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Research Article

Partial Sex-Role Reversal of the Pink Bollworm Moth (Pectinophora gossypiella)

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Complete and partial sex role reversals, where males are selective and females compete, are common in species in which males contribute more than just sperm to reproduction. In the Lepidoptera order, and particularly in the pink bollworm moth, both sexes invest significantly in reproduction. Therefore, we hypothesized that both females and males would exhibit some degree of mate selectiveness. Our study found that males delayed mating with smaller, less fecund females when larger, more fecund females were present in their surroundings. In contrast, males raised without exposure to females mated indiscriminately with both large and small females. Additionally, larger, more fecund females were more selective than their smaller, less reproductive counterparts. Even though large females exhibited greater selectiveness than small females, their selectiveness appears to be an indirect form of mate choice, as they did not choose based on the males' size but rather rejected a higher number of males overall.

Introduction

The different reproductive roles of males and females have long captivated researchers in the field of sexual selection, tracing back to Darwin's pioneering work[1]. Darwin observed that typically, males compete for access to females, while females are generally selective. This was initially explained by the theory of female parental investment[2]. Trivers further posited that if males contribute more to the offspring than females, males are expected to be the choosier sex, with females becoming more competitive. Male investment in reproduction can take various forms, such as courting, providing costly ejaculates, or offering nuptial gifts to females[3][4][5][6][7][8][9]. Indeed, complete and partial sex role

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reversal, where males are choosy and females compete, is frequently observed in species where males contribute in various ways beyond merely providing sperm to the female[10][11][12][9][13].

In the Lepidoptera, both males and females can exhibit selectivity[5][6]. In most moth species, sexual communication is initiated by pheromones emitted by the females and perceived by conspecific males[14]. The female's volatile sex pheromone attracts males from long distances and elicits males' courtship behaviors[15]. Female sex pheromones are costly and condition-dependent and serve as an honest signal of the female's quality[16]. There is evidence that the pheromone amount and blend in the female's gland changes in relation to her age, size, and hunger status[17][18].

Given that females have limited reproductive resources[19][20], they may be selective in choosing males they encounter[21][22]. Upon detecting a pheromone-emitting female, the male approaches and initiates courtship, typically using visual, chemical, or tactile signals, depending on the species. In some species, these cues allow the female to assess his quality.[23][24]. During courtship, females may seem passive, but receptive females often adopt typical postures that facilitate coupling[5][6]. One example of female moths that are choosy of males is the noctuid moth *Chloridea virescens,* in which females actively accept or reject courting males and prefer to mate with larger males[25]. Female selectivity may vary according to their quality, with higher-quality females often being more selective[26].

Male choosiness is expected in moths. During mating, male moths provide females with a spermatophore containing sperm and additional secretions that may offer protection to the female or eggs, as well as supplemental nutrients. Both sperm, additional secretions, and nutrients are limited resources and depend on the male's condition, size, age, and mating history[27][5][6][28][25][29]. Female fecundity is typically linked to body weight and size[30], so if males are selective, they are likely to prefer larger females. Examples of selective male moths include the Mediterranean flour moth, *Ephestia kuehniella*[31], the Winter moth, *Operophtera brumata*[32], and the pink bollworm moth (*Pectinophora gossypiella*) which, when given a choice, prefer larger, better fed and younger females[18]. Selectiveness based on female size has also been demonstrated in the European berry moth (*Lobesia botrana*) where males allocate larger ejaculates to larger females compared to smaller ones[29].

Since the pheromones of the female moths disclose their quality[16][18] and males are often selective, inferior females may face difficulty attracting a mate when competing with preferred females. Female moths are known to detect their species' sex pheromone and are therefore likely to be aware of the presence of competing females[16][33][34]. Inferior individuals may adopt alternative strategies to attract mates when competing with superior conspecifics[35]. One such strategy is when females adjust their calling times to reduce competition with other females. This behaviour has been described as an alternative strategy in several species of moths*:* *Helicoverpa armigera* moths infected with the *Ophryocystis elektroscirrha*-like parasite, which reduces their reproductive success, begin calling significantly earlier when housed with uninfected females. This may be an attempt to reduce competition and increase their mating opportunities[36]. The onset of the calling period of the female *Platynota stultana* moth, as well as that of *Agrotis ipsilon* [37] and *Chilo suppressalis*[38], advances with age, suggesting that older, less preferred females increase their chance of mating by early calling, reducing the competition with younger females[39](.

Pink bollworm females predominantly call for males in the second half of the night[40]. Once a male detects a desired female, he begins courting her by vibrating his wings and tapping her extended ovipositor with his antennae. Non-receptive female pink bollworm moths are known to escape from males that try to mate with them[41].

We observed that small female moths begin mating later than larger females. This led us to hypothesize that (1) small pink bollworm females initiate calling later at night to minimize competition with larger, more preferred females. Alternatively, or additionally, (2) male moths delay mating with less fecund small females in favor of larger, higher-quality females. We also hypothesized that both males and females would exhibit selectiveness in mate choice. Uncovering how both sexes navigate mate selectiveness in the pink bollworm moth could provide new insights into the complex strategies of sexual selection. This research uniquely explores the intricate interplay between male and female mate choice. By distinguishing between the two, it provides new insights into moth reproductive strategies, thereby contributing to our broader understanding of sex role evolution.

Methods

Breeding and maintenance

Pink bollworm moths were reared in climate-controlled rooms at 25±1°C, with a 14:10 light: dark cycle and 60% relative humidity, at our Department of Entomology.. Larvae were fed an artificial diet (Stonefly Heliothis diet, Ward's Science) and separated by sex based on the presence or absence of a black line on the 6th abdominal segment, indicating developing testicles in males. Males and females were housed in separate cages during the final larval stage to prevent mating. Adult moths were provided with a 10% sugar solution *ad libitum*.

Experimental design

Experiment 1. Causes of Delayed Mating in Small Females

To investigate why small females begin mating later than large females, we compared the initiation time of mating between large and small females across three treatments:

Treatments description:

1. **Moths reared all together:** Large females, small females, and males were reared in separate net cages within the same room (*n* = 10 trials).
2. **Females Separately:** Large and small females were separated into different rearing rooms together with males, so that small females were unaware of large females and vice versa. Participating males were reared with females of all sizes (*n* = 10 trials).
3. **Males Separately:** Participating males were reared in the absence of females. Large and small females were reared in different net cages together in the same room with non-participating males. In this treatment, males were unaware of the female range of sizes before the experiment, but females were exposed to males and females of all sizes (*n* = 10 trials).

Small and large females were obtained by separating female pupae into two size groups: large females (0.017–0.022 g) and small females (0.007–0.011 g). Medium sized females were excluded from the experiment. Males were not separated by size and were collected randomly before the experiment. Emerged adult moths were sorted daily into age-based net cages (20X20X20 cm). Virgin male and female moths, 3–4 days old, were used for the experiment.

For each trial, we used two groups of 40 randomly collected males. One group of males was presented with 20 large females, and the other was presented with 20 small females. Each group was observed in a separate dark room at 25°C simultaneously. All trials began 3–4 hours before "sunrise”. The mating starting time for each couple was recorded, and each couple that began mating was placed in a glass tube inside the cage, plugged with cotton wool, allowing other moths to continue sensing their presence. We recorded the mating initiation time until half of the females in the cage had mated.

Statistical analysis

For each trial, mating initiation was measured using two variables:

1. **Time until half of the females (i.e., 10 out of the 20 females) began mating.**
2. **Mating magnitude during the first 15 minutes.** Females were graded based on when they began mating, from 0 (did not mate within 15 minutes) linearly to 15 (mated within the first minute of the experiment). Grades were summed for all 20 females of the trial.

Two-sided paired samples *t*-tests were used to compare the mating initiation between the large and small females within each treatment, for each of these two variables.

Experiment 2. Females' choosiness

To investigate whether female choosiness depends on their own size and the sizes of available males, we conducted mating trials by pairing small and large females with either small or large males and observed which males were accepted. To minimize male choosiness affecting female behavior, males were reared separately from females to ensure they were unfamiliar with female size variations prior to the experiments and were therefore indifferent to female sizes (based on the results of Experiment 1). The experiment included the following four treatments:

Treatment description

- 5 large females with 10 large males (*n* = 15 trials),
- 5 large females with 10 small males (*n* = 15 trials),
- 5 small females with 10 large males (*n* = 15 trials),
- 5 small females with 10 small males (*n* = 17 trials).

Female and male pupae were weighed and separated into two size groups: large (0.017–0.022 g) and small (0.007–0.011 g). Medium-sized pupae were discarded. Emerged adult moths were further separated daily into age-based net cages (20×20×20 cm). Virgin moths, 3-4 days old, were used for the experiment.

In each trial, we placed 5 females with 10 males in a cage. We recorded the number of successful and unsuccessful mating attempts. An attempt was deemed unsuccessful if a male approached a calling female, courted her, and failed to mate for more than 5 minutes. Each trial lasted 40 minutes.

Statistical analysis

Acceptance was defined as the proportion of successful mating events relative to the total number of mating attempts made by males. For each treatment, this measure was calculated as the ratio of the total number of accepted matings by females to the total number of male attempts, summed across all *n* trials for that treatment. Due to significant deviations from normality of the data, we employed bootstrap procedures to test the differences in acceptance between large and small females within each of the two male size categories.

Ethical Note

The pink bollworm moth (*Pectinophora gossypiella*) is a well-known agricultural pest. Consequently, research involving this species typically does not require specific ethical permits. Nonetheless, all experimental procedures were conducted in adherence to ethical standards. The insects were reared in climate-controlled rooms maintained at a constant temperature of 25°C and were consistently provided with appropriate food corresponding to their developmental stages. Throughout the study, the moths were handled gently and with care. After mating trials, they were released outdoors. At no point were the insects harmed or subjected to detrimental conditions.

Results

Experiment 1. Causes of Delayed Mating in Small Females

1. The time until half of the females began mating

Treatment 1: When males and females were all reared together so that females had full information about the sizes of their female competitors, and males had full information regarding the different sizes of available females, the time until half of the small females began mating was significantly longer than the time until half of the larger females began mating (p = 0.040, Table 1, Figure 1).

Treatment 2: When small females were reared apart from large females so that small females were unaware of the presence of larger, superior competitors, and large females were unaware of the small, inferior females, but the males had full information about the different sizes of available females, the time until half of the small females began mating was also significantly longer than the time until half the larger females began mating (p = 0.036, Table 1, Figure 1).

Treatment 3: When females were reared together, but males were reared separately to ensure they were unaware of the presence of higher- or lower-quality females, there was no significant difference in the time until half of the females, whether large or small, began mating (p = 0.248; Table 1, Figure 1).

2. Mating magnitude during the first 15 minutes

Treatment 1: When all females and males were reared together, large females scored slightly higher points (based on the timing of when they began mating) than small females, although this difference was not statistically significant (p = 0.064; Table 1, Figure 2).

Treatment 2: When small and large females were reared separately, large females scored significantly higher points than small females ($p = 0.010$, Table 1, Figure 2).

Treatment 3: When males were reared apart from females, the mating magnitude of large and small females did not differ significantly ($p = 0.912$, Table 1, Figure 2).

	Time until half of the females started mating (Small vs. Large)		**Mating magnitude during the first 15 minutes (Large vs. Small)**	
Reared all together	$t_9 = 2.403$	$p = 0.040$ $D = 0.760$	$t_9 = 2.107$	$p = 0.064$ $D = 0.666$
Females separately	$t_9 = 2.457$	$p = 0.036$ $D = 0.777$	$t_9 = 3.258$	$p = 0.010$ $D = 1.030$
Males separately	$t_9 = -1.235$	$p = 0.248$ $D = 0.391$	$t_9 = -0.113$	$p = 0.912$ $D = -0.036$

Table 1. Paired-sample *t*-tests were used to analyze the time until half of the females started mating and the mating magnitude during the first 15 minutes. *p*-values are for two-tailed tests. *D* denotes Cohen's *D* effect size.

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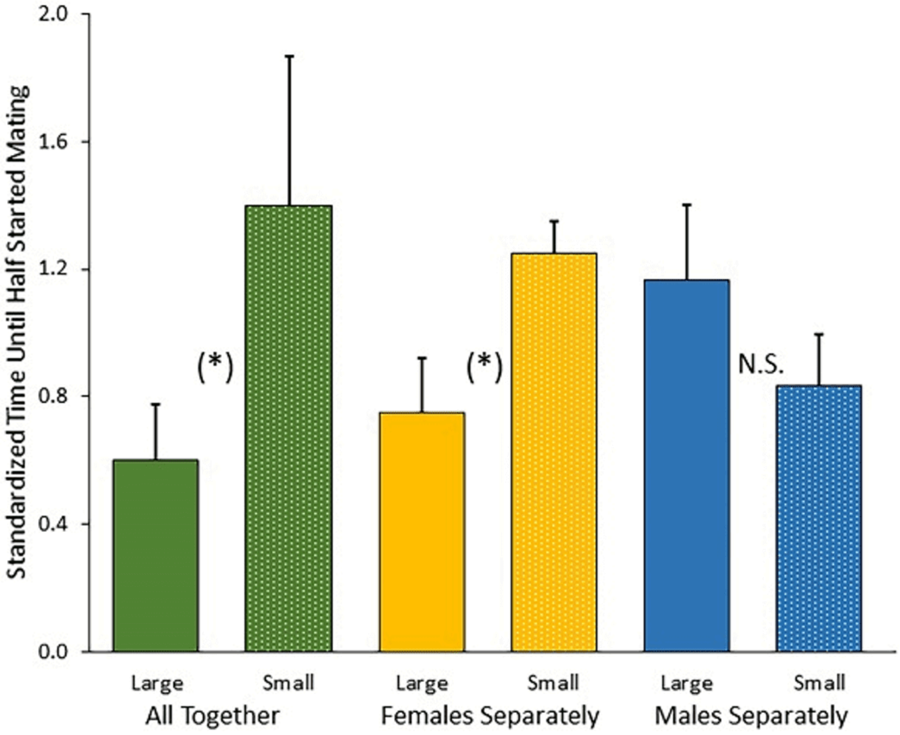

Figure 1. Time until half of the females started mating. For each treatment, Time was standardized by dividing it by the average time of all trials of that treatment. (*): $0.01 < p \leq 0.05$; N.S.: $p > 0.05$.

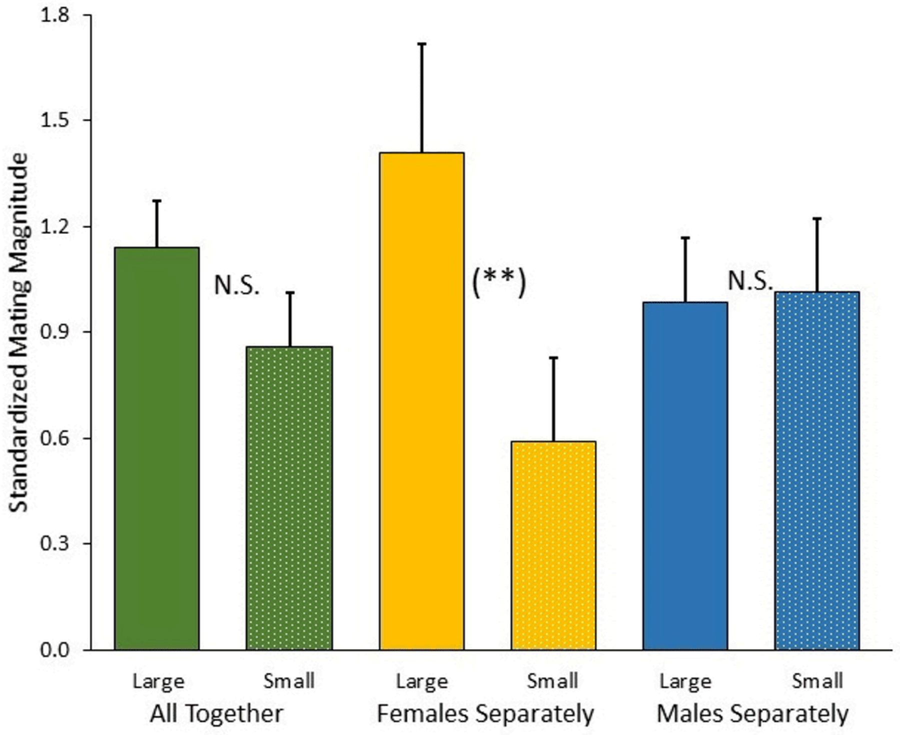

Figure 2. The Mating Magnitude (see text). For each treatment, Mating Magnitude was standardized by dividing it by the average Mating Magnitude of all trials of that treatment. (**): $p \leq 0.01$; (*): $0.01 < p \leq 0.05$; N.S.: $p > 0.05$.

Experiment 2. Females' choosiness

In both treatments where females were presented with large males, small females accepted males at a higher rate than large females (two-tailed p = 0.008). Similarly, in the treatments where females were presented with small males, small females also accepted males at a higher rate than large females (two-tailed p = 0.031). Each comparison was conducted using the bootstrap method with 1,000 simulated samples (Table 2).

	Large Males	**Small Males**
Large Females	12.08%	13.55%
Small Females	55.17%	36.49%

Table 2. Percentage of females' acceptance of male mating attempts

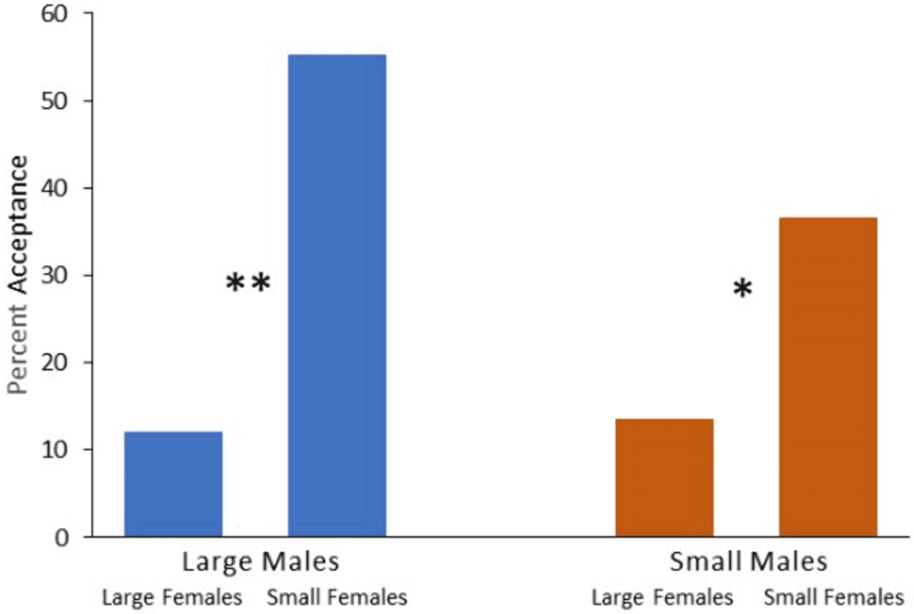

Figure 3. Percent of males mating attempts accepted by females of different sizes. In blue, attempts by large males and in brown, attempts by small males. (**): $p \leq 0.01$; (*): $0.01 < p \leq 0.05$.

Discussion

Mate choosiness varies between sexes across different species, primarily due to differences in their reproductive investment[2][42]. Both females and male moths have restricted amounts of reproductive resources: Female and male gametes are limited and are not renewable[27][28], males invest energy in producing a spermatophore[5][6][43], and sex pheromones of the female is costly[16]. Accordingly, our findings have demonstrated a partial sex role reversal in the pink bollworm moth, with both females and males exhibiting selectivity when choosing a mate. Males delayed mating with smaller, less preferable females when both small and large females were present. Interestingly, males that had not been exposed to female volatiles since pupation mated with both large and small females at similar rates when presented with either option as adults.

Females in many moth species are known to detect their own species-specific pheromones and adjust their calling behavior based on the perceived risk of competition for mates and resources[17][44][45]. Based on this, we hypothesized that small pink bollworm moth females delay their calling to reduce competition with larger, more attractive females. However, we rejected this hypothesis, since, when small females were reared separately from large females, thus limiting their awareness of potential larger competitors, they still initiated mating significantly later than the large females. Because males and females initiated mating simultaneously when males were reared separately from females, unaware of any size differences amongst females, we accepted the second hypothesis whereby males delay mating with smaller females in anticipation of larger, more fecund females when they are aware of their presence in their environment.

To assess female selectivity, we introduced males that had not been exposed to females and therefore lacked a preference for female size. This approach minimized male choosiness, enabling us to focus on the selectivity exhibited by females. We found that larger females exhibited greater choosiness compared to smaller females. While larger females generally rejected all males, smaller females were more accepting of males in general, showing some preference for larger males over smaller ones. Female mate choice can vary depending on their current physical condition. Females in better condition may exhibit stronger preferences and invest more time and energy in evaluating potential mates[46]. For example, female *Schizocosa* wolf spiders that were fed on a higher-quality diet were more selective in accepting courting males than those reared on a lower-quality diet[47]. Similarly, reproductive aging due to delayed mating decreased the choosiness of female cockroaches (*Nauphoeta cinerea*)[48].

Although large pink bollworm female moths rejected males significantly more often than small females, their selectivity was not based on the males' size. Instead, they rejected over 85% of large males and over 85% of small males within the first hour of mating (the duration of our experiment), while small females rejected only about 45% of the large males and about 63% of the small males. The observed tendency of large females to reject males may serve as an indirect strategy to select higher-quality mates. By delaying mating, these females provide larger males the opportunity to compete, thereby increasing the likelihood of mating with superior partners. Indirect mate choice fosters competition among the opposite sex, enhancing the chances of mating with a successful competitor, thereby allowing females to mate with superior genotypes without directly choosing a mate.[49] For example, female northern elephant seals (*Mirounga angustirostris*) enhance their chances of mating with high-ranking males by typically rejecting early mating attempts without distinguishing between subordinate and dominant males. Their loud protests trigger male competition, favoring dominant ones over lower-ranked rivals[50]. Another example of indirect mate choice is seen in female eastern gray squirrels (*Sciurus carolinensis*), who attract many males during their single day of estrus. After being pursued and cornered by males, the female bolts and avoids them. She then stays motionless, usually low on a tree trunk, and the first male to find her after these breakaways, mates with her[51].

Female moths use sex pheromones to attract potential mates, with these signals evolving alongside highly sensitive receptors in males. The pheromones draw many mates, encourage intra-male competition, and triggering rivalry among males[49]. In the pink bollworm moths, males are also attracted to mating pairs[52]; personal observations, submitted). Males are often observed interrupting and attempting to displace the first male in order to mate with the receptive female (personal observations, submitted). The combination of pheromone signaling, a general rejection of arriving males, and synchronized mating times among females can lead to indirect mate choice, encouraging competition and allowing larger, more competitive males to outcompete rivals and succeed in mating.

Our research uncovers an intriguing pattern in the mating dynamics of pink bollworm moths, revealing a partial sex role reversal in mate selection. Both males and females display selective behavior: males delay mating with smaller females when larger options are available. Small females generally accept most males, showing a slight preference for larger ones. In contrast, large females often reject most males initially, a strategy likely aimed at securing higher-quality mates. In conclusion, our findings offer new insights into the complexities of mate choice in this species, enhancing our understanding of its reproductive strategies.

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