An ESS Treatment of the Pattern of Female Arrival at the Mating Site in the Yellow Dung Fly *Scathophaga stercoraria* (L.)

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In most previous work on the yellow dung fly *Scathophaga stercoraria* (L.), as on other species, adaptive explanations have been sought for male behaviour whereas female behaviour has not been examined in similar detail. Here, the arrival of females at the mating site, fresh cattle droppings, is investigated. While almost all males are present shortly after pat deposition females arrive at a low, decreasing rate over an interval of about 5 hours. We propose that the distribution of female arrival times represents a mixed Evolutionarily Stable Strategy (ESS), formed by different trade-offs between costs and benefits of early and late arrival. Early arrival could be favoured by advantages due to better conditions for oviposition, faster egg development or reduced larval competition. Late arrival could be favoured by negative effects on females of male–male competition being weaker later after deposition. Computer simulations with distributions of arrival times deviating from the natural one were performed to "measure" the costs for females arriving at different times. These costs were compared with estimated benefits corresponding to the females' arrival times. This procedure revealed that females coming to the pat later in a population of females arriving shortly after deposition would be favoured. In a population arriving according to a uniform distribution, early females would have fitness advantages. Thus, evolution should lead to an intermediate distribution of arrival times, as in nature, i.e. female arrival behaviour is probably adaptive. The simulations also revealed that the intensity of sexual selection through male–male competition is highest with the natural pattern of female arrival. Therefore, natural selection generating this pattern amplifies the intensity of male–male interaction as a by-product.

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Introduction

Sexual conflict over mating has been studied in many animal groups (e.g. Bateman, 1948; Beach & LeBoeuf, 1967; Thornhill & Alcock, 1983; Clutton-Brock *et al.*, 1992; Rowe *et al.*, 1994; Thornhill & Gangestad, 1996). These studies have mostly focused on male behaviour, which has been seen as adaptive whereas females were considered passive or their action to be formed by constraints. However, female choice is now well-documented [see O'Donald (1983) and Andersson (1994) for reviews] but some aspects remain controversial as "male control is

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sometimes assumed even when male and female morphology indicate female influence is far more likely" (Eberhard, 1996; cf. Eberhard, 1990). Thus, subtle female adaptations may still be commonly undetected.

One of the classic studies on male behaviour is that on the yellow dung fly *Scathophaga stercoraria* [sometimes *Scatophaga*, but see Kloet & Hincks (1975)]. Parker investigated this species in detail, focusing on sexual selection by male–male competition [see Parker (1978) for a review of the early work]. Males are larger than females and so able to force females to copulate (Borgia, 1980). Sexual selection favours large body size in males as larger males have advantages in competition for mates (Borgia, 1980, 1982; Parker, 1970a; Parker & Thompson, 1980; Sigurjónsdóttir & Parker, 1981). Borgia (1980) says active female choice occurs, but the evidence is weak, being based on few observations.

The natural history of *S. stercoraria* is well known (Hammer, 1941; Parker, 1970a–d, 1971, 1978). Freshly-deposited cow pats are rapidly colonized by males, which wait for arriving females. Males have a higher potential reproductive rate (Clutton-Brock & Parker, 1992) than females in this species. Therefore, the operational sex ratio (OSR) is strongly male biased (4m:1f) during the time flies are present on a pat, about 5 hours. Newly-arriving females are grabbed by males and copulation begins immediately. Copulation lasts about 35 min and takes place either on the dung surface or in the surrounding grass. Emigration from the pat is mostly by pairs with a relatively small male, as on the dung surface a pair may be attacked by single males trying to take over the female. Struggles are risky for females because they may be damaged physically. If a take-over occurs, there is also a time cost since the female has to copulate with the new mate. After copulation, the female lays eggs into the dung, with the male still guarding her. After oviposition, the female leaves the pat but the male may stay to search for another mate.

The patterns of male and female arrival at dung pats are extremely different, males arrive very quickly after pat deposition but females arrive over a period of about 5 hours at a much lower, negative exponentially decreasing rate (Parker, 1970b; Fig. 1). If males and females are both equally attracted by the odour emitted from the pat it is difficult to see why this is so. It is possible that females are attracted from further away, i.e. outside the pasture, whereas males may wait on it. However, Gibbons (1987) showed that flies found in the surrounding vegetation are mostly immature.

Males are probably strongly selected to arrive early as female arrival rate is highest then; moreover, early arrival may increase a male's chance of mating with more than one female (Parker 1970b). For females, there may be two opposing selection pressures: possible benefits of early arrival include lower impact of competition among larvae and predation during development (Parker, 1970b). Larval competition strongly influences adult size (Amano, 1983; Sigurjónsdóttir, 1984), a feature important for both male and female fitness [the number of eggs in a clutch is correlated with female body size (Parker, 1970e; Blanckenhorn, 1997) and larger males have a higher probability of succeeding in struggles (Sigurjónsdóttir & Parker, 1981)]. Larvae hatching from eggs laid early may be favoured as they will be larger in the early stages of competition. Despite an overall development time of ca. 3 weeks, larvae accumulate most of their body mass in the first 5 days of their life in a rapid, exponential manner (Blackenhorn, 1998). So a head start of only a few hours could convey substantial advantages in a situation of high larval competition (Wall & Begon, 1987).
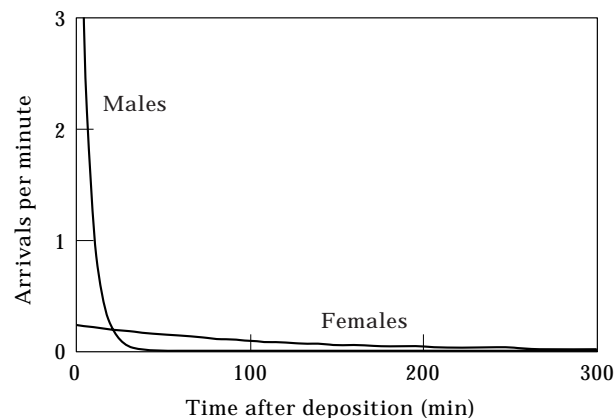

FIG. 1. The rate of male and female arrival with time after deposition (modified from Parker, 1970c).

This benefit may be amplified by the fact that, initially, the dung is warmer, thus accelerating development (Ratte, 1985; Blanckenhorn, 1997). The latter effect may also, to a smaller extent, act independently of competition, as faster development reduces the time the larvae are exposed to predators. Furthermore, there could be an additional benefit to the females themselves: the progressive hardening of the pat surface makes oviposition increasingly difficult (Parker, 1970a). Conversely, females may also experience costs associated with early arrival. The absolute number of males is highest soon after pat deposition, increasing the likelihood of an encounter (Parker, 1970b). As the numbers of encounters and struggles are correlated (Parker, 1970a), the increased chance of being damaged in a struggle may be such a cost. Therefore, different trade-offs between direct or indirect benefits and costs in terms of risk of physical damage and loss of time could lead to a distribution of equally-successful arrival times among females, i.e. a mixed ESS [Evolutionarily Stable Strategy, sensu Maynard Smith & Price (1973)]. This would imply that female behaviour is adaptive.

If the natural distribution of female arrival was an ESS, any deviation from it should favour the strategies under-represented in the deviating distribution. We therefore simulated the phase of fly mating for the natural and two plausible deviating patterns of female arrival: one similar to that of the males (i.e. a deviation towards earlier arrival times) and a uniform distribution over time (i.e. a deviation towards later arrival times). The simulations yielded estimates of the females' costs due to struggles and take-overs. Costs together with estimated benefits yielded rough fitness measures for females arriving at any particular time in each of the three patterns. The benefit functions were chosen under the assumption of an ESS in nature, i.e. the net benefits were equal for all arrival times under natural conditions. We then examined whether either mutants for delayed arrival in the male-like pattern or early-arriving females in the uniform pattern would be favoured. If one or both of these conditions is not fulfilled, we would have to reject our ESS hypothesis.

The Simulation

The program written was an individual-based simulation, i.e. flies were represented as interacting entities with individually differing properties (Huston *et al.*, 1988). As the program contained many elements of stochasticity it may be called a Monte-Carlo simulation. However, this is not true for every view of the meaning of this term [see Judson (1994) for a review]. The code was written in C and run on a UNIX system. Copies can be made available from the first author.

The male population on the model pat consisted of 30 individuals, representing a medium density (Parker, 1970b; Otronen, 1995). The individuals were assigned sizes randomly sampled from a realistic normal distribution (Kraushaar, unpubl. data), and stay times (the amount of time a male spends on the pat waiting for a female) were appropriately chosen as described below. To simplify the simulation, all males were assumed to be present immediately after deposition. A male was removed from the simulation (i.e. left the pat) when his waiting time exceeded his individual stay time. Newly-arriving females were randomly assigned an unpaired male. A pair copulated on the pat if the male's size was greater than (mean male size − SD), otherwise they emigrated to the grass. A pilot simulation revealed that this threshold value yields mean sizes of males copulating on the pat and in the grass that correspond well to field data given by Sigurjónsdóttir & Snorrason (1995). Copulation lasted for 30 min on the pat and 35.5 min in the grass [due to the higher temperature, copulations on the pat surface are known to be shorter (Parker, 1971)]. All pairs had to be on the pat during oviposition which was assumed to take 16.5 min (Parker, 1970c). When a female had finished oviposition, she was removed from the simulation and the male was returned to the pool of searchers.

Time was modelled in steps of 30 s. During each time step, every pair either copulating on the pat or ovipositing encountered a single male with a certain probability being a function of the number of searching males present at that time [deduced from Fig. 2 in Parker (1970a)]. A struggle followed if the size-ratio of owner to
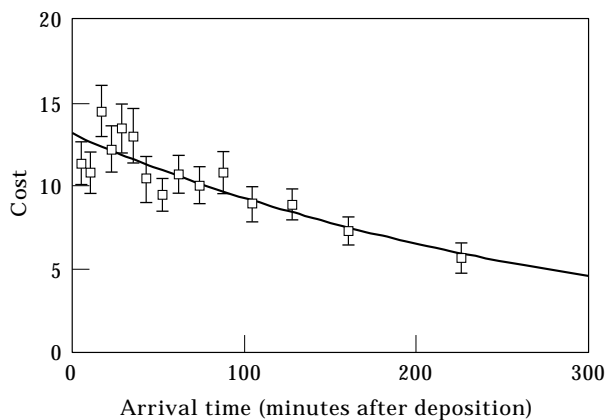
FIG. 2. Struggle and take-over cost with arrival time in the natural treatment. Means and SE over 100 simulation runs are shown.

attacker was less than 0.9. This reflects the fact that in nature attackers are almost always larger than defenders (Sigurjónsdóttir & Parker, 1981). Pairs copulating in the grass were considered to be safe from encounters. Struggles incurred no time cost and lead to a take-over with a fixed probability of 15%; the probabilities of take-overs given in the literature range from 6 to 25% (Borgia, 1980; Parker, 1970a; Sigurjónsdóttir & Parker, 1981).

If a take-over occurred, the newly-formed pair copulated on the pat. This could be assumed because nearly all males winning a struggle had a size greater than the emigration threshold. The duration of oviposition was assumed to be the fixed 16.5 min, regardless of whether the female had already been ovipositing before the take-over or not. The former owner of the female was returned to the pool of single males. During simulations, the program recorded individually the number of struggles and take-overs each female experienced, the total time spent on the pat and the size of the male she finished mating with. The simulation was stopped when no more animals were present at the pat. We did 100 simulations (i.e. 100 pats) for each pattern of female arrival. Within one pattern, arrival times were the same for all 100 runs.

In the natural case (="natural" treatment), 15 females arrived as given by Parker (1970b). As in nature, males in this treatment had negative exponentially distributed stay times which were generally longer than 15 min (Parker, 1978). With the male-like distribution of arrival times

(="synchronous" treatment), 14 females were assumed to be present immediately after deposition of the pat. To measure the benefits of a mutant for delayed arrival, the 15th female arrived after 24.5, 49.5 or 99.5 min (we did 100 simulations for each delay). Corresponding to the shortened presence of the majority of females, males in this treatment had shorter but nevertheless negative exponentially distributed stay times. In the uniform distribution (="uniform" treatment), 15 females arrived at a constant rate over 300 min. All males were present over the whole time but in a smaller number of only 16 animals. As the distribution of male stay times depends solely on the pattern of female arrival, changing the latter while keeping the former constant would lead to ecologically unreasonable results. Therefore, adjustments of male behaviour were performed in accordance with Parker (1970b). He argued that evolution should lead to an equilibrium distribution of male stay times with all males experiencing the same female quota, i.e. female arrivals per male and time. This means that the number of males has to decrease rapidly relatively shortly after deposition in a population with females arriving mainly at the time of deposition whereas male number has to be constant with a uniform distribution of female arrival times. By reducing the number of males in the latter case, the total time spent by all males on the pat was held in the range of that in the simulations with the other patterns of female arrival. This reduction thus follows from straightforward OSR theory as the sex ratio must become relatively less male-biased if the mean male staying time increases (Sutherland, 1987).

All statistical analyses were run using the SPSS for PowerPC package (Norusis, 1994).

Results

COSTS

To estimate a female's cost due to male fights were derived an index from simulation data. It consisted of three times the number of struggles plus once the number of take-overs an individual female experienced. This measure assumed that

injury is more costly for the female than time loss due to repeated copulations; we therefore assumed a linear relationship between fitness and our measure of cost, the simplest case possible. In the following, we will refer to this index simply as cost. For all following analyses on data from the uniform treatment we discarded the last two values for every pat. This is because the females arriving late were still at the pat when all unsuccessful males were removed (i.e. at a pat age of 300 min). As a result of this the probability of encountering a single male and therefore of experiencing a struggle and take-over dropped.

As simulation runs in the natural treatment did not differ in costs the females had (ANOVA, cost by simulation run with arrival time as a covariate, $F_{99, 1399} = 1.23$, $p = 0.068$), we performed the regression analysis with data averaged for arrival times. Costs decreased negative exponentially with arrival time (Fig. 2; nonlinear regression analysis, $y(X) = 13.079*$ $\exp(-0.003*x)$, $F_{2,13} = 574.26$, $R^2 = 0.740$). In the synchronous treatment delayed females experienced lower costs than those arriving simultaneously at time zero [Table 1(a)]. The effect of time of arrival (at time zero vs. any delay) was significant (ANOVA, cost by time of arrival, simulation run and length of delay, $F_{1,3900} = 81.24$, $p < 0.001$ for time of arrival, all other factors and interactions not significant). With the delay getting longer, on more and more pats all males had left when the latecoming female arrived (see sample sizes in Table 2). These females therefore could not experience any struggles at all. In the uniform treatment, cost did not change with arrival time while simulation runs differed (ANOVA, cost by simulation run with arrival time as a covariate, run:

TABLE 1

Synchronous treatment: cost and time dependent benefit (time benefit) for females arriving simultaneously at time 0 or delaying their arrival. Mean ± SE is given

Arrival	At time zero	Delayed
N	4200	300
(a) Cost	3.73 ± 0.09	0.64 ± 0.15
(b) Time benefit	9.34 ± 0.09	10.15 ± 0.15

TABLE 2

Synchronous treatment: benefit due to larval competition (competition benefit) for females arriving simultaneously at time 0 or delaying their arrival for 24.5, 49.5 to 99.5 min. Mean ± SE is given. The numbers in parentheses following the sample sizes indicate the number of females which did find the pat already abandoned of males

Delay (min)	0	24.5	49.5	99.5
N	4200 (0)	100 (5)	100 (35)	100 (97)
Benefit	5.23 ± 0.08	6.16 ± 0.32	6.91 ± 0.32	7.5 ± 0.00

$F_{99,1299} = 1.48$, $p = 0.002$, regression with arrival time: $t = -1.53$, $p = 0.126$).

Selection differentials for last male size (sensu Brodie *et al.* (1995)] were calculated per pat and varied significantly with treatment ($F_{2,499} = 142.72$, $p < 0.001$). The differential was largest for the natural distribution of arrival times (natural: 0.79 ± 0.03, synchronous: 0.29 ± 0.02, uniform: 0.69 ± 0.04).

TIME-DEPENDENT BENEFIT

In a first step we assumed the benefit to be a function of pat alone, e.g. due to beneficial effects of the softness of the dung surface. Because of the assumption of an ESS in nature, i.e. costs equal benefit for all arrival times, were used the regression equation of the cost for the natural treatment as function of the benefit on time (cf. Fig. 2). The net benefit for each female was calculated by subtracting her cost from the value of the benefit function corresponding to her arrival time. This procedure revealed that females who delay their arrival in the synchronous treatment had a higher net benefit than those arriving at the time of pat deposition [Table 1(b); ANOVA, net benefit by time of arrival, simulation run and length of delay, $F_{1,3900} = 5.66$, $p < 0.017$ for time of arrival, all other factors and interactions not significant]. For the uniform distribution, net benefit decreased significantly with time and again simulation runs differed (ANOVA, cost by simulation run with arrival time as a covariate, run: $F_{99,1199} = 1.48$, $p = 0.002$, regression on arrival time: beta = -0.14, $t = -5.17$, $p < 0.001$).

FREQUENCY-DEPENDENT BENEFIT

To test for beneficial effects due to larval competition we performed a second analysis of the cost data. A benefit in terms of reduced larval competition by earlier arrival should depend on both the reduction in number of competitors and the time larvae have to deal with this reduced number of competitors. To determine its value we used the function of the number of females still having eggs to lay over time. For each arrival pattern we separately calculated the mean time of oviposition for every arrival time. As oviposition duration is about 16 min, the mean time of oviposition of females arriving at a certain time equals the average of the time of their departure (i.e. the end of oviposition) minus eight (i.e. half the oviposition duration). For each arrival pattern we then plotted the number of unlaid clutches over these means. A female's benefit equalled the integral of this function from the mean time of oviposition corresponding to her arrival time to the time where the function's value becomes zero (which is when the last of the 15 females to arrive at the pat lays her eggs) (see Fig. 3 for an example). The function of this benefit did not exactly fit the cost function for the natural pattern. We therefore sought constants to correct the function so that the mean benefit did not differ significantly from the mean cost for each arrival time for the natural pattern. The benefits of females in the other two treatments
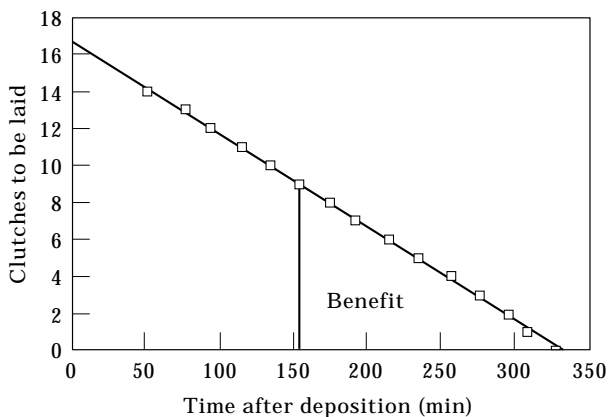

FIG. 3. Number of unlaid clutches with time after deposition. The estimate of benefit due to larval competition for the 6th female to lay eggs equals the size of the area of the triangle formed by the vertical line, the lower part of the curve and the right part of the *x*-axis.

were then treated with the same constants. In the synchronous treatment again all late-coming females had a higher net benefit than those arriving at time zero and the effect of delay varied with length of delay (Table 2; ANOVA, cost by time of arrival, simulation run and length of delay; interaction of time of arrival and length of delay: $F_{2,3900} = 10.00$, $p < 0.001$; all effects involving simulation run not significant). In the uniform treatment net benefit significantly decreased with time and runs differed as in the other analyses (ANOVA, cost by simulation run with arrival time as a covariate, run: $F_{99,1199} = 1.46$, $p = 0.003$, regression on arrival time: beta $= -0.18$, $t = -6.58$, $p < 0.001$).

Discussion

Under the assumption of either of the two benefit functions we used, populations showing deviating patterns of female arrivals would evolve back to the one found in nature. In a population of females arriving right after deposition of the pat, i.e. as males do, a female arriving late would gain a higher net benefit than her conspecifics, i.e. have a higher fitness. In a population of females arriving at a constant rate, those individuals coming early would be favoured. As it is most probable that either of the two benefits or a mixture of both (which would not alter our results) exists in nature, our work suggests that the natural pattern is evolutionarily stable and female arrival behaviour is adaptive.

There are two restrictions to the evolutionary process maintaining the intermediate arrival pattern. First, the delay in the synchronous case would have to be a moderate one. This is because with increasing delay the time dependent benefit decreases, ruining the bonus of fewer costs, and the bonus for early arrivers due to reduced larval competition increases; thus, there would be selection against long delays. Additionally, the chance of being inseminated decreases considerably, as very late females find the pat abandoned of males which would be important at least for virgin flies. However, the majority of virgin flies appear to engage in extra-dung matings, reducing the proportion of virgin females arriving at a pat to as low as 3%, (Parker *et al*.,

1993), and so this may not be a serious problem. The second restriction is that the natural pattern would not be maintained if male behaviour did not adapt to female arrival rates. However, as selection on male behaviour is strong, it seems reasonable to assume that a change in female arrival pattern would lead to a change in the distribution of male stay-times.

Our results raise the question about the proximate mechanism triggering female behaviour. One possibility is that the volatile chemical cues coming from a pat change with pat age and that females vary in the cue composition which attracts them to a pat. Females waiting for varying times after having sensed the presence of a pat is another possible mechanism.

The mean size of the males females completed oviposition with was largest in the natural treatment, i.e. sexual selection on male size was most intense with this pattern of female arrival. This implies that the intensity of sexual selection acting on males is partly mediated by the pattern of female arrival which is itself formed by selection pressures independent of the advantages of mating with large males for the females' offspring. Evolution from the uniform to the natural pattern would increase the selection intensity by almost 14%. It would almost triple in a population changing from a synchronous to the natural female arrival pattern. However, the selection intensity depends very much on operational sex ratio (Emlen & Oring, 1977; Arnold & Duvall, 1994), i.e. the absolute number of single males and the number of females they compete for. The accuracy of the detected difference in intensity between treatments thus depends strongly on how realistic the adjustment of male behaviour was. The adjustments we performed were relatively crude, making the calculated changes in selection intensity only rough estimates of what would happen in reality. Despite this, our study shows that besides active female incitation of competition among males (e.g. Cox & LeBoeuf, 1977), selective pressures acting on unrelated features of female behaviour could have important consequences on male–male interactions.

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