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Polyandry as a Signal of Phase Shift in Female Desert Locust *Schistocerca gregaria*

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Abstract

The multiple mating by female (polyandry) is a widespread behavior in insect species. This behavior is known to be a kind of fitness maximization, but some case of sexual selection factors can explain the evolution of this behavior in relation with the phenotype plasticity model. In this paper, we analyze the role of polyandry in the reproductive success and in the phase shift process in the gregarious desert locust. In an applied perspective, knowledge on the reproductive success and in the phase shift process is essential to perform mass rearing for human food production. Our results suggest that multiple mating is not associated with fitness benefits. Polyandry acts as a signal of phase shift through offspring. We showed that hatchlings of gregarious females mated only once are smaller and green at 87.2% in first egg pods and produced the solitary form of the desert locust. The coloration of offspring in females mated with two males reaches only 15.2% of green forms versus 84.8% of mostly blacks. In this study, we showed that females mated more than two times with different males produce larger eggs, heavier, and black hatchlings characteristic of gregarious phase known in *S. gregaria*.

Keywords: polyandry, phase polyphenism, phenotypic plasticity, fitness, *Schistocerca gregaria*

1. Introduction

In males, the number of matings (polygyny) determines the reproductive success and the ability to transmit its own genes to the next generation [1, 2]. Things are less clear in females, as multiple matings (polyandry) represent a loss in time and energy [2]. Several hypotheses have been proposed to explain why natural selection had favored the evolution of polyandry in

animals [3, 4]. Polyandrous females may gain direct benefits in fitness maximization, genetic benefits, or reduction of harassment [5]. For example, polyandry stimulates ovulation [6], ensures fertilization, or brings nuptial gifts [2]. Genetic benefits could be paternity choice [6]), sex ratio manipulation particularly in haplodiploid insects [7], inbreeding avoidance by mixed paternity [8], and sperm stored renewal [3].

In *Orthoptera*, for female, multiple mating has many advantages [9]: preventing the females from sperm depletion [10], increasing the rate of oviposition [11–15], or providing material incorporated into eggs or female biomass [16, 17]. Since the 1950, it has been shown that desert locust copulation occurs frequently, and multiple copulation appears to serve mainly as a stimulant to egg-laying [18]. However, until now, adaptive significance of polyandry is poorly understood in *Schistocerca gregaria*. According to our previous results, multiple mating did not seem to be necessary for avoiding sperm depletion [19]. Three other hypotheses can be stated to explain polyandry in this species: (1) an increase of female fitness (fecundity, fertility, and lifespan), (2) an increase in offspring viability as observed in other species [20, 21], and (3) the provision of additional nutrients [22].

At the same time, the mechanisms underlying the phase polyphenism in desert locusts have been studied since many years and various aspects of this phenomenon have been clarified [23–30]. However, multiple matings and male harassment could be also an indication of overcrowding and thus of phase shift. In that context, the role of multiple mating for females in the phase polyphenism determination was never investigated in detail. It is the main objective of this work.

Recently, it has been discovered that progeny characteristics such as egg size, hatchlings body color are predetermined in the ovaries of the mother in *S. gregaria* [31–35]. They underlined a strong evidence of maternal effect controlling egg production and egg size [34, 35].

Green and small hatchings are solitarious locusts, whereas black and heavy hatchings are gregarious individuals [34–39]. In 1932, Faure has already suggested that small hatchlings appear from small eggs produced by solitarious form, whereas large hatchlings are from large eggs produced by gregarious form. Although eggs size alone is inadequate to explain completely the locust polyphenism phenomenon, it remains very important to understand if multiple-mating behavior may influence egg size and thereafter, phase shift.

In this study, we examined the adaptive significance of polyandry of desert locust and more particularly, the impact of multiple mating on phase shift and eggs biomass. In practice, we determined the effects of multiple mating on female fitness components (fecundity, fertility, female longevity, and offspring survival) and offspring phase (egg sizes hatchlings body color and body size).

As this species is usually consumed by human population [40] and may even be a source of dietary or therapeutic sterols [41], a better knowledge of its mating strategies may improve possible mass rearing systems.

2. Materials and methods

Under laboratory conditions, we tested the benefits for a female *S. gregaria* to mate with several males. Five treatments have been analyzed during this survey: a female mated with only one male, or successively with two, three, and four males. We also noted the effect of promiscuity on the fitness traits of a female in presence of four males after mating. As number of egg pods per females varies, we analyzed and compared only the two first egg pods that were laid.

2.1. Insect rearing

S. gregaria individuals were provided by the Laboratory of Entomology of the Zoological Institute of KUL (Leuven, Belgium). These individuals descend from locusts that were originally collected in Nigeria [42]. Rearing of gregarious *S. gregaria* was conducted in cages (50 × 60 × 80 cm) containing 100–200 individuals per cage. Rearing temperatures were 35 ± 2°C (12 h day) and 28 ± 2°C (12 h night) with a relative humidity of 60%. Locusts were fed on fresh cabbage leafs and rolled oats. Females and mature imago were collected in cages few days before sexual maturation and separated by sex to ensure virgin status.

2.2. Mating test and fitness analyses

Mature females were placed individually with mature males in experimental cages for mating. Pairs were observed until the male disengaged his genitalia and males were then removed to prevent re-mating. To ensure that mated females were inseminated, only females that copulated for more than 4 h according to our previous results [19] were used. Among these females, single-mated ($n = 23$) have been considered as control. Plastic cups filled with clean, moist sand were placed in cages to collect egg pods. Egg pods were incubated at 30°C, and cages were checked daily for the hatched larvae. After hatching, the oothecae were removed from the sand the number of nonhatched eggs was counted.

The total number of first-stage larvae plus nonhatched eggs represents the female fecundity and the proportion of hatched larvae and its fertility.

The once-mated remaining females were marked with a red permanent marker (Artiline®-70N) for the re-mating tests. Marked mated females were placed with a virgin male 24 h after the first mating. After the second copulation, females ($n = 26$) were allowed to lay eggs until death. Third ($n = 21$) and fourth ($n = 27$) re-mating events were conducted in the same way. In the last treatment, females ($n = 24$) were allowed to mate once and stay in contact with a group of four males until female death. Fecundity and fertility were examined as explained above.

Polyandrous females, used in re-mating tests, were monitored daily to measure their lifespan. Survival of offspring produced by multiple or a one-time-mated female was also determined until imaginal moult. Offsprings were maintained in the same conditions of rearing as explained above, and dead individuals were counted.

2.3. Effects of multiple mating on phase transformation

To characterize the phase transformation, we considered three parameters: egg size, hatchling body color, and body weight.

2.3.1. Eggs collection and eggs weight measurements

Three treatments were used: females mated with single males, females mated with two males, and females mated with three males.

After copulation, females were removed from copulation cage and held individually in small cages.

Plastic cups filled with clean, moist sand were placed in cages to collect egg pods. Cages were observed, and eggs were carefully collected from egg pods after 6–12 h. Eggs were washed with distilled water to remove ovipositing substrate or sand and then separated individually and put in marked Petri dishes (9 cm in diameter; 1.5 cm in height), according to the number of males that female has been mated. Eggs were then weighed individually using a Taledo balance at 0.1 mg.

2.3.2. Hatchling body color and body weight

Five treatments were used: females mated with single male, females mated with two males, females mated with three males, females mated with four males, and females allowed to mate once and stay in contact with a group of four males until female death. Mating tests and eggs incubation until hatchling were conducted as explained above. The body color of hatchlings was observed 6 h after hatching. Nymphs from single mating and multiple mating were divided into two hatchling color groups: green and black including dark spots to entirely black. Hatchlings from single and multiple matings were weighted 6 h after hatching using Ohaus Explorer balance (0.01 mg) to analyze body weight.

2.4. Statistical tests

Repeated measures analysis of variance (ANOVA) with multiple matings as a factor was performed on fitness data characteristics: fecundity, fertility, and hatchling body weight. Univariate analysis of variance was used to compare egg size produced by females mated with single male or more than one male. For offspring survival, the log-rank test was used to compare survival curves with GraphPad Prism. In all experiments, an assumption of normality of residuals was tested and statistic significance was 0.05.

3. Results

3.1. Fecundity

The fecundity did not differ between the treatment in first egg pods (one-way ANOVA $F_{4,116} = 0.37\ P = 0.82$), with a mean ranging from 60.9 ± 10 ($n = 23$) eggs in single-mated to 60.6 ± 8.3

($n = 26$), 59.2 ± 6.8 ($n = 21$), 59 ± 8.1 ($n = 27$), and 61.3 ± 8 ($n = 24$) eggs in multiple-mated treatment. Fecundity did not differ also in second egg pods (one-way ANOVA $F_{4,65} = 0.32$, $P = 0.85$) with a mean ranging from 58.9 ± 7.2 ($n = 11$) eggs in single-mated to 57.3 ± 7 ($n = 13$), 57.7 ± 6.8 ($n = 14$), 58.7 ± 9 ($n = 15$), and 56.2 ± 5.5 ($n = 16$) eggs in multiple-mated treatment.

3.2. Fertility

In two first egg pods, we found no significant difference among treatment. Fertility in first eggs pods did not differ between the treatment (one-way ANOVA $F_{4,116} = 0.49$ $P = 0.73$). For the first egg pods, a mean (±SD) of 55.4 ± 9.5 larvae were observed in single-mated ($n = 23$) and 55.8 ± 7.2 ($n = 26$), 53.4 ± 6 ($n = 21$), 54.1 ± 6.7 ($n = 27$), and 55.8 ± 7.3 ($n = 24$) larvae, respectively, in multiple-mated treatments; indicating the hatchling success of $90.9 \pm 5\%$ in single-mated, $92.3 \pm 4.1\%$ in two males mated, $90.4 \pm 5.5\%$ in three males mated, $91.6 \pm 4.7\%$ in four males mated, and $91.1 \pm 5.6\%$ in male promiscuity mating.

No statistical differences appeared among treatments in second egg pods (one-way ANOVA $F_{4,64} = 0.24$ $P = 0.91$). The hatchling success of $90.7 \pm 7.5\%$ in single-mated, $92.3 \pm 5.1\%$ in two males mated, $92.7 \pm 6.3\%$ in three males mated, $91.2 \pm 5.4\%$ in four males mated, and $92 \pm 5.1\%$ in male promiscuity.

3.3. Female longevity

The female life span after copulation was 37.1 ± 21.9 days (mean ± SD) in single-mated and 45 ± 18.6, 38.1 ± 18.5, 44.3 ± 23.1 days, respectively, in two, three, and four males mated treatments. The life span was 44.7 ± 23.8 if female mated stay with a group of four males.

There was no significant difference between the five treatments (one-way ANOVA $F_{4,116} = 0.76$, $P = 0.54$).

## 3.4. Offspring survival

With a log-rank test, no difference was found among offspring whose mother has been mated once or multiple times (Chi-square: 2.372 df: 5, $P > 0.05$). Survival rate at imaginal moult was 77% in single-mated offspring ($n = 44$), 73% in two males mated offspring ($n = 52$), 80% in three males mated offspring ($n = 50$), 79% in four males mated offspring ($n = 62$), 74% in one male and one female pair offspring ($n = 54$), and 85% in one female paired with four males offspring ($n = 60$).

3.5. Phase transformation

3.5.1. Eggs weight

The number of matings had a highly significant effect on the eggs weight (likelihood ratio test: 14.82, d$f = 2$, $P = 0.0006$). The females mated once have an estimated mean egg weight of 6.69 mg. Our results showed a significant relationship between eggs weights and the number of males mated with the females ($a = 0.47$ $t = 32.17$, $P < 0.0001$) (**Figure 1**).
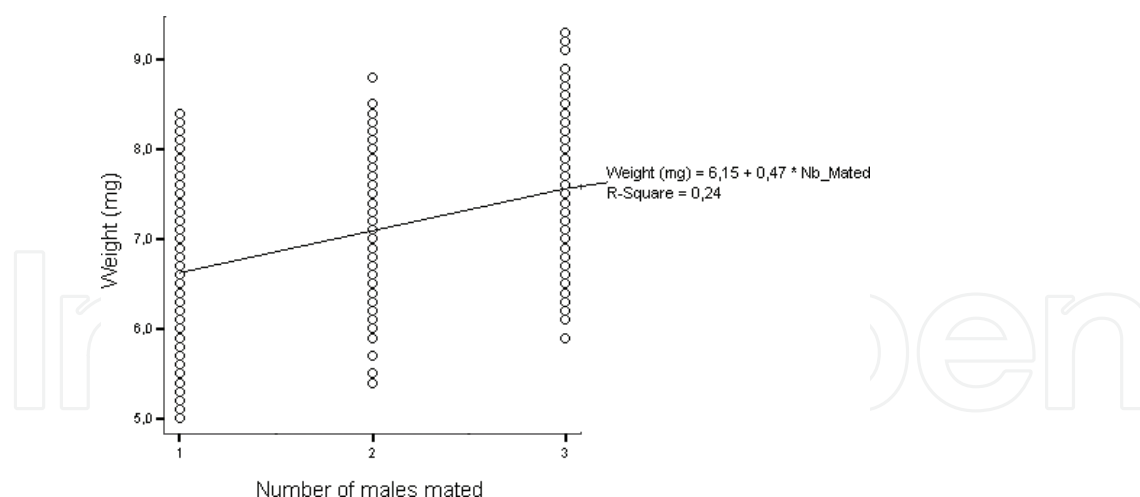
Figure 1. Relationship between number of males mated by the female and eggs weight.

3.5.2. Nymphs weight

Our results showed that hatchlings from single male-mated females are smaller than the hatchlings from the females mated with more than two males (Student-Newman-Keuls multiple comparisons test $P < 0.0001$). Hatchlings weight was 12.4 ± 1.3 mg, $n = 80$ (mean $\pm$ SD) in single-mated, 16.1 ± 1.8 mg, $n = 78$ in two males mated, 16 ± 1.2 mg, $n = 74$ in three males mated, and 15.9 ± 1.2 mg, $n = 77$ in four males mated treatment. Hatchlings weight of female mated and stay with four males was 16.2 ± 1.5 mg, $n = 76$.

3.5.3. Hatchling coloration

Hatchlings from single-mated female were green at 87.2% ($n = 23$) in first egg pods (**Figure 2**) and 85.5 ($n = 11$) in second egg pods (**Figure 3**). The coloration change in females mated with two males was only 15.2% green versus 84.8% black in first egg pods ($n = 26$) (**Figure 2**), 13.6% green
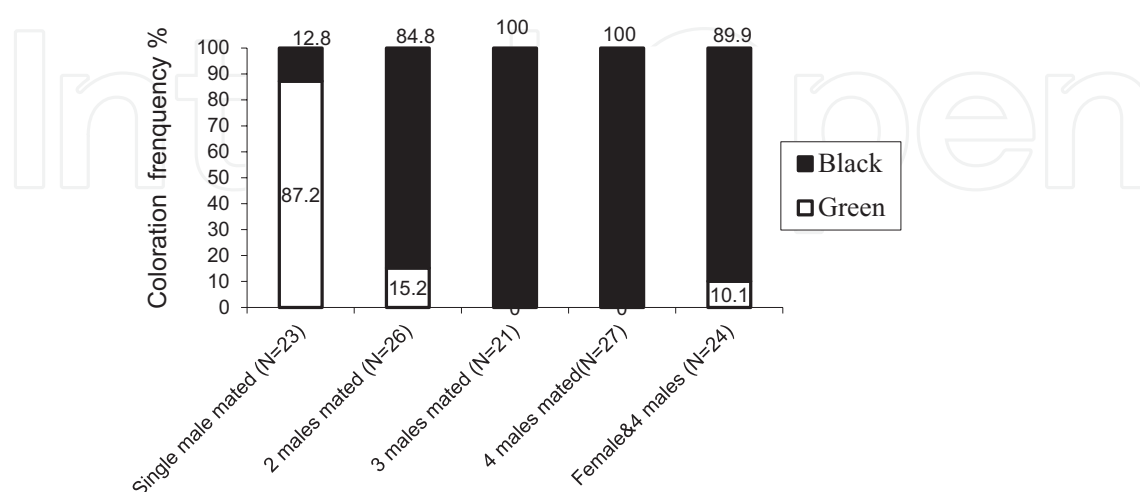
Figure 2. Hatchling coloration in first egg pods of gregarious desert locust *Schistocerca gregaria*: green hatchlings are represented as green color; black hatchlings are represented by black color. Numbers inside columns indicate the percentage of coloration. *N* indicates number of gregarious females tested.
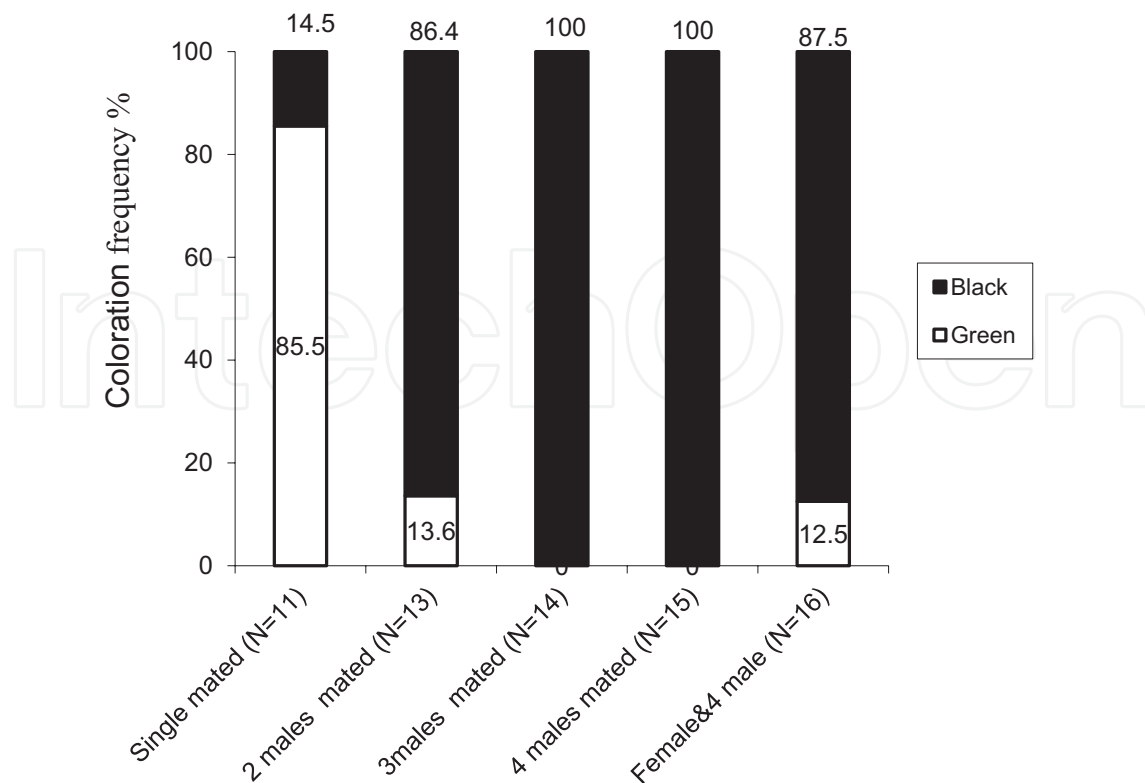
Figure 3. Hatchling coloration in second egg pods of gregarious desert locust *S. gregaria*: green hatchlings are represented as green color; black hatchlings are represented by black color. Numbers on columns indicate the percentage of coloration. *N* indicates number of gregarious females tested.

larvae versus 86.4% black larvae in second egg pods (*n* = 13) (**Figure 3**). Hatchlings from females mated with three and four males were 100% black in first and second egg pods (**Figures 2** and **3**).

4. Discussion

In this paper, we experimentally varied the number of copulations with different males to elucidate the significance of polyandry in gregarious desert locust *S. gregaria*. *S. gregaria* is a very important agronomic pest but presents also many possibilities in terms of food production with an average of 76% of protein content [40]. Our most important finding is that desert locust polyphenism may be induced by multiple matings that act as a signal of phase shift. We show that when a female is mated with two or more males, she produced a majority of black hatchlings with a higher biomass, which correspond to the gregarious phase. On the contrary, females mated only once produce smaller hatchlings with the green coloration of the solitary phase.

Many factors have been proposed to explain the parental effect by which desert locust control their progeny phase: (1) rearing density [18, 43]; (2) pheromonal factor derived from the accessory gland of the female parent [36–39, 44]; (3) ovary influence [32]. Multiple mating can be considered as a reliable signal of overcrowdings leading on a biparental influence on egg size and thus on phase transformation. The desert locust polyphenism is a case of phenotypic plasticity with a numerous convergent evolutionary events [27, 35, 37, 45]. Recent investigations on insect polyphenism have concluded that the expression of a polyphenism is governed by one or more

hormones secretion [46]. Thus fluctuations in the concentration of hormones can be a regulator of polyphenism expression. This concentration can be modulated by multiple mates in three main processes in desert locust: (1) males ejaculate signal; (2) males courtship and mating femur stimulating; and (3) male-derived nutrients. In the first hypothesis, males introduce sperm with a hormonal factor, which could have a gregarizing effect at some concentration level [4, 32, 37] or a hormonal factor that acts on the ovarioles to control egg size [35]. In the second hypothesis, female femur is stimulated during male courtship and mating [4, 32]; a stimulus is transmitted to the locust brain and causes a hormonal factor controlling egg size [35, 47]. Both processes are not mutually exclusive. Finally, male-derived nutrients during multiple mates could influence quantitatively egg size, polyandrous female receiving more nutrients, and produce larger eggs producing the gregarious forms. More experimental studies must be made to confirm these hypotheses. However, the egg weight significantly increases in the progeny of females mated more than once but irrespectively of the number of matings. This indicates that it is the fact to mate at least twice that induces a change in egg size and progeny color more than the number of matings. A potential nutritive contribution of each male ejaculate is probably thus not the main factor.

Polyandry is known to increase fitness [1, 48–51], and numerous cases were reported in *Orthoptera* [12, 15, 52–54]. However, except egg size, no fitness benefits could be underlined. Indeed, none of the life-history traits investigated (i.e., female fecundity, fertility, lifespan, and offspring survival) were improved by multiple mating. This could be linked to the fact that the number of eggs produced is less important than their size and the possibility it confers to hatchlings to migrate under stressful conditions. These results may help to improve mass rearing of this species as a source of food or nutrient.

In conclusion, we showed another form of phenotypic plasticity of desert locust in which the expression of numerous physiological, morphological, and behavioral traits occurs in response to multiple matings behavior.

Acknowledgements

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