1978. The evolution of sex. Cambridge University
Press, Cambridge.
- Schoener, T.W. 1971. Theory of feeding strategies. Ann. Rev.
Ecol. Syst. 2:369-404.
- Smith, C.C. and S.D. Fretwell. 1974. The optimal balance between
size and number of offspring. Am. Nat. 108:499-506.
- Summerlin, C.T. and J.L. Wolfe. 1973. Social influences on trap
response of the cotton rat, Sigmodon hispidus.
Ecology 54:1156-1159
- Trivers, R.L. 1972. Parental investment and sexual selection. Pages
136-179 in B. Campbell, ed. Sexual selection and the descent
of man 1871-1971. Aldine, Chicago.

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APPENDIX

The expression for determining the rate at which an animal moves as a function of food and mate availability is as follows:

$$r = s_1 t + s_2 (p - t)$$

where s_1 increases linearly with b_1 (energy gathered per unit time) and s_2 increases linearly with b_2 (successful copulations achieved per unit time). The model predicts that t will decrease with increased b_1 , while $p - t$ will decrease with increased b_2 . Hence dr/db_1 , the rate at which the movement changes with changes in b_1 , such as food supplementation, will include the following terms:

$$dr/db_1 = t(ds_1/db_1) + s_1(dt/db_1) + s_2(d(p-t)/db_1)$$

When b_1 is increased, the only positive term will be $d(p-t)/db_1$. Hence whether dr/db_1 is positive or negative will depend on the ratio of the positive term $s_2(d(p-t)/db_1)$ to the negative terms $(t(ds_1/db_1) + s_1(dt/db_1))$. ds_1/db_1 is independent of sex. dt/db_1 and $d(p-t)/db_1$ will be of opposite sign and equal, but greater for males than for females.

$$s_1 < s_2$$

$$\text{Hence } |s_1(dt/db_1)| < |s_2(d(p-t)/db_1)|$$

So in general dr/db_1 will tend to be positive given food supplementation unless t is large. However, the greater the value of dt/db_1 and $d(p-t)/db_1$, the greater absolute difference is indicated here. Hence males are more likely to increase their movement in response to food than females. The predicted value of t is also

smaller for males, so therefore both negative terms will be less.
Hence males should probably increase their movement with food
supplementation while females should decrease if their t is
sufficiently large.

A TEST OF BATEMAN'S HYPOTHESIS IN TERMS OF
MALE AND FEMALE TIME DIVISION STRATEGIES

by

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ABSTRACT.

Male and female cotton rats were provided with increased food density to determine whether a) the two sexes divide their time differently between foraging and mating activity and b) whether males would use the increased time thus made available to further pursue mates. Results are consistent with the existence of time division strategies as predicted by a simple model developed in order to test Bateman's hypothesis. However, it appears that the time spent in foraging activity may be of minimal cost to male fitness. Thus it need not follow that because of an ultimate time limitation on fitness, the fitness of either sex will be limited by either or both resources. Bateman's prediction is confirmed in its original form, indicating that males cannot benefit in fitness through the reduction in the time required to do a small but necessary amount of foraging.