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Mating behaviour of the tiger blue butterfly (*Tarucus theophrastus*): competitive mate-searching when not all females are captured

Steven P. Courtney* and G.A. Parker
Department of Zoology, University of Liverpool, P.O. Box 147, Liverpool, England

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Summary. Females of the tiger blue butterfly (*Tarucus theophrastus*) fly upwind in search of the larval hostplant. Males perch or patrol the downwind edges, searching for incoming females or those already on the bush. A model of competitive mate-searching is developed for the case where not all receptive females are contacted by searching males: the model differs from the earlier ones of Parker (1970, 1974), particularly when few males are involved. Observed distributions of males upon bushes of different sizes agree better with the predictions of the game theory model than with a random distribution of males. The described model may be widely applicable to populations where females remate, but frequently evade detection by searching males.

Introduction

Much interest focuses on the ways in which the sexes of mobile animals distribute themselves. Parker (1978) has reviewed the mate-location behaviours of insects; in many species "mate-encounter-sites", such as hilltops or the oviposition plant, are used as conventional aggregation areas for individuals of either sex who wish to mate. Studies of the dungfly *Scatophaga stercoraria* indicated that intensive inter-male competition may occur at such sites, and that the distribution of males around them conforms well to that expected from game theory (Parker 1974, 1978).

We report here a study of the tiger blue butterfly, *Tarucus theophrastus,* a widespread insect of arid zones of North Africa, where its hostplant *Zizyphus vulgaris* (crown of thorns bush) may grow in monoculture on open plains. Males wait on or near the bushes for arriving females. The questions addressed by this study were then: Do male *T. theophrastus* distribute themselves so as to maximize contact with receptive females (Parker 1978)? Are the observed distributions of males, on bushes of different size, consistent with the equilibrium distribution from competitive mate-searching theory, i.e. are males distributed in such a way that all individuals achieve equal rates of encounter with receptive females? The ecology and behaviour of the butterfly are undescribed; some information on these aspects is included.

Methods

Investigations were carried out by SPC during April 1983 at Oulad Berehil, Region de Taroudannt, south Morocco. Densities of the butterfly were high with, at any one time, most thorn bushes having one or more insects. The butterfly is strongly dimorphic, males having bright blue upper wing surfaces, whilst females are brown; lower surfaces are white with blackish-brown spots in both sexes. Casual observation in previous years had indicated that *T. theophrastus* shows a form of host and mate location reminiscent of the dungfly *Scatophaga stercoraria.* Females fly upwind towards thorn bushes, to search amongst the bush for suitable oviposition sites, and to deposit small batches (1–4) of eggs. Males "patrol" or "perch" (sensu Scott 1974) near or on the downwind side of bushes so as to intercept incoming females: frequent male/male interactions also occurred. It was also noted that different sized host plants had differing numbers of attendant males.

Both sexes basked or rested in two ways: with wings held open and horizontal to the body (called "top-basking") or with wings closed ("side-basking"). In side-basking the wings were not oriented to the sun, unlike similar basking in other butterflies. Closed-wing basking is not distinguishable from the stationary strategy of mate location in males, and was designated as "Side-Bask/Perch." Figure 1 shows that both male and female *T. theophrastus* increase the proportion of time spent "top-basking" under less sunny conditions, consistent with the view that an open-wing position is adopted to raise body temperature, whilst a closed-wind position is primarily a resting

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* Current address: Department of Biology, University of Oregon, Eugene, Oregon 97403, USA

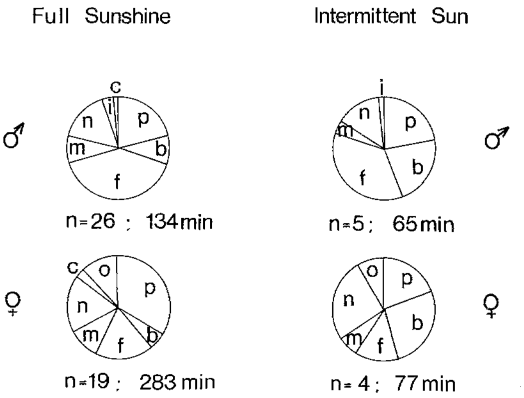

Fig. 1. The percentage of time spent in different activities by males and females, under conditions of constant or intermittent sunshine. The number of individuals, and total observation time are given below each figure. "Oviposition" includes occasions when no egg was deposited (see text). Courtship includes all such behaviors, successful or not. Observations on one female, which commenced copulation whilst under scrutiny, are included until the onset of copulation. p = side bask/perch; b = top bask; f = flight in bush; m = flight between bushes; n = feeding; c = courtship; i = ♂/♂ interaction; o = oviposition

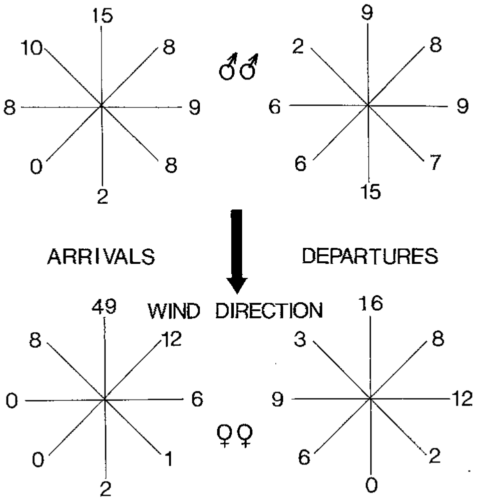

Fig. 2. Directions of flight at arrival and departure from the bush by males and females. n (arrival) males = 60, females = 78; n (departure) males = 62, females = 56. All directions relative to wind direction at time of observation (assessed to nearest compass point). Observed heterogeneities are high: χ^2 (compared to random allocation of directions) are: male arrival = 20.56 $P<0.01$; male departure = 12.35 NS; female arrival = 195.10 $P<0.001$; female departure = 28.85 $P<0.001$; 7 *df* in all cases

posture. Closing the wings whilst resting prevents individuals of either sex from being detected and harassed by patrolling males. Because of differences in butterfly activity between sunny and shaded conditions, all subsequent observations were carried out only in full sunshine.

Observations were made on both sexes by following individuals and making real-time records of behaviour using a portable tape-recorder. Details noted included the type of behaviour seen, the outcome of intra- and inter-sexual contacts with other individuals, the estimated dimensions of hosts encountered, the direction of flight relative to wind direction, and (for females) the duration of visits to hosts. Individual females were readily followed for long periods, but males involved in encounters with other males "spiralled" vigorously, making individual identity uncertain. The procedure followed was to continue recording the behaviour of the nearest individual (after a spiral) as if it were the original male. This procedure is necessary to avoid any bias against recording such male/male interactions. In addition to these recordings, surveys of *Z. vulgaris* bushes were made on 3 dates, and the number and location of *T. theophrastus* individuals of either sex recorded, together with the dimensions of the thorn bush. Bushes were sampled in the same area on all three dates, by walking the study site on a north-south transect and recording every bush encountered. Any bushes which could not be unequivocally scored for dimension at the downwind edge, or which were separated from a neighbour by less than 1 m were excluded.

Results

Behavioural components

1. Movement between bushes. Females spend more time than males in moving between bushes, relative to the time spent in the vicinity of bushes (Fig. 1). this is consistent with their search for suitable oviposition sites, which contrasts with the mate searching behaviour of males which may be carried out in a small area (c.f. Parker 1978).

2. Flight direction and area of activity. In Fig. 2 are shown the directions of flight of individuals when entering and leaving bushes, relative to the wind direction. Upwind flight is typical of entry into bushes, most strikingly by females. Directions of departure are more evenly spread, though there is a tendency for females to continue flying upwind through and away from the bush. During the surveys of bushes 284 males and 55 females were encountered in the following areas of bushes: within 1 m of the upwind edge (2 males, no females) in the bush interior (41, 16), within 1 m of the downwind edge (209, 39) or perched on soil or grass outside the downwind edge (32, 0). Ground perching was most noticeable in strong wind conditions. Males are concentrated around downwind edges, where females arrive. Females, too, tend to be found near the downwind edge; this may represent nothing more than that individuals remain near their point of entry for the period necessary for oviposition.

3. Bush size preferences. Females found during surveys of bushes (Fig. 3b) tend to be associated with larger *Z. vulgaris*. Similarly, females under observation (Fig. 3c) found large hosts disproportiona-

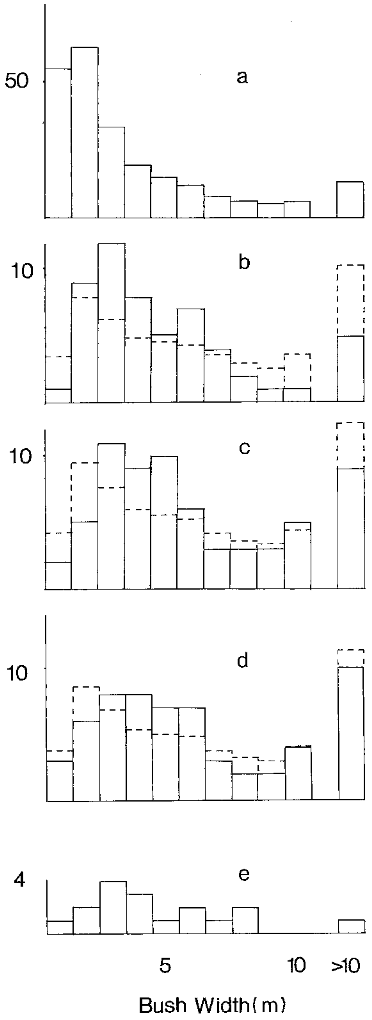

Fig. 3. **a** The distribution of bushes by widths (assessed to nearest *m*) along downwind edge. Data for the three dates of survey summed ($n=239$). **b** The distribution of females discovered on bushes during the three surveys ($n=55$). **c** The distribution of bushes discovered by females during taperecorded observations ($n=66$). **d** The distribution of bushes discovered by males during taperecorded observations ($n=60$). **e** The distribution of bushes on which copulating pairs were seen. For **b–d**, the expected distributions, given random allocation of individuals (by target theory and bush abundance) are indicated by dotted lines

tely often. In both cases, female distribution agrees well with that predicted from simple target theory, i.e. a bush of twice the width received twice the number of incoming females. Bush height did not seem to influence females, who are typically flying at 0.5 to 1 m above the ground and never flew over a bush without landing. Note that in both Figs. 3b and 3c there is an under-representation of the smallest bushes of less than 1 m on the downwind side. Males, when followed, equally found hosts of different sizes much as predicted from the random model (Fig. 3d). The seventeen copulations observed were distributed amongst bushes much as were individuals of the sexes (Fig. 3e).

4. *Mate searching.* Male *T. theophrastus* spend a large proportion of their time (41.0%) flying around the surface of *Z. vulgaris* bushes, periodically landing, and investigating any conspecific found, whether basking or in flight. If another male is found, "spiralling" may take place, the two males circling very rapidly one another. Occasionally a male locates another which is top-basking, and which may then respond by fluttering his wings several times; the first male then flies away. Male/male interactions also frequently occur when a patrolling individual is noticed by another which is "side-basking/perching."

5. *Courtship and copulation.* During their time spent at the bushes, females are often encountered by searching males. If the female does not evade the male, she may land and adopt a "mate-refusal" posture, with depressed, vibrating wings; the male does not then persist in courtship for more than a few seconds. However if the female lands but does not adopt this posture, the male will either continue to flutter around her, or will land below or behind her, bend his abdomen, and attempt to copulate. This may prompt the female to flight. The male then pursues; frequently the process is repeated several times over many metres until the male either loses contact with the female, or copulates successfully. The time from landing to attempted copulation may be very brief (<3 s). On one occasion (of 6 complete copulation sequences observed) a male landed and moved up behind a female, and grasped her with his claspers before she could fly away. The female then attempted to detach herself from the male for 15 min (until killed by SPC). This female, and another found behaving similarly whilst in copulation (1 of 11), proved to have large sperm reserves remaining from a previous copulation; this perhaps indicates that the second males had achieved an enforced mating. Copulation lasted 44 and 53 min in two cases observed from start to finish. Most females are *not* contacted by males, either when they enter the bush, or during their stay in it.

Analysis of competitive mate-searching

Most of 72 contacts between males and females were initiated as the female entered the bush ($n=37$; 51.4%) and was contacted by a patrolling or perching male, or whilst she remained near the

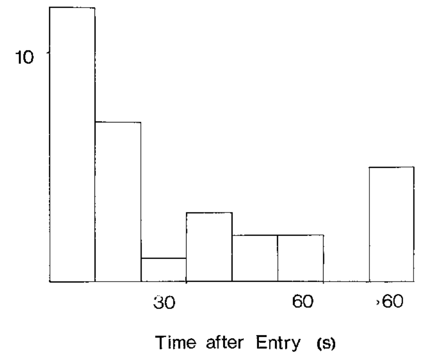

Fig. 4. The times after entry into a bush at which a female is contacted by a male $n=32$

downwind edge ($n=28$; 30.6%) (usually being contacted by a patroller). Most contacts were with flying females ($n=64$), (the remainder being basking individuals). Thus most male – female contacts occur soon after female arrival (Fig. 4). Very few contacts result in copulation ($n=5$; 6.9%) most contacts being resolved by females refusing ($n=16$) or evading males ($n=37$) by flying into the bush. Other outcomes were: interference from another male ($n=6$); emigration of the female ($n=5$) or of both male and female ($n=3$).

In order to investigate the strategies employed by searching males, the numbers of individuals on bushes of different sizes were counted (Fig. 5). It may be seen that on three different days, under differing wind directions, intermediate-sized bushes had most males. This is in opposition to the expectations of simple target theory: both the smallest *and* largest bushes have fewer males than expected.

Since males encounter bushes much as expected under such a random model, the observed distributions of males over bushes must be due to differential residence times on different sized bushes. This effect could not be demonstrated directly, due to the high frequency of male/male encounters (which prevented accurate individual identification). These may influence male residence times: interactions can be lengthy (Fig. 6) and frequently (13.7% of occasions) lead to one or both individuals leaving the bush (Table 1). Interactions of over 4 s (34.7% of all interactions) may exceed the time needed to ascertain sexual identity, and perhaps indicate a form of territoriality as in the butterflies *Aglais urticae* (Baker 1972) and *Pararge aegeria* (Davies 1978; Wickman and Wiklund 1983).

Model of male mating behaviour

The models that follow seek to find the "equilibrium" distribution of males upon bushes of different

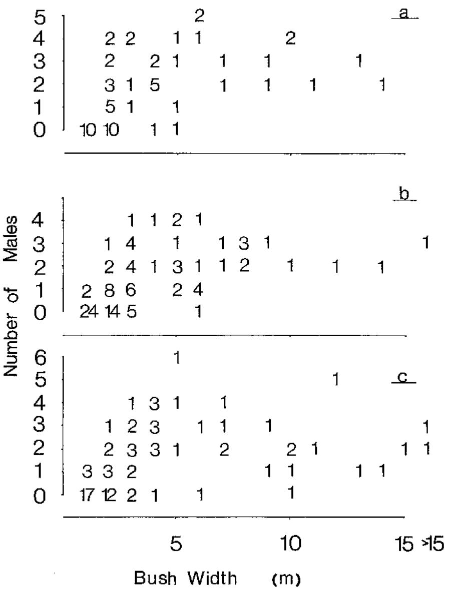

Fig. 5a–c. The distributions of males over bushes of different widths, on three dates. **a** 15 April 1983 ($n=60$); **b** 19 April 1983 ($n=100$); **c** 20 April 1983 ($n=80$)

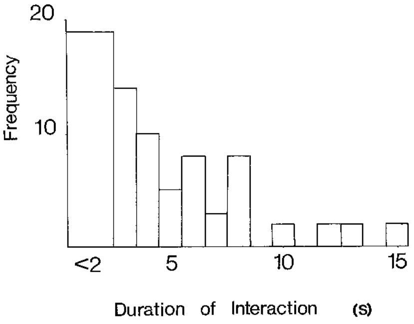

Fig. 6. The frequency of male-male interactions of different durations. Interactions of less than 2 s duration are summed, and the histogram averaged in height (n for $d<2$ s$=38$)

Table 1. The outcome of male/male interactions (all observations summed). A distinction is made between situations where an apparently perching male resumes position on the bush periphery after "spiralling", and cases where a male flew in amongst the thorns to evade pursuit. Interactions with no evasive behaviour (a, b, c) are shorter than those where one male flies into the bush (d) ($t=6.33$ $P<0.001$ at 80 *df*), and also are shorter than interactions where one or both males leave the bush (e, f) ($t=9.99$ $P<0.001$ at 79 *df*)

		No. of observations	Mean duration
(a)	Basking male "flutters"	4	1.9
(b)	Both males resume patrolling	52	2.6
(c)	One male patrols; one perches	12	3.8
(d)	One male settles in bush	14	5.6
(e)	One male leaves bush	10	9.8
(f)	Both males leave bush	3	11.3

sizes, so that no male can profit by a change in strategy. The models are constructed in one dimension only, since bush height does not appear to influence any aspect of courtship or residence. The models likewise assume a random spacing of males within bushes – this seems reasonable on the basis of observation.

Model 1: Coexistence of the two mating strategies

Males can capture females either from a resting position ("perching") or whilst "patrolling" in flight along the downwind side of the bush. We make the following assumptions to facilitate analysis:

1. Incoming females (females arriving at the bush) are caught by both patrollers and perchers; neither mating strategy has an advantage over the other.
2. Within-bush females (females that have not been captured as they arrive at the bush) are caught only by patrollers.
3. Both types of female are equally valuable to a male.
4. Females are unreceptive to further courtship after mating.

All assumptions seem justified as approximations from the field observations.

Let:

n_a = the number of patrollers at a bush
n_e = the number of perchers
n = the total males (n_a+n_e)
$P(n)$ = the probability that a female is captured as she arrives (a function of n)
$Q(n_a)$ = the probability that a female that has moved within the bush is captured before she leaves the bush (a function of n_a). Hence the probability that a given female is caught within the bush is $(1-P(n))\,Q(n_a)$
$c(n)$ = the cost (lost matings) felt by a patroller compared to a percher.

Now, each patroller's payoff will be:

$$\frac{P(n)}{n}+\frac{Q(n_a)\,(1-P(n))}{n_a}-c(n). \tag{1}$$

Each percher's payoff is simply

$$\frac{P(n)}{n} \tag{2}$$

and for patrolling and perching to coexist as a mixed evolutionarily stable strategy we need (1) = (2), i.e.

$$\frac{Q(n_a)\,(1-P(n))}{n_a}=c(n) \tag{3}$$

As yet, we have no adequate way of estimating $c(n)$, but anticipate that c is only dependent on n by virtue of interaction costs, which would increase with n. We envisage such a dependence to be extremely weak, so that c could be regarded as constant. Value $1-P(n)$ is also constant with respect to n_a. Hence stability in (3) depends on $Q(n_a)/n_a$; $Q(n_a)$ must therefore be non-linear to generate a stable solution. It is shown below (Eq. 6) that it is plausible that $Q(n_a)$ should increase with n_a, but with a slope that decreases as n_a increases; if so, there will be a stable mixed strategy.

Model 2: Distribution of males on different sizes of bush

Males of the dungfly, *Scatophaga stercoraria* L. distribute themselves so as to maximize individual rates of contact with females, taking into account the competitive effects of other males (Parker 1970, 1974, 1978). The equilibrium distribution is said to be "ideal free" (Fretwell and Lucas 1970; Fretwell 1972) if all males achieve equal fertilization rates (Parker 1970). Does the distribution of *T. theophrastus* over different-sized thorn bushes similarly reflect competitive mate searching? Suppose that the number of females attracted to a bush i is proportional to its width, w_i. Then the number of matings obtained by *each* of n_i males on bush i is proportional to

$$M_i=w_i\left\{\underbrace{\left[\frac{P_i(n_i)}{n_i}+\frac{Q_i(n_{ai})\left[1-P_i(n_i)\right]}{n_{ai}}\right]\frac{n_{ai}}{n_i}}_{\text{payoff to each male while it is patrolling}}+\underbrace{\left[\frac{P_i(n_i)}{n_i}\right]\frac{n_{ei}}{n_i}}_{\text{payoff to each male while perching}}\right\}-\underbrace{c_i}_{\text{cost of patrolling}} \tag{4}$$

and from ideal theory we require

$M_i=M_j=M_k\cdots=M_n=$ constant K,

i.e. payoffs must be equal whatever the bush widths $w_i, w_j, w_k\cdots w_n$.

$P(n)$ is calculated as follows. Consider a bush w units wide, where each unit represents the width limit for sensory perception by a male of a female as she arrives at the bush (approximately 1 m).

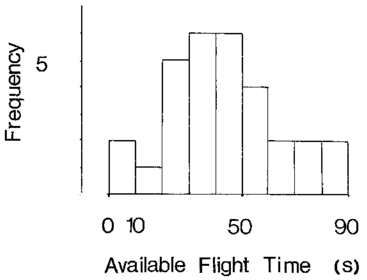

Fig. 7. The frequency of "available-flight-times" of females, calculated as the time spent in flight within 1 m of the downwind edge

The chance that a given male is within the "correct" unit when a female arrives is therefore $1/w$, which is the chance that a single male searching on bush (w units wide) captures a female as she arrives. Thus if $n=1$, $P=1/w$. If there are two searching males, P will generally be less than $2/w$ because both males could be within the same unit of the bush at the time the female arrives. If there are n males searching at random, it is easy to show that

$$P(n)=1-\left(1-\frac{1}{w}\right)^{n}. \tag{5}$$

Calculation of $Q(n_a)$ is more complex. However, if $q(w)$ is the chance that a single male patrolling a bush of width w will capture a within-bush female before she leaves, then by analogy with (5)

$$Q(n_a)=1-(1-q(w))^{n_a} \tag{6}$$

assuming again that patrolling is random. The value of q is calculated as follows. Within-bush females are captured only when flying, and the mean available flight time between entering and leaving a bush is approximately 46 s (calculated from Fig. 7). Each separate burst of flight activity has a mean duration of approximately 7 s, so that an average of 6.6 bursts of activity are undergone before the female leaves the bush. The time t taken for a male to patrol the full width w of a bush is given by $t=2.172\ \exp(0.469w)$, from the best exponential curve fit (least squares) to the data in Fig. 8. Thus the proportion of the entire bush width "covered" by a patrolling male during one bout of activity is $7/t$, which will equal the probability that the female will be captured on her first bout of flight. The probability that she isn't captured during this bout is $(1-7/t)$, and the probability that she isn't captured after 6.6 bouts is $(1-7/t)^{6.6}$. Thus the probability q that she will be captured within the bush is

$$q=1-(1-7/t)^{6.6}.$$

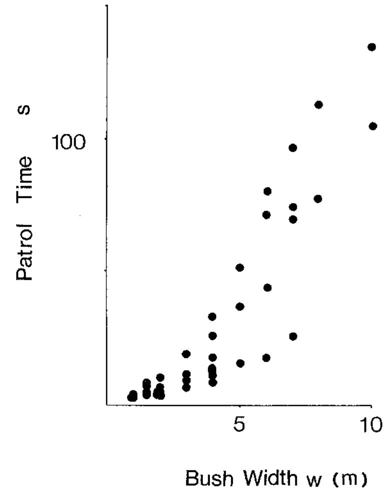

Fig. 8. The times taken for males to patrol the full width of a *Z. vulgaris* bush of width w. The best exponential fit to the data is $t=2.172\ \exp(-0.469w)$. $r^2=0.848$

Table 2. The proportion of time spent by males in perching and patrolling on bushes of different widths

Bush width class	No. of observed males	Proportion of time	
		Patrolling	Perching
1–2 m	9	0.436	0.564
3–5 m	23	0.451	0.549
6+m	28	0.521	0.479

The data for calculation of $q(w)$ are given in Table 1. If $t<7$ s, $q=1$.

Table 2 shows that males spent approximately equal times patrolling and perching, whatever the bush width. The cost c of patrolling relative to perching is measured in terms of the "time out" of reproductive activity (and hence missed mating opportunities) due to using extra energy while patrolling. If the proportion of time spent in each strategy is independent of bush width, we can also regard c as independent of bush width. From Eq. (4) we can therefore set:

$$M_i=\frac{W_i}{n_i}\left[P_i(n_i)+Q_i(n_{a\,i})[1-P(n_i)]\right]$$
$$=M_j=M_k\cdots=K. \tag{7}$$

Substituting (5) and (6) into (7) gives

$$\frac{W_i}{n_i}\left[1-\left(1-\frac{1}{w}\right)^{n_i}(1-q(w_i))^{n_i/2}\right]$$
$$=K \text{ for all } w_i,\ w_j,\ n_i,\ n_j. \tag{8}$$

Taking values for $q(w_i)$ from Table 3, and finding the distribution of n_i for bush size w_i (from Fig. 3a) we can now estimate the value of K for

Table 3. Calculation of $q(w_i)$. For explanation of terms see text. n is too low to analyse date beyond $w=10$. $t=2.17e^{0.47w}$. Probability of capture on first bout$=7/t$. $q=1-(1-7/t)^{6.6}$

w	t	$7/t$	q
1	3.47	1.0	1.0
2	5.56	1.0	1.0
3	8.86	0.79	1.0
4	14.16	0.49	0.99
5	22.63	0.31	0.91
6	36.17	0.19	0.76
7	57.80	0.12	0.57
8	92.37	0.08	0.41
9	147.61	0.05	0.27
10	235.90	0.03	0.18

Table 4. Calculation of $\bar{K}$; for explanation of terms see text

Bush width w	Observed mean no. of males n	Weighted mean payoff $\bar{K}$
1	1.16	0.86
2	1.59	1.26
3	2.19	1.37
4	2.72	1.47
5	2.79	1.67
6	2.70	1.79
7	2.63	2.03
8	2.60	1.96
9	2.40	1.76
10	2.20	1.59

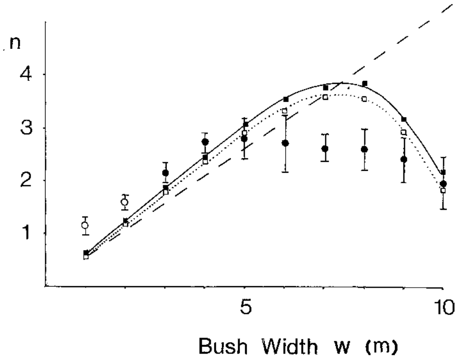

Fig. 9. The predicted values of n, the number of males on a bush under various conditions, and the observed values in the field. Unbroken line: predicted n when weighted mean K used. Dotted line: predicted n when direct mean used. Dashed line: predicted n from random, "target-theory." Circles: observed values of n ($\pm$SE). Open circles for $w=1,2$ indicate that these values should be treated cautiously. Because of the method of analysis, zero numbers of males are excluded; n cannot therefore be less than 1. This is of importance only on the smallest bushes which rarely have males. Values of correlation coefficient r between predicted and observed results ($df=8$ in all cases): weighted mean K $r=0.888$ $P<0.001$; direct mean K $r=0.886$ $P<0.001$; random distributions $r=0.569$ NS

each bush observed in the study (Table 4). Bushes on which no males were observed are, of course, omitted. We then calculate the mean number, $\bar{n}$, of males observed on each bush width, again omitting all bushes on which there were no males. We next find the weighted mean payoff value, $\bar{K}$, for each bush width (Table 4). If ideal free theory holds, the K values should be equal for all bush widths. (Too few samples were available to carry the analysis above $w=10$ m). K varies only between 1.4 and 2 if we exclude $w=1$ and 2. The reason for excluding $w=1$ and 2 is that, unlike other bush widths, males appear actively to avoid them. (50/56 bushes of $w=1$ had no males; 36/63 bushes $w=2$ had no males). Finally, we calculate an expected mean payoff (weighted mean K for all $w=3$ to 10); it is 1.615. This value for K is inserted into Eq. (8), which can then be iterated to give a predicted solution for n_i.

The predicted number of males which should be found on different-sized bushes is compared with the mean observed numbers in Fig. 9. Also included in Fig. 9 is the predicted curve calculated from the direct mean K for all bush widths $w=3$ to $w=10$ (mean $K=1.706$). The fit between the predicted n and the observed n (Fig. 9) is certainly not a perfect one, though both curves follow the same pattern; i.e. n initially increases with w, then peaks, then decreases with w. Peak numbers occur for $w=6$–8, and the mismatch between observations and predictions stems mainly from the fact that the observed mean n values for these bush sizes were lower than expected. If males were to spend a fixed time on bushes, independent of bush size, we would expect $n(w)$ to be linear increasing. The residence times of males may, therefore, be adapted to the selective pressures of competitive mate searching. The fit between the observed distribution of males and that expected purely by random is very poor.

Competitive mate-searching theory predicts that males should avoid spending time on the very smallest bushes, which are always unprofitable. However this is a "perfect-information" model – in reality, males are unlikely to be able accurately to assess bush size immediately on arrival. This will lead to a few encounters with males on such small bushes, as we observed. These limitations of male sensory capability may also explain the remaining variance between our results and those predicted from game theory. If males cannot recognize bush size, then the only available cue as to bush suitability may be the frequency of conspecific encounters (Dethier and MacArthur 1964).

We might then predict males remaining longer on medium-sized bushes (high rate of encounter) than on large-bushes (low rate) – exactly the pattern seen here.

Discussion

Males of many insect species appear to distribute themselves so as to maximize their individual rates of encounter with receptive females. Individual males of the dungfly *Scatophaga stercoraria* adopt a number of behaviours which cause an approximation between their distribution and that expected from "ideal-free" theory (Parker 1978). However dungflies differ from tiger blues in two respects: all females mate when contacted or captured by a males; virtually all females are captured by males. Female unreceptivity need not alter the ideal free distribution of males. The rate of encounter with all females can be profitably used as an index of encounter rate with mates, provided that recapture or virgin females do not qualitatively differ in behaviour (e.g. Wiklund 1982).

However in many insect populations using mate-encounter sites, as in *T. theophrastus*, receptive females may frequently remain uncontacted by males, at least temporarily. This may often be the case when encounter/oviposition sites are relatively large, and where males search randomly within them for mates, as opposed to perching on a few restricted sites. In such populations, models of the form developed here will be appropriate for calculating ideal free distributions of searching males; the standard models which assume that a receptive female will be mated at her first visit to a mate-encounter site (Parker 1978) will overestimate benefits if many females are not contacted.

If all female *T. theophrastus* were to be caught on or after arrival at a bush, the predicted distribution of males over bushes of different sizes, from ideal free theory, would be linear, and identical to the prediction from "target theory." At low bush widths, virtually all females are caught, and the predicted number of males from ideal free theory increases linearly. However at intermediate bush widths, a significant number of females will escape capture, because many of the males will overlap spatially in their sensory ranges. This effect is greatest at high bush widths, and must be compensated for by a reduction in the number of competing males so that payoffs can be equilibrated over all bush widths.

The fit between our results and those expected from ideal-free theory is reasonable, and much better than that of a random "target-theory" model. However the fit is far from perfect; various ad hoc rationalisations can be proposed to explain this, but it is perhaps best to emphasize that the sensory capabilities of these butterflies are not great. It is probably impossible for a male accurately to assess either the number of other, competing males, or the size of the bush on which he patrols or perches. In both cases, the larger the bush, the less easy for an animal to assess – it is extremely unlikely that a male can detect the number of other males on a 20 m bush. The reactions of males to intra-sexual interactions indicates that they do react to male density – often *both* males leave the bush on which contact is made (Table 1). The fit between our predicted and actual results is probably as good as might be expected in an organism which lacks a good mechanism for responding to pertinent environmental cues.

The data of Fig. 6 show that "interaction times" between males fit well to a negative exponential distribution. A prediction from "war of attrition" models of animal contests, is that durations of fights should follow such a pattern (Maynard Smith 1974; Parker and Thompson 1980). Whilst there is no evidence that tiger blue males are showing any vigorous form of territoriality or aggression, the duration of the longer interactions does seem too long simply to ascertain sexual identity, the usual cause of butterfly male/male interactions. Since the emigration of one male from a bush significantly raises the pay-off for both males (assuming the emigrant finds a vacant spot relatively quickly) but also involves a cost of movement, it may be of advantage to males to engage in intensive spiralling. Note that in Table 1 there is a trend that the longer the interaction, the more likely one or both males will emigrate; Baker (1972) obtained similar results with *Aglais urticae*.

In many territorial systems, including the butterfly *Pararge aegeria,* there is a relationship between male "quality" or fighting ability, and occupation of territory (Wickman and Wiklund 1983). Males of differing status then occupy different positions and may experience considerable differences in pay-off. In *T. theophrastus*, a number of different options are available for searching males: patrolling or perching; perching on several different substrates; remaining on bushes for different residency times. No correlation could be found however between any of these behaviours and either male size or age (as indexed by wing wear). Our results suggest that all males in the population use a mixture of the various behavioural options open to them.

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