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# EFFECT OF BODY WEIGHT ON REPRODUCTIVE FITNESS IN *Spodoptera Litura* (LEPIDOPTERA: NOCTUIDAE)

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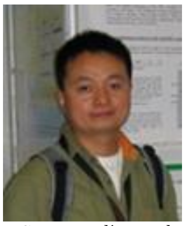

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## ABSTRACT

The exact nature and even existence of the balance between natural and sexual selection are still controversial. Body size is a key determinant of an organism's ecological and physiological properties. It is widely accepted that selection for higher fecundity is the main force behind the selection for larger body size. However, there are conflicting selection pressures operating on body size of both sexes in many organisms, for instance, natural selection for higher survival might reduce body size. In the present study, we found that in the common cutworm moth, *Spodoptera litura*, female fecundity and fertility significantly increased with her body weight, while male body weight or female–male weight interaction had no effect on female reproductive output. Results of this study also showed that heavier parents have heavier male and female offspring than those from lighter parents. Although not statistically significant, offspring from heavy and light parents showed lower survival rate than those from average weight parents.

**Contribution/Originality:** The paper's primary contribution is finding that heavier parents have heavier male and female offspring than those from lighter parents, i.e. body size is heritable in *Spodoptera litura*.

## 1. INTRODUCTION

Body size is a key determinant of an organism's ecological and physiological properties [1-5]. Larger females often have more eggs available for laying and are able to regenerate eggs faster when required than smaller ones [6, 7]. A growing list of empirical studies in Lepidoptera has demonstrated a positive correlation between female weight and fecundity [1-3, 8-11].

The reproductive advantages of being a large male are not as clear as those of large females. This may be because measurements of the reproductive success of males over their entire lifespan are extremely uncommon compared with females [12-14]. Nevertheless, large size has been used as an indication of "good quality" in males, such as having better genes and more ejaculate supply over smaller ones [15-18]. In some species of insects, larger males have a higher probability of obtaining mates [12, 19-22] and probably mate more often [12, 23-25].

It is widely accepted that selection for higher fecundity is a major evolutionary force that selects for larger body size (directional selection) in most organisms [1, 26-29]. Nevertheless, organisms do not increase in size continuously [27, 30, 31] because selection for large body size is eventually counterbalanced by opposing selective forces, such as higher mortality rates due to longer juvenile developmental times, resulting in stabilized selection for optimal intermediate size with maximum lifetime fitness (e.g. [32]). However, counterbalancing selection favoring smaller body size is often masked by the good condition of the larger organism and is therefore less obvious, particularly when the evidence for selection favoring larger body size is overwhelming [27].

The common cutworm moth, *Spodoptera litura* (Lepidoptera: Noctuidae) is a serious agroforestry pest worldwide [33, 34]. The aim of this section was to determine whether and how conflicting selection pressures act on body size in *S. litura* by testing two hypothesis (1) selection for higher reproductive success favors larger individuals [4] and (2) selection for higher survival favors smaller individuals [32]. To test these hypotheses, we carried out a series of experiments in the laboratory to determine whether larger individuals of sexes have higher fecundity, larger parents have larger progeny, and larger progeny suffer higher mortality rates during juvenile stage.

## 2. MATERIALS AND METHODS

### 2.1. Effect of Body Weight of Both Sexes on Female Reproductive Output and Offspring Fitness

Insect rearing, body weight weighing and categorizing followed the methods described in Li, et al. [35]. The effect of body weight on female fecundity and fertility was studied by confining 213 breeding pairs of 1-d-old moths individually for the duration of their lifespan in plastic boxes (25 cm long, 15 cm wide, 8 cm high). A complete factorial block design was used for this experiment, where each sex (factor) had three different weights: light, average and heavy. Thus, this experimental design produced nine treatments (3 female weights × 3 male weights) of breeding pairs (Table 1). Fecundity and fertility were recorded as described in Li, et al. [35].

**Table-1.** Number of *S. litura* breeding pairs in different bodyweight combinations

| Male class | Female class | n |
|---|---|---|
| Light | Light | 25 |
| Light | Average | 25 |
| Light | Heavy | 27 |
| Average | Light | 26 |
| Average | Average | 24 |
| Average | Heavy | 21 |
| Heavy | Light | 20 |
| Heavy | Average | 21 |
| Heavy | Heavy | 24 |

To test whether parental bodyweight affected offspring weight and survival, newly hatched larvae (< 24 h old) from three size combinations, light×light, average×average and heavy×heavy (male×female), were randomly selected and reared in plastic boxes, respectively. For each box or a replicate, 50 larvae were introduced into the box and reared under the same conditions as described in Li, et al. [35]. Ten boxes (replicates) were set up for each of the three weight combinations. Newly eclosed moths were collected and weighed. Survival rate (no. of adult moth/no. of larvae introduced) was recorded.

### 2.2. Statistics

Data on the effect of body weight on female fecundity and fertility were analyzed using a two-way analysis of variance (ANOVA) followed by Tukey's studentized range test. Offspring survival rate and body weight were analysed using a one-way analysis of variance (ANOVA) followed by Tukey's studentized range test. Data on survival rate were arcsine transformed prior to analysis. All analyses were made using SAS 9.1 (SAS Institute, Cary, NC, U.S.A.) [36]. Rejection level was set at $\alpha < 0.05$.

## 3. RESULTS

Results show that neither male weight nor female–male weight interaction had any effect on female lifetime fecundity ($DF = 2, 204$; $F = 0.93$; $P = 0.396$ for male weight, and $DF = 4, 202$; $F = 0.39$; $P = 0.815$ for female-male interaction) and fertility ($DF$ = 2, 204; $F$ = 0.93; $P$ = 0.396 for male weight, and $DF$ = 4, 202; $F$ = 0.37; $P$ = 0.769 for female-male interaction). However, heavy females had significantly higher fecundity and fertility than light and average females (Table 2).

**Table-2.** Reproductive output of *S. litura* females of different weights*

| Output | Female weight | | | | |
|---|---|---|---|---|---|
| | **Heavy** | **Average** | **Light** | ***F*** | ***P*** |
| Fecundity | 1307.9±118.2A | 1103.3±97.4B | 981.4±102.1B | 165.97 | < 0.0001 |
| Fertility | 1259.9±115.4a | 1056.3±102.1b | 945.4.1±96.3b | 155.21 | < 0.0001 |

* Numbers with different letters in rows are significantly different ($P$ < 0.05).

Heavier parents have significantly heavier offspring than lighter ones ($DF$ = 2, 105; $F$ = 79.95; $P$ < 0.0001 for male offspring and $DF$ = 2, 105; $F$ = 25.84; $P$ < 0.0001 for female offspring; Fig. 1). However, parents' body weight did not show significant effect on offspring's survival rate ($DF$ = 2, 27; $F$ = 0.47; $P$ > 0.05; Fig. 2) in *S. litura*.

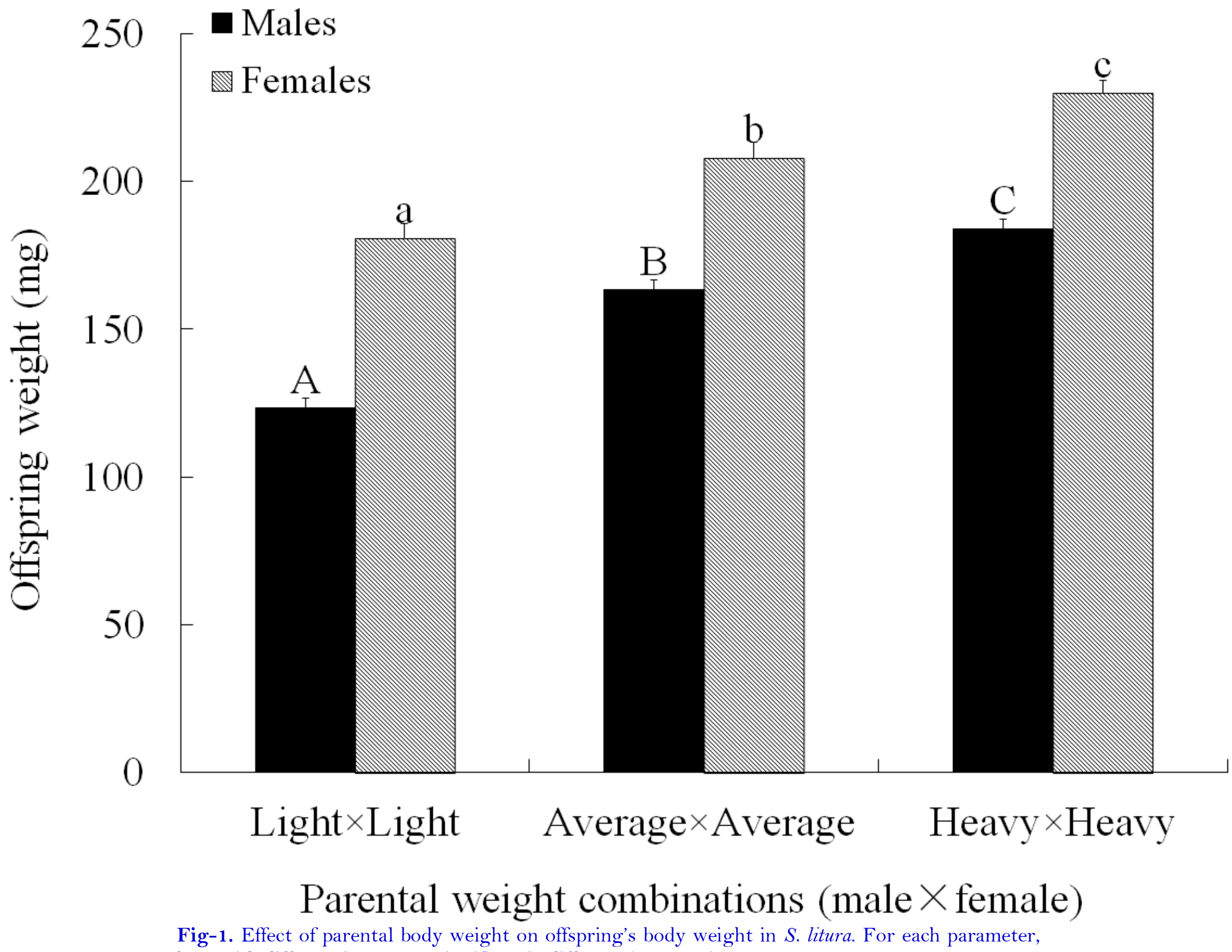


**Fig-1.** Effect of parental body weight on offspring's body weight in *S. litura*. For each parameter, bars with different letters are significantly different ($P$ < 0.05)

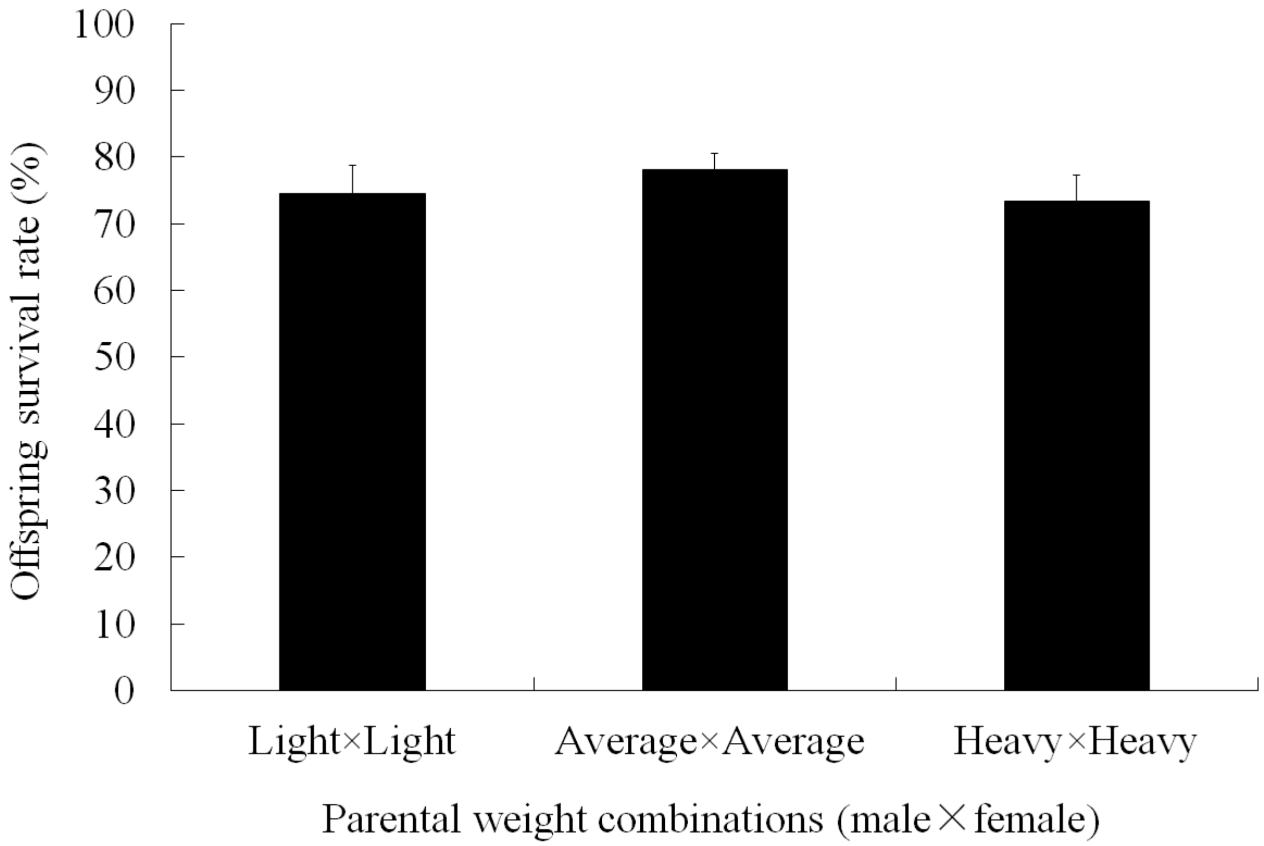


**Fig-2.** Effect of parental body weight on offspring's survival rate in *S. litura.*

## 4. DISCUSSION

Similar to many empirical studies in other insect species [1-3, 8-11] our study demonstrates that female fecundity and fertility significantly increased with her body weight. Consistent to Jiménez-Pérez and Wang [8] work on *Cnephasia jactatana*, the present study shows that male body weight or female–male weight interaction had no effect on female reproductive output in *S. litura*. These results support the notion that natural selection for higher fecundity is a major evolutionary force that selects for larger body size in females [1, 26-29].

The reproductive advantages of being a large male are not as clear as those of large females, which may be because measurements of the reproductive success of males over their entire lifespan are extremely uncommon compared with females [12-14]. Nevertheless, studies have revealed that large males may have better genes and more ejaculate supply [15-18] higher probability of obtaining mates [12, 19-22] and probably mate more often [12, 23-25] than smaller ones.

In the present study, we found that heavier parents have heavier male and female offspring than those of lighter parents (Fig. 1), i.e. body size is heritable in *S. litura*, which is consistent with the results of other studies (e.g. [37-39]). According to Fisher [40] genetic model, a female mate with a large male will have large offspring and thus will gain indirect genetic benefit because her large sons and daughters possess higher fitness [1, 3, 26].

Sexual conflict theory suggests that there are conflicting selection pressures operating on body size of both sexes in many organisms [41-45]. For example, in the Mediterranean flour moth, *Ephestia kuehniella*, heavy offspring from larger parents have lower survival rate than average and light ones, suggesting that natural selection for higher survival might reduce body size. In the present study, we found, although not statistically significant, offspring from heavy and light parents have lower survival rate (Fig. 2). To achieve a larger size, organisms have to grow for longer time or grow faster. Longer prereproductive period increases cumulative mortality due to predation, parasitism and starvation, giving nonzero mortality rates at all times [46, 47]. Faster growth also is likely to increase mortality rate because of higher metabolic demands under resource limitation [48, 49]. Moreover, *S. litura* is a protogynous species—females emerge earlier than males [50]. As a consequence, larger males of this species may have a mating disadvantage due to late reproduction because of possible longer juvenile development stage [27].

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**Competing Interests:** The authors declare that they have no competing interests.
**Contributors/Acknowledgement:** All authors contributed equally to the conception and design of the study.

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