Plasticity in reproductive effort of male dung flies (*Scatophaga stercoraria*) as a response to larval density

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Summary

1. Explaining variation in reproductive effort is fundamental to understanding diversity in male mating and life-history strategies, although relatively little is known about environmental influences on such variation and associated trade-offs.

2. Plasticity in reproductive effort was examined in male Yellow Dung Flies (*Scatophaga stercoraria*) reared under two larval density treatments. Relative testis size, thorax size and mate-searching effort were compared, and relationships between these traits examined to look for correlational evidence of predicted trade-offs in gonadal and mate-searching expenditure.

3. Males reared under high larval density conditions developed relatively larger testes than those reared at low density but no evidence was found for a corresponding reduction in mean mate-searching effort at the population level.

4. A negative relationship was found between testis size and mate-searching activity among males within the high larval rearing density treatment but not among those reared at low density.

5. Willingness to engage in struggles for possession of females increased in relation to body size among males reared at high larval density, and the opposite relationship was found among those reared at low density.

6. Plasticity in male reproductive effort in relation to environmental conditions may be more widespread among insects than has previously been appreciated.

Key-words: Ejaculate expenditure, phenotypic plasticity, *Scathophaga*, testis size, trade-offs

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Introduction

Explaining how males optimize investment in reproduction is fundamental to understanding diversity in mating and life-history strategies (Stearns 1992; Parker 1998). Within a fixed energy budget, effort spent on one trait to increase fertilization success should reduce the success of alternative traits with the same function. It is often assumed, therefore, that ejaculate expenditure is limited by investment in behaviours aimed at increasing copulation rate, such as mate-searching or direct competition with other males (Parker 1990a,b, 1998; Parker *et al.* 1996, 1997). Empirical studies of ejaculate expenditure at an intraspecific level have focused almost exclusively on patterns of discontinuous variation in body size and gonadal expenditure associated with alternat-

ive mating tactics (Taborsky 1994, 1998). However, continuous variation in testis size both within and between populations may also be adaptive (Stockley & Purvis 1993; Gage 1995). Although environmental causes of variation in male reproductive effort have not yet been widely investigated, two recent studies suggest that ejaculate expenditure may vary in relation to population density. In both studies, male moths were shown to invest more in sperm production under high population density conditions, where anticipated future mating frequency and risk of sperm competition is high (*Pseudaletia separata*, He & Tsubaki 1992; *Plodia interpunctella*, Gage 1995). Such plasticity in male resource allocation strategies may be widespread in insects, particularly among species that regularly experience fluctuations in population density.

Population density is highly variable in natural populations of the Yellow Dung Fly, *Scatophaga stercoraria* L. (or *Scathophaga*), making this an ideal subject for studies of phenotypic plasticity (Parker 1970a; Gibbons 1987; Blanckenhorn 1997). The

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number of adult dung flies found on dung peaks during spring and autumn months, around April and October, respectively, and then decreases drastically during the summer and winter (Parker 1970a; Gibbons 1987). The reproductive behaviour of *S. stercoraria* is well documented. Males gather on and around fresh dung, where they search for and copulate with incoming gravid females (Parker 1970b). Following copulation the female oviposits in the dung and is guarded by the paired male from attempted 'take-overs', where attacking males try to displace him and copulate to fertilize the remaining ova (Parker 1970b; Sigurjónsdóttir & Parker 1981). Copulation in *S. stercoraria* leads to displacement of previously stored sperm at a constant rate from the female sperm storage organs. Copula duration (and hence ejaculate size) is optimized according to the marginal value theorem to displace around 80% of previously stored sperm at typical female encounter rates (Parker 1970c; Parker & Simmons 1991; Simmons *et al*. 1999).

In this study we investigate variation in reproductive effort of adult male Yellow Dung Flies reared under differing larval density conditions. We compare relative testis size, thorax size and mate-searching effort of males reared under high and low larval density treatments, and examine relationships between these traits to look for evidence of predicted trade-offs between ejaculate expenditure and mate-searching effort. Our investigation provides evidence of both plasticity and trade-offs in the reproductive effort of male dung flies in relation to larval rearing density.

Materials and methods

REARING FLIES

Dung flies were reared under laboratory conditions from eggs collected at Woodpark Farm, Wirral, Cheshire, UK, between October 1994 and 1996. Small batches of eggs, taken from cowpats across the area, were transferred to moist filter paper in Petri dishes. The Petri dishes were then stored in a constant temperature room at 20 °C for ≈48 h, by which time the eggs had all hatched. For each of three replicate experimental populations, larvae were divided between two density treatments in groups of 5 (low density) or 30 (high density); each group was placed in a 100-ml plastic pot with 20 g of homogeneously mixed fresh cow dung. Care was taken to mix larvae from across the field site within each treatment and within jars. Potential pseudoreplication was also minimized by using large numbers of jars (≈50 for each density treatment replicate). Jars were secured with metal lids pierced with small air holes and were maintained at 20 °C for approximately 3 weeks until adult flies began to emerge. By repeating this process using dung varying naturally in quality, it was possible to produce variation in the body size of adult male dung flies reared at the same larval density

(Hammer 1941; Sigurjónsdóttir 1980). Jars were checked daily for emerging adult flies, which were each transferred to separate 150-ml jars containing two small cotton-wool balls – one soaked in water and the other in sugar solution. The flies were maintained at constant temperature (20 °C) on a 12-h/12-h light/dark cycle. They were fed *ad libitum* by providing ≈10–15 live *Drosophila melanogaster* twice weekly. Jars were checked 4 to 5 days a week for the presence of excess *Drosophila*. Fresh water was provided by regularly remoistening the cotton-wool balls. Feeding was maintained in this way for approximately 6 weeks, which allowed ample time for full sexual maturation of both sexes (Foster 1967).

BODY, THORAX AND TESTES MEASUREMENTS

Measurements were made on three replicate populations, which differed in mean body size because of natural variation in dung quality. Mature male dung flies were killed by freezing. Right hind tibia lengths were measured to the nearest 0·05 mm at ×25 magnification. Hind tibia length cubed (htl^3 mm^3) correlates well with other measures of body size (Sigurjónsdóttir 1984). Length of the testes was measured to the nearest 0·01 mm at ×40 magnification (testes were put in a drop of Barth-X solution to prevent them from drying out). Measurements of testes length did not include the area identified by Ward & Simmons (1991) which shrivels in relation to recent mating activity. Additionally, for the final replicate, body and thorax mass were recorded to the nearest 0·1 mg, thorax length to the nearest 0·05 mm, and paired wet testis mass was recorded to the nearest µg immediately after dissection.

MEASURING BEHAVIOURAL EFFORT GAINING MATES

Experimental flies for behavioural analysis were reared as described above, except that on the first day of emergence, each male was anaesthetized with CO_2 and weighed to the nearest 0·1 mg. Mature males within each density treatment were matched in pairs according to body size. At the start of the experiment, one male from each pair was introduced into a 150-ml glass jar containing a large smear of fresh cow dung and a sexually mature female which had not previously oviposited. The size of females introduced to males of both density treatments was randomized, as differences in ova number associated with female body size can influence the likelihood of struggles occurring or their duration (Sigurjónsdóttir & Parker 1981). Temperature was constant at 19 ± 1 °C throughout the experiment. Once the first male had begun to copulate, the subject male was introduced to the jar and its behaviour recorded for 30 min. Activity scores of subjects were

recorded as the number of times the male crossed each of two boundary lines marked on the outer circumference of the jar to divide it into three equal sections. Any physical contact with the copulating pair was also recorded. Three categories of encounter were distinguished (after Parker 1970b): (i) touch – the subject male touches but makes no further contact with the copulating pair; (ii) mount – the subject male mounts and orientates but then immediately separates from the copulating pair; and (iii) struggle – the subject male mounts the copulating pair and initiates a struggle. The duration of each struggle was also recorded. All experimental males were killed by freezing and measurements taken of body and testis size as described above. Behavioural data were analysed in a general linear model using the GLM option in MINITAB (MINITAB Inc., PA, USA).

Results

RELATIVE TESTIS SIZE

Relative testis size of sexually mature male dung flies fed *ad libitum* varied significantly in relation to larval rearing density. Males reared under conditions of high larval density were smaller than those reared at high density, and had absolutely smaller testes (Tables 1 and 2). However, relative to body size, males reared at high density had significantly larger testes than those reared at low density (Tables 1 and 2). Mean body size and absolute testis size also differed significantly between replicates because of natural variation in the quality of dung in which larvae were reared (Table 2). This variation was used to compare the mean testis size of male populations with similar body size (all individuals included) that had been reared at different larval densities. In these populations, absolute testis size also differed significantly in relation to larval rearing density (Fig. 1). It appears therefore that male dung flies adjust relative investment in the testes according to conditions of larval rearing density rather than body size *per se*. Length measurements of body and testis size were also strongly correlated with corresponding mass measurements (hind tibia length and adult body mass: $n = 73$, correlation = 0·82, $r^2 = 0·68$; $P = 0·0001$; total testes length and combined testis mass: $n = 58$,

Table 2. Results of analysis of variance for body and testis size of adult male dung flies from three replicate populations, within which approximately half were reared under conditions of high larval density and half under conditions of low larval density. Body size was measured as hind tibia length and testes size as total length. Relative testis size was calculated as the ratio of total testes length to hind tibia length

| Source	df	SS	MS	F	P
Hind tibia length					
Larval density (A)	1	6·18	6·18	255·45	0·0001
Replicate (B)	2	5·46	2·73	112·83	0·0001
AB	2	1·21	0·61	25·04	0·0001
Error	175	4·23	0·02		
Total testes length					
Larval density (A)	1	2·23	2·23	15·29	0·0001
Replicate (B)	2	13·62	6·81	46·56	0·0001
AB	2	0·45	0·23	1·54	0·22
Error	148	21·64	0·15		
Relative testes length					
Larval density (A)	1	0·13	0·13	6·87	0·01
Replicate (B)	2	0·07	0·04	1·85	0·161
AB	2	0·10	0·05	2·66	0·07
Error	147	2·79	0·02		
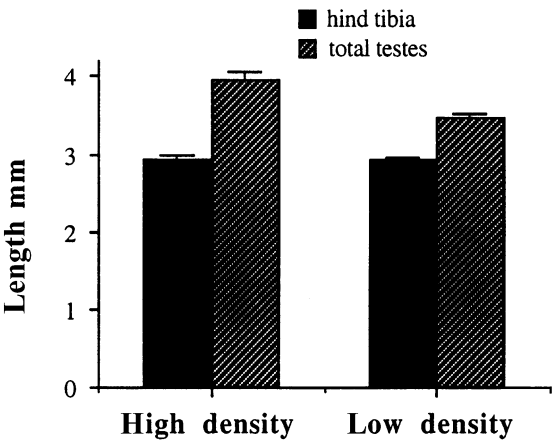
Fig. 1. Male dung flies reared under high larval density conditions have significantly larger testes than those of comparable body size reared under low larval density conditions (unpaired t-test: body size (htl³): $t_{64} = -0·86$, $P > 0·40$; total testes length: $t_{54} = 2·93$, $P < 0·005$).

correlation = 0·49, $r^2 = 0·24$; $P = 0·0001$). For males reared under conditions of high larval density, testis size (log total length mm) increased significantly with body size (log htl³ mm³) (simple least-squared linear regression analysis within largest replicate population: $y = 0·24x - 0·08$; $r^2 = 0·22$; $F_{1,30} = 8·54$, $P = 0·006$), whereas for males reared at low density, this relationship was not significant ($r^2 = 0·04$; $F_{1,46} = 2·12$, $P = 0·15$).

RELATIVE THORAX SIZE

In accordance with overall differences in body size, male dung flies reared at high larval density had absolutely smaller thorax lengths than those reared at low

Table 1. Mean length measurements and ratios of morphological traits for adult male dung flies reared under different larval density conditions

	High density			Low density		
Measurements	n	Mean	SE	n	Mean	SE
Hind tibia length mm	82	2·66	0·03	99	3·06	0·02
Total testes length mm	65	3·39	0·06	89	3·71	0·05
Thorax length mm	35	2·68	0·02	35	3·05	0·02
Ratio testes to hind tibia length	64	1·30	0·01	89	0·73	0·02
Ratio thorax to hind tibia length	34	0·95	0·01	35	0·97	0·01

Table 3. Results of general linear model to investigate effects of rearing density on relationships between behavioural measures of mate-searching effort (activity in the context of mate-searching and number of struggles initiated) and body size or testes size of male Yellow Dung Flies

Dependent variable	Source	df	MS	F	P
General activity in context of mate-searching	Density	1	181·2	0·38	0·543
	Body size	1	77·3	0·16	0·690
	Density × body size	1	93·2	0·20	0·662
	Error	22	474·8		
Residual number of struggles initiated	Density	1	13·7	3·83	0·063
	Body size	1	0·02	0·01	0·944
	Density × body size	1	14·7	4·11	0·055
	Error	22	3·6		
General activity in context of mate-searching	Density	1	2363·5	5·83	0·026
	Testes size	1	64·3	0·16	0·695
	Density × testes size	1	1967·8	4·85	0·040
	Error	19	405·7		
Residual number of struggles initiated	Density	1	12·1	3·26	0·087
	Testes size	1	0·2	0·06	0·807
	Density × testes size	1	13·5	3·64	0·072
	Error	19	3·7		

density (Table 1; unpaired $t_{68} = -13·20$, $P = 0·0001$). There was no difference in the relative thorax size of flies reared under different larval density treatments (Table 1; unpaired $t_{67} = -1·45$, $P = 0·15$), and thorax measurements (log length mm) were significantly related to male body size (log htl^3 mm^3) in both of the larval density treatments (simple least-squares linear regression: high-density treatment: $y = 0·26x + 0·07$; $r^2 = 0·51$; $F_{1,31} = 32·01$; $P = 0·0001$; low-density treatment: $y = 0·14x + 0·27$; $r^2 = 0·16$; $F_{1,33} = 6·40$; $P < 0·02$). Measurements of thorax length were also strongly correlated with corresponding mass measurements ($n = 61$, correlation $= 0·69$, $r^2 = 0·47$; $P = 0·0001$).

TRADE-OFFS WITH BEHAVIOURAL EFFORT GAINING MATES

For males reared at different densities there was no difference in mean activity scores (unpaired *t*-test: $t_{30} = 0·48$, $P > 0·60$), number of struggles initiated ($t_{30} = -0·09$, $P > 0·90$), or total duration of struggles ($t_{30} = 1·31$, $P > 0·20$). For all males, the number of struggles initiated increased significantly in relation to activity scores ($r^2 = 0·55$, $F_{1,30} = 36·7$, $P = 0·0001$). The residual number of struggles was therefore taken from this relationship as an index of male willingness to initiate struggles independent of activity. In contrast, the total duration of struggles was not predicted by activity scores or the number of struggles initiated (multiple regression analysis: $r^2 = 0·08$, $F_{2,29} = 1·26$, $P > 0·25$; activity scores: partial regression coefficient $= 7·45$, $t = 1·12$, $P > 0·25$; number of struggles: partial regression coefficient $= -2·71$, $t = 0·08$, $P > 0·90$).

Results of a general linear model showed that testes size affects activity differently according to rearing density ($F = 4·85$, df $= 1$, $P = 0·04$; Table 3; Fig. 2). In individual regression analyses, both absolute
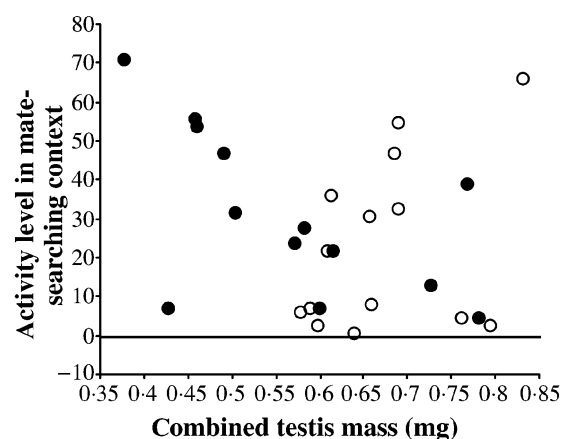
Fig. 2. The relationship between activity levels in the context of mate searching and testis size of male dung flies was affected by rearing density: ● males reared at high density; ○ males reared at low density (see also Table 3).

and residual testis mass of high-density males were negatively related to activity in the context of mate-searching (absolute: $r^2 = 0·32$; $F_{1,12} = 5·23$; $P < 0·05$; residual: $r^2 = 0·30$; $F_{1,11} = 4·71$; $P = 0·05$). In contrast, testis mass of low-density males did not predict activity in the context of mate-searching when analysed separately ($r^2 = 0·10$; $F_{1,13} = 1·40$; $P > 0·25$). No other interaction terms are significant (Table 3), although the effect of density in the relationship between residual number of struggles and body size approaches significance at $P = 0·055$. When males reared at high density are analysed separately, body size (htl^3) predicts the number of struggles initiated independent of activity, with larger males generally more likely to engage in struggles ($r^2 = 0·30$; $F_{1,13} = 5·19$; $P < 0·05$). In individual regression analyses for males reared at low density, body size (htl^3) predicts both the number of struggles initiated after control for activity ($r^2 = 0·25$; $F_{1,14} = 4·74$; $P < 0·05$) and a similar

trend with the total duration of struggles ($r^2 = 0.23$; $F_{1,14} = 4.19$; $P = 0.06$). In contrast to males reared at high density however, these relationships were in a negative direction. That is, larger males reared at low density were generally *less* likely to engage in struggles following encounters with copulating pairs, and their struggles were generally of shorter duration than those of smaller males.

Discussion

Male dung flies reared under conditions of high larval density developed relatively larger testes as adults than did those reared at low larval density. This pattern was repeated for males of comparable body size emerging from different larval density treatments, suggesting that variation in relative testis size is a response to conspecific density rather than body size or food availability *per se*. This pattern is consistent with results found by Ward & Simmons (1991), who showed that fluctuations in body size do not fully account for observed seasonal variation in testis size within natural populations of *S. stercoraria*. Although there is no direct evidence that selection has been operating, results of the present study are strongly suggestive of an adaptive response by which investment in the testes is varied in relation to local environmental conditions.

Plasticity in ejaculate expenditure has been described previously for male insects that regularly experience fluctuations in population density. He & Tsubaki (1992) found that male Armyworms, *Pseudaletia separata*, reared at high larval density produce significantly larger spermatophores than those reared at low density. Also, Gage (1995) found that adult male Indian Meal Moths, *Plodia interpunctella*, invest more in testes and produce larger ejaculates with increasing larval rearing density. Increased ejaculate expenditure revealed by these studies may be an adaptation to elevated sperm competition risk at high population density (Parker *et al*. 1997) and/or anticipated high copulation frequency, both of which result from increased female encounter rates (Gage 1995). In the case of *S. stercoraria*, however, it is unlikely that increased ejaculate expenditure is a response to sperm competition because the mechanism of sperm displacement in this species offers little or no advantage for increased ejaculate size under conditions of high sperm competition risk (Parker 1970c; Parker & Simmons 1991; Simmons *et al*. 1999).

It is unlikely also that the variation in relative testis size observed here is a simple response to anticipated copulation rate. Development of dung flies until adult eclosion takes around 30 days at 15 °C (Larsen & Thomsen 1940), after which a minimum period of around 4 weeks is required for adult males to achieve sexual maturity (Foster 1967). Peaks of seasonal abundance in autumn and spring therefore

lead to some asynchrony in larval and adult population densities, such that males experiencing low larval density conditions in the dung will often reach sexual maturity during adult population peaks, and those experiencing high larval density conditions will be more likely to mature as the adult population is in decline. A predictable and likely important correlate of larval rearing conditions for Yellow Dung Flies is therefore the anticipated duration of their reproductive life span. Males developing under low larval density conditions will have a potentially long reproductive life span coinciding with optimal conditions for reproduction, whereas those which develop at high larval density will experience a relatively short reproductive life span when environmental conditions are in decline. The relatively large testes of high larval density males may therefore reflect an increased overall reproductive effort in response to a relatively short anticipated reproductive life span. This idea could be tested further by comparing the longevity under controlled conditions of male dung flies from high and low larval density treatments. Gage (1995) also found that male Indian Meal Moths reared at high population density had relatively larger testes but survived for shorter periods than those reared at low density.

There was no difference in the mean overall activity scores or rate of attempted take-overs for male dung flies reared at differing larval densities. Activity levels recorded in the present investigation are a good indicator of likely male success in mate-searching on the dung, as Otronen (1995) found that males are most successful in mate-searching when they walk more, make more short flights and attack other males frequently. That no difference in mean activity levels was found here in relation to larval rearing density suggests therefore that increased investment in the testes at a population level is not achieved at the expense of behavioural reproductive effort. No difference was found either in the mean thorax sizes of male dung flies reared under differing larval density conditions. These results contrast with those of Gage (1995) for *Plodia interpunctella*, where males increased investment in the testes at high population density, but simultaneously decreased investment in the thorax, and hence, presumably, flight for mate-searching. Overall, therefore, results of the present study provide no evidence of population-level trade-offs between gonadal and mate-searching effort in *S. stercoraria*. Rather, males reared under high larval density conditions apparently raised their overall reproductive effort by increasing investment in the testes.

The results of our experiments designed to investigate variation in mate-searching activity are based on relatively small sample sizes and should therefore be interpreted with caution. However, evidence for some potentially significant interactions with larval rearing density did emerge from the analyses. Slopes

for the relationship between testes size and activity levels were significantly different for the two density treatments. Among males reared at high density, those with larger testes were generally less active in mate-searching, whereas the same trend was not evident among males reared at low density. This suggests that there may be a trade-off between ejaculate investment and mate-searching activity, which is dependent on rearing density. Such a trade-off could potentially result from competition for resources during development of the structures involved and/or more directly during the adult phase via a shared resource pool, although we are unable to suggest which mechanism is likely to be most important on the basis of current evidence. Competition for resources during development would be consistent with results of previous work (e.g. Gage 1995), although a more direct physiological trade-off between energy allocated to sperm production and mate-searching activity is possible in *S. stercoraria* because resources used in reproduction are accrued and stored during the adult phase (Otronen 1995).

We also found some evidence to suggest that rearing density may influence the relationship between male body size and willingness to engage in struggles over females. Within the high larval density treatment, large males were generally more likely to initiate struggles with a competitor of equal body size than were small males. This result is interesting because it suggests that large males may gain disproportionate reproductive pay-offs from aggressive behaviour, and previous studies have shown that they have a higher success rate in take-over attempts (Sigurjónsdóttir & Parker 1981). For males reared under low-density conditions, the reverse relationship was found. In this case, large males were *less* likely to initiate struggles with competitors of equal body size than were small males. It is possible then that large males reared at low density may be investing relatively more effort in searching for females. Otronen (1995) found that males successful in mate-searching have higher energy stores, and that both carbohydrate and lipid stores are positively related to male body size. Alternatively, overall reproductive effort might decrease in relation to body size among males from the low-density treatment, with larger males investing more in somatic maintenance and survival to extend their reproductive life span.

In conclusion, relatively little is known about environmental influences on variation in male ejaculate expenditure. While previous studies have found evidence of reproductive plasticity in semelparous species among which resources for reproduction are accrued exclusively during development (He & Tsubaki 1992; Gage 1995), results presented here for *S. stercoraria* suggest plasticity and trade-offs in ejaculate expenditure may be more widespread among insects. Investigation of plasticity in male resource allocation decisions with respect to environmental

conditions is therefore a potentially rewarding area for direction of future research effort.

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