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Mating with a large male yellow dung fly: costs or benefits in terms of clutch size?

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ABSTRACT

Mating, and mate choice, typically carry benefits as well as costs for the female, which can be manifested in certain fitness components but not others. Both fecundity benefits and costs have been reported in some species for females that mate with larger males. The former has been interpreted as cryptic female choice, whereas the latter indicates sexual conflict. Using four independent data sets, we examined whether female clutch size varies with the size of her mate in the yellow dung fly *Scathophaga stercoraria*, a classic model species for studies of sexual selection and conflict. We found that clutch size depends strongly on female size but not male size, revealing neither costs nor benefits. It is possible that female dung flies are constrained in modifying their clutch size, or that this sort of strategic oviposition does not pay in this species. We suggest that mating costs or benefits in terms of fecundity may be relatively rare compared with corresponding effects on survivorship.

Keywords: body size, cryptic female choice, fecundity, mating costs, *Scathophaga stercoraria*, *Scatophaga*, sexual conflict, sexual selection.

INTRODUCTION

Traits that affect mating success can evolve by sexual selection or sexual conflict (Partridge and Hurst, 1998). Several sexual selection mechanisms may operate that are generally difficult to discriminate empirically (notably good genes models, Fisherian runaway selection, direct benefits; Andersson, 1994; Kokko, 2001). Distinguishing between sexual selection and inter-sexual conflict (or chase-away sexual selection; Parker, 1979; Holland and Rice, 1998; Partridge and Hurst, 1998) is also problematic, as their predictions often coincide. For example, most of the above-mentioned models predict co-evolution of, and hence a (genetic) correlation between, male and female sexual traits (Andersson, 1994; Bakker and Pomiankowski, 1995; Holland and Rice, 1998). Unique predictions of inter-sexual conflict (as opposed to sexual selection) are female resistance to (rather than choice of) particular males, and costs (rather than benefits) when mating with those males (Holland

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and Rice, 1998). Although resistance and choice can be difficult to disentangle in practice (e.g. Arnqvist, 1989; Crean and Gilburn, 1998; Blanckenhorn *et al.*, 2000), demonstrating mating costs or benefits seems straightforward.

Mating, and mate choice, carries benefits as well as costs for the female, and these can be manifested in unpredictable ways in some fitness components but not others (cf. Kokko, 2001). Mating often, and sometimes severely, reduces female survivorship (e.g. Rowe, 1994; Chapman *et al.*, 1995, 1998; Blanckenhorn *et al.*, 2002) but may also increase it (e.g. Brown, 1997; Hayashi, 1998). Similarly, female fecundity may increase (reviewed by Andersson, 1994) or decrease (e.g. Arnqvist *et al.*, 1997; Reyer *et al.*, 1999) after mating with particular males. A reduction in fitness due to mating is indicative of sexually antagonistic co-evolution driven by sexual conflict (Holland and Rice, 1998), whereas a fitness gain is the expected outcome of traditional sexual selection models (Andersson, 1994). This interpretation may be clear with regard to survivorship, but for fecundity the situation is more complex. For example, Reyer *et al.* (1999) interpreted reduced fecundity of female water frogs after mating with an undesirable (i.e. small) male as a case of cryptic female choice by strategic resorption of eggs (cf. Eberhard, 1996). Conversely, increased oviposition by *Drosophila melanogaster* and some other flies can be caused by male accessory substances transferred during mating, and hence may be a result of male manipulation and conflict (Chapman *et al.*, 1995, 1998). At least with regard to fecundity, therefore, the same response may indicate female choice or sexual conflict, depending on the species, presumed selection mechanism and trait in question. Moreover, whether and how much fecundity is increased or decreased should, at least theoretically, depend on male quality: females might strategically increase egg output after having mated with a high-quality male, and higher quality males may also be better at manipulating females into laying more eggs fertilized by their sperm.

The yellow dung fly *Scathophaga stercoraria* (sometimes *Scatophaga*) is a classic model system for studies of sexual selection (Parker, 1979). As in many species (Andersson, 1994), large males enjoy a mating advantage (Jann *et al.*, 2000). Sexual selection is primarily mediated by male–male competition (Parker, 1979), but subtle forms of female choice and sexual conflict also occur (Borgia, 1981; Reuter *et al.*, 1998; Ward, 2000; Hosken *et al.*, 2001). Here we examine whether female clutch size varies with the size of her mate, testing multiple hypotheses at the same time. On the one hand, females might strategically allocate more resources to their clutch after mating with larger males, a possible result of cryptic choice (Eberhard, 1996; Reyer *et al.*, 1999; Cunningham and Russell, 2000) or, alternatively, size-dependent male accessory substances (cf. Chapman *et al.*, 1998). On the other hand, clutch size might decrease with male size, as has been found in *D. melanogaster* and water striders (Pitnick, 1991; Arnqvist *et al.*, 1997). Although the causal mechanisms are not known, this may result from size-dependent physiological or mechanical damage of females by males, which might depend on copula duration. The null hypothesis is that male size has no effect on female fecundity.

MATERIALS AND METHODS

We used four independent data sets comprising 391 clutches in total. Two sets stem from studies previously published (Ding and Blanckenhorn, 2002; Martin and Hosken, 2002) and two from unpublished studies. In two studies, we analysed only the first clutch of each female mated to a randomly allocated male of varying size (Martin and Hosken, 2002;

Y. Teuschl and C. Reim, unpublished). In a third study (Ding and Blanckenhorn, 2002), females of two size classes (small and large) were each mated to one male of each size class 7 days apart, and their first and second clutches laid thereafter were analysed. In a fourth study (Meile, 1996), females of five size classes were, at intervals of 4–5 days, mated each to the same males of five size classes in a completely crossed, repeated-measures design ($n = 4$ individuals per size class), and their five clutches laid thereafter were analysed. The latter two studies are strong tests of the theory because the same female mated with males of different sizes in randomized order.

Using standard techniques (for details, see Ding and Blanckenhorn, 2002; Martin and Hosken, 2002), all flies were reared in the laboratory at various temperatures and larval food availabilities to generate a wide range of body sizes. Adults were well fed with sugar, water and *D. melanogaster ad libitum*. Flies mated first when 10–20 days old, ensuring sexual maturity (Jann and Ward, 1999). All pairings took place singly in the laboratory in 100 ml bottles containing a smear of fresh cow dung, at 18–21°C. As is natural, males were introduced first into the bottle and females thereafter. After copulation (the duration of which was measured by direct observation) and oviposition, all eggs laid were counted and the dung was removed. We used hind tibia length as an index of body size.

RESULTS

We first analysed all 391 clutches combined with male and female hind tibia length plus their interaction as continuous factors and study as a blocking variable. Clutch size was positively related to female size ($F_{1,387} = 59.7$, $P < 0.001$, partial $r = +0.38$) but not male size ($F_{1,387} = 0.43$, $P = 0.513$, partial $r = +0.03$; interaction and study: $P > 0.2$). However, sometimes ($n = 79$) females did not lay at all after copulation, and sometimes they laid only a partial clutch. This may have occurred because females had no eggs to lay or because of a strategic decision. We therefore performed the same analysis with a reduced sample, removing all zero clutches and all those (partial) clutches that were 2 standard errors smaller than the clutch size expected from an overall regression of clutch size on female hind tibia length. The results of this analysis were qualitatively the same (female size effect: $F_{1,286} = 127.0$, $P < 0.001$, partial $r = +0.59$; male size effect: $F_{1,286} = 0.91$, $P = 0.334$, partial $r = +0.05$; interaction and study: $P > 0.2$; Fig. 1).

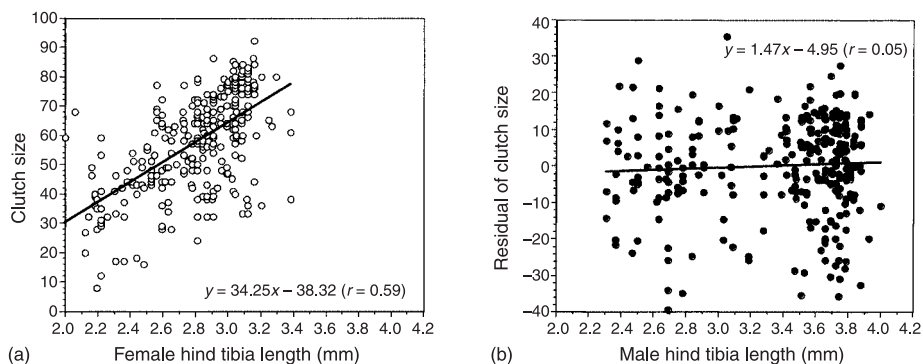


Fig. 1. (a) Clutch size as a function of female hind tibia length and (b) the residuals of this relationship as a function of male hind tibia length (reduced data set with zero and partial clutches excluded).

The results for individual studies 3 (Ding and Blanckenhorn, 2002) and 4 (Meile, 1996) were similar. For study 3, analysis of variance (ANOVA) with female size class as a repeated measure revealed effects of female size class ($F_{1,50} = 7.19$, $P = 0.01$) but not male size class ($F_{1,50} = 3.44$, $P = 0.070$; interaction $P > 0.1$). Note, however, the trend for smaller clutches with larger males (Fig. 2a). For study 4, ANOVA with both male and female size class as repeated measures showed effects of female size class ($F_{4,12} = 4.46$, $P = 0.019$) but not male size class ($F_{4,12} = 1.15$, $P = 0.380$; interaction: $P > 0.3$; Fig. 2b). Again, reducing the data set as described above did not qualitatively change these results. Copula duration never had a significant influence on clutch size ($P > 0.1$) and did not affect the results; this covariate was therefore removed from the final model in all analyses.

DISCUSSION

The clutch size of yellow dung flies depends strongly on female body size but generally not on the size of her mate. Body size dependent female fecundity is common in ectotherms and, therefore, not surprising (Wootton, 1979; Honek, 1993). Our study focused on the possibility that male body size also influences female clutch size. This had been found previously for one of our data sets (Martin and Hosken, 2002), but could not be verified here using a much larger data set. Martin and Hosken (2002) removed more covariates and factors in their analysis, which could explain the difference in results, but theirs may also be a case of falsely rejecting a true null hypothesis, which is more likely at lower sample sizes. We therefore conclude that female dung flies do not allocate more resources to reproduction after mating with a large (i.e. high-quality) male. This form of cryptic female choice has been observed in at least one frog and one bird species (Reyer *et al.*, 1999; Cunningham and Russell, 2000). Even though female yellow dung flies have few means of rejecting (i.e. choosing) the typically larger males (Ding and Blanckenhorn, 2002), subtle pre-copulatory female preferences of large males have been described or invoked previously (Borgia, 1981;

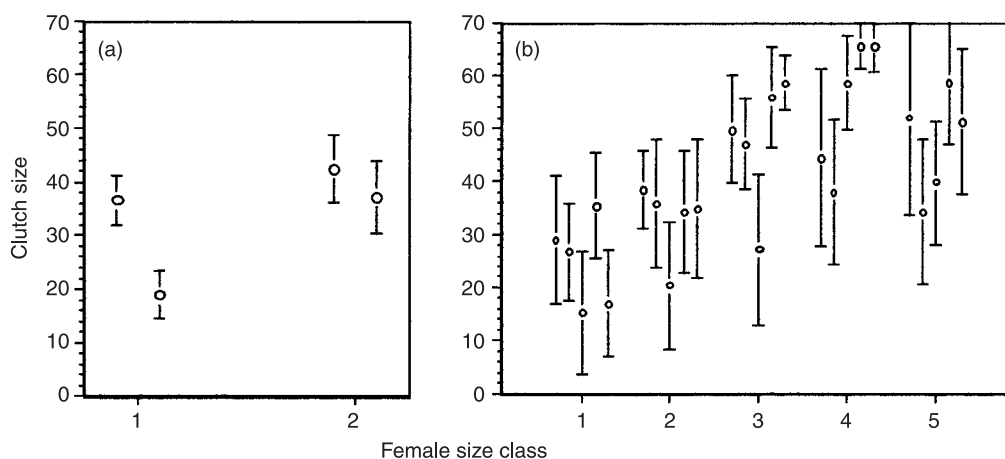


Fig. 2. Clutch size of females from (a) two size classes (study 3; 1 = small, 2 = large) and (b) five size classes (study 4; 1 = smallest, 5 = largest) laid after copulating with males from two or five size classes, respectively (male size increases from left to right for each group of data points; full data set including zero clutches).

Reuter *et al.*, 1998). Moreover, Ward (1998, 2000) has demonstrated in this species that females may cryptically choose males based on their genotype at the PGM enzyme locus. Nevertheless, modification of strategic female clutch size apparently does not occur in yellow dung flies, nor does size-dependent action of potential male accessory products that could affect female oviposition (cf. Chapman *et al.*, 1995, 1998). It is possible that modification of strategic female clutch size may not pay in this species. Depending on foraging success in the field, inter-clutch intervals are at least 3–5 days but may be considerably longer (Gibbons, 1980). If there is a low probability of surviving to the next oviposition, a female should lay as many eggs as soon as possible after being fertilized by whichever male.

It is also possible that female yellow dung flies are physiologically constrained in modifying their clutch size. In insects, (maximal) egg output is set during juvenile development in relation to environmental factors ultimately determining final body size (Bennettova and Fraenkel, 1981). Nevertheless, the clutch size of yellow dung flies decreases both with limited adult food and with female age (Jann and Ward, 1999; Blanckenhorn, 2000), presumably by resorption or abortion of some eggs at some point during egg development, although this was apparently not the case here with regard to male size. Presumably, variation in female age, nutritional status, dung quality and, in particular, the timing of the copulation relative to a female's gonotrophic (egg ripening) cycle can explain most of the residual clutch size variation apparent in Fig. 1.

Hosken *et al.* (2002) recently showed a longevity cost of multiple mating in the laboratory in female yellow dung flies. Here we did not find that larger males inflict greater costs of reproduction on females in terms of clutch size. Although the mechanism is unclear, such an effect has been observed in some other insect species and may result from inter-sexual conflict (Pitnick, 1991; Arnqvist *et al.*, 1997). What remains is the long-term benefit females enjoy when mating with large males because body size is heritable and thus passed on to her offspring. We could not find short-term costs in terms of clutch size counterbalancing this benefit, and suggest that mating costs or benefits in terms of fecundity may be relatively rare compared with analogous effects on survivorship.

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