

Article

Mating Behavior and Sexual Selection in *Monochamus saltuarius* (Gebler)

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Abstract: The Sakhalin pine sawyer *Monochamus saltuarius* (Gebler) (Coleoptera: Cerambycidae) is a new vector of pine wood nematode in China, which has caused huge economic losses in the forestry industry. The mating process of *M. saltuarius* has been described in detail. However, mate choice and sexual selection in this species are not fully understood. In this study, we quantitatively evaluated the characteristics associated with contact between the sexes in mating and inferred the sex-specific characteristics under selection. We detected positive correlations between the morphological characteristics of females and males. Most female traits and all male traits differed significantly between mated and unmated individuals. The results of this study provide evidence for the selection of the mating preferences in *M. saltuarius*.

Keywords: mating behavior; sexual selection; elytra length; antennal length; hind tibia length



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1. Introduction

Darwin [1] formulated the concept of sexual selection, which included two principal mechanisms: intrasexual competition (usually between males) for breeding access and mate choice (usually by the female) based on desirable traits in the opposite sex. Sexual selection theory predicts that females should be the more selective sex in choosing mates and show a preference for particular sexual ornaments and signals [2] due to their relatively greater investment in gametes [3]. Where females can choose a male among numerous males, they will commonly increase their fitness and that of their offspring by selecting genetically compatible mates, or mates with ‘good genes’, which the offspring may inherit [4].

Increasing evidence now shows that males can be choosy, too, even in apparently unexpected situations, such as in the absence of male parental care [5,6]. Males may exhibit mate choice for a variety of reasons, including seeking mates with greater fecundity [7]. For males, reproductive success tends to increase with the number of mates acquired [8], while males will inevitably reject available females if they lack the resources required to mate with them. Therefore, mate choice comprises not only decisions about whether to mate but also how many resources to allocate to each mate or mating [9]. In fact, regardless of whether the mate choice occurs in males or females, it is a central component of sexual selection theory [1,8,9], and understanding mate choice and the underlying preferences that lead to choice is, therefore, central to understanding sexual selection.

Sexual selection can lead to the rapid diversification of reproductive traits in both males and females. Such selection is often proposed as an explanation for the evolution of external morphological traits that confer a mating advantage upon their carriers of different genders. Sexual selection has diverse effects on individual traits, either by promoting success in competition for mates or by facilitating mate attraction and copulation. These

traits can either be morphological or behavioral in nature and are subject to selection pressures [10].

The Sakhalin pine sawyer *Monochamus saltuarius* (Gebler) (Coleoptera: Cerambycidae) is widely distributed in Central and Eastern Europe, Siberia, the Russian Far East, and East Asia [11]. In China, *M. saltuarius* is mainly distributed in the Heilongjiang, Jilin, Liaoning, Hebei, Shaanxi, and Gansu provinces, Inner Mongolia Autonomous Region, and Xinjiang Uyghur Autonomous Region [12]. *M. saltuarius* has one generation per year in China and overwinters as larvae in the xylem canals of their host trees [13]. The second instar larvae of *M. saltuarius* feed on the sapwood, and the fourth instar larvae begin to drill the xylem [13]. The number of invasion holes of *M. saltuarius* increased first and then decreased with the increase in the trunk height of the host trees [14]. *M. saltuarius* began to emerge in early May; adults feed on the cortex of host tree branches to supplement nutrients and then spread to mate and lay eggs [15]. The oviposition groove of the female is a long prismatic. After eclosion, the *M. saltuarius* entered the stage of supplementary nutrition, gnawing bark and needles on host trees to cause wounds [16]. In the Japanese pine sawyer *M. alternatus* Hope, an insect vector of the pine wood nematode *Bursaphelenchus xylophilus* (Steiner and Buhner) Nickle has higher CO₂ concentrations, resulting from the respiration cycles and bursts of CO₂ that occur during maturation feeding, which drives the pine wood nematode off its insect vector [17]. Plausibly, a large number of pine wood nematodes carried by *M. saltuarius* were immediately introduced into healthy pine trees through the wound in the same way. Pine trees usually die 2–3 months after being infected by pine wood nematodes. The most important management action to control the pine wilt disease spread is based on the felling and elimination of declining trees during winter since the removal and destruction of these trees during winter months (before pine sawyer emergence) eliminates the pine wood nematode and the immature stages of pine sawyers that are still inside the pupal chambers [18]. *M. salternatus* is mainly spread by flight; the longest flight distance of *M. saltuarius* adults is about 5 km throughout their whole life cycle [19]. As a vector insect, *M. salternatus* has a great ability to transmit pine wood nematodes, which brings challenges to the prevention and control of pine wilt disease [12].

M. saltuarius mainly colonizes Korean white pine *Pinus koraiensis* Sieb. et Zucc., Chinese pine *P. tabulaeformis* Carr. [20], and Mongolian Scots pine *P. sylvestris* var. *mongolica* Litv. [21]. In 2018, *M. saltuarius* was first identified as a new vector of pine wood nematode in China, which has resulted in huge economic losses to forestry production and development [16,22–24]. The mating process of *M. saltuarius* has been characterized in detail. Mating in the species could be divided into three stages: pair bonding, ejaculation, and post-copulatory guarding. The mating and spawning behaviors of *M. saltuarius* have circadian rhythms. The male remains motionless with an outstretched antenna or shows slight movement. The male mounts the approaching female upside down or turns the female so that they are facing the same direction. The male then grasps the female's metathorax with the fore tarsal and holds the metasternum on either side. The male genitalia protrude during copulation. During mating, the male grasps the back of the female firmly using the forelegs and midlegs, with the hind legs on the bark of the tree [25,26].

We observed mating behavior in the species to determine the sequence and key body parts related to mate evaluation in both sexes. Next, we inferred sexually selected traits based on mate choice experiments, recorded successful matings, and measured traits that were in frequent contact between the sexes prior to insemination.

2. Materials and Methods

2.1. Sample Collection and Rearing Conditions

Wood segments (length: 57.6–74.3 cm) of *P. koraiensis* containing *M. saltuarius* larvae were collected from Dahuofang Forest Farm, Fushun City, Liaoning Province, China. (41°56'23.028" N, 124°13'3.925" E). The two ends of the wood segments were sealed with wax in order to prevent water loss. The temperature and relative humidity in the room were controlled at 22.3 ± 2.3 °C and 33.0% ± 7.0%, respectively. To ensure that

M. saltuarius was unmated, newly emerged adults were obtained daily and placed in 800 mL plastic boxes. Individuals were fed cotton bales soaked in water with honey (10% concentration) [27] and young shoots of *P. koraiensis* separately, and foods were replaced every other day. Females of *M. saltuarius* are sexually mature at approximately 7-day-old post-emergence [28]; 14-day-old virgin females were used in the mating test. Males of *M. saltuarius* are sexually mature after emergence [29]; thus, 5-day-old virgin males were used in the mating test.

2.2. Mating Test

To determine female traits associated with mating success and to identify traits that might be affected by directional selection, mating was allowed at a female-biased sex ratio with a total of 45 replicates. To observe mating behavior, one 5-day-old virgin male and two 14-day-old virgin females were placed in an 800 mL plastic container for each replicate. To establish the male traits linked with successful mating and to identify characteristics that may undergo directional selection, mating experiments were carried out, releasing one 14-day-old virgin female and two 5-day-old virgin males in each replicate. Observations are usually conducted from 12:00 to 14:00, the time period coinciding with the peak period of mating activity of *M. saltuarius* [25]. A total of 45 replicates were conducted in this experiment. All individuals in the mating test were photographed, and body weights were measured before the mating test.

2.3. Morphological Measurements

ImageJ (NIH, Bethesda, MD, USA) was used to measure morphological parameters based on photos like body length, antennal length, elytra length, elytra width, head width, abdomen length, fore femur length, fore tibia length, fore tarsal length, hind femur length, hind tibia length. All length and width measurements reported here are the maximum values. For example, body length was defined as the length between the head and the abdomen.

2.4. Data Analyses

An index of body size for both sexes was generated by a principal component analysis based on five morphological characters of body parts: body length, elytra length, elytra width, head width, and abdomen length. A scatter plot of the relationship between body weight and body size was generated. We checked the normality of morphological data and conducted a multicollinearity analysis. To determine whether these morphological features are related to each other in both sexes, Spearman correlation coefficients were evaluated, and a Spearman correlation matrix was generated. To determine whether a morphological feature differs significantly between selected and unselected individuals, independent-sample *t*-test was performed when data satisfied the normal distribution. For the data that did not satisfy the normal distribution, we carried out $\ln(x)$ transformation before independent-sample *t*-test. Mann–Whitney *U* test was performed for the data that still did not meet the normal distribution after data transformation. Values of $p < 0.05$ indicated that a morphological feature was significantly correlated with mating success. Excel 2019 (Microsoft, New York, NY, USA) and IBM SPSS 23 Statistics (IBM, Armonk, NY, USA) were used for data processing and analysis, and Origin 2023b (Origin Lab, Northampton, MA, USA) was used to draw plots.

3. Results

3.1. Sexual Selection on Female Traits

Mating was successful in all 45 replicates. Based on multicollinearity analysis, only the variance inflation factor (VIF) value for body length (10.667) was more than 10 (Table 1), so we removed it [30]. Spearman correlation coefficients showed there were positive correlations among the 12 traits measured, and the correlation coefficient between antennal length and elytra length was highest at 0.817 (Table 2). The first principal component for females explained 68.984% of the total variance and was regarded as an index of the

body size of females (Table 3). For females, body size PC1 = $0.517 \times \text{body length} + 0.475 \times \text{elytra length} + 0.424 \times \text{elytra width} + 0.443 \times \text{head width} + 0.362 \times \text{abdomen length}$. Female body weight and female body size were positively correlated ($r = 0.338$, $p < 0.01$, $n = 90$ females) (Figure 1a).

Table 1. Multicollinearity analysis for morphological traits in females.

	B	SE	Beta	<i>t</i>	<i>p</i>	VIF
Weight	0.984	0.025	1.013	39.020	0.000	1.581
Body length	−0.004	0.002	−0.154	−2.291	0.025	10.667
Antennal length	0.002	0.001	0.126	2.598	0.011	5.527
Elytra length	-2.896×10^{-5}	0.001	−0.001	−0.025	0.980	4.493
Elytra width	−0.006	0.004	−0.051	−1.584	0.117	2.415
Head width	0.007	0.004	0.064	1.789	0.078	3.020
Abdomen length	0.000	0.002	−0.004	−0.082	0.935	4.298
Fore femur length	0.001	0.003	0.009	0.262	0.794	2.757
Fore tibia length	−0.007	0.002	−0.103	−2.928	0.004	2.887
Fore tarsal length	−0.004	0.004	−0.039	−0.871	0.386	4.723
Hind femur length	0.000	0.002	0.004	0.112	0.911	2.949
Hind tibia length	0.005	0.002	0.077	2.283	0.025	2.700
Hind tarsal length	0.006	0.004	0.060	1.266	0.209	5.243

Table 2. Spearman correlation matrix for morphological traits in females (* $p < 0.05$; ** $p < 0.01$).

	Weight	Antennal Length	Elytra Length	Elytra Width	Head Width	Abdomen Length	Fore Femur Length	Fore Tibia Length	Fore Tarsal Length	Hind Femur Length	Hind Tibia Length
Antennal length	0.089										
Elytra length	0.097	0.817 **									
Elytra width	0.355 **	0.594 **	0.583 **								
Head width	0.083	0.686 **	0.777 **	0.456 **							
Abdomen length	0.287 **	0.523 **	0.492 **	0.374 **	0.388 **						
Fore femur length	0.367 **	0.466 **	0.378 **	0.331 **	0.254 *	0.704 **					
Fore tibia length	0.285 **	0.485 **	0.517 **	0.432 **	0.431 **	0.638 **	0.544 **				
Fore tarsal length	0.108	0.614 **	0.591 **	0.362 **	0.454 **	0.777 **	0.696 **	0.649 **			
Hind femur length	0.342 **	0.514 **	0.529 **	0.417 **	0.422 **	0.748 **	0.501 **	0.652 **	0.661 **		
Hind tibia length	0.192	0.426 **	0.469 **	0.256 *	0.301 *	0.556 **	0.476 **	0.714 **	0.661 **	0.472 **	
Hind tarsal length	0.123	0.642 **	0.629 **	0.355 **	0.550 **	0.762 **	0.630 **	0.647 **	0.820 **	0.686 **	0.649 **

Table 3. Component score coefficient matrix of morphological characters on the first principal component and proportions of variance explained by these components.

Morphological Characters	Female Body Size PC1	Male Body Size PC1
Body length	0.517	0.486
Elytra length	0.475	0.485
Elytra width	0.424	0.451
Head width	0.443	0.462
Abdomen length	0.362	0.334
Proportion of variance	68.984%	79.775%

Independent-sample *t*-tests revealed that significant differences existed in body weight ($t = 2.010$, $p = 0.047$), fore femur length ($t = 2.335$, $p = 0.022$) and fore tibia length ($t = 2.576$, $p = 0.012$), and extremely significant differences existed in body length ($t = -3.696$, $p = 0.000$), antennal length ($t = 13.804$, $p = 0.000$), abdomen length ($t = 2.978$, $p = 0.004$), fore tarsal length ($t = 7.596$, $p = 0.000$), hind femur length ($t = 2.805$, $p = 0.006$), and hind tibia length ($t = 2.686$, $p = 0.009$) between chosen and nonchosen females (Figure 2a,b). Mann–Whitney *U* test revealed that extremely significant differences existed in elytra length ($z = -3.389$, $p = 0.001$) and body size PC1 between chosen and nonchosen females ($z = -3.623$, $p = 0.000$) (Figure 2a).

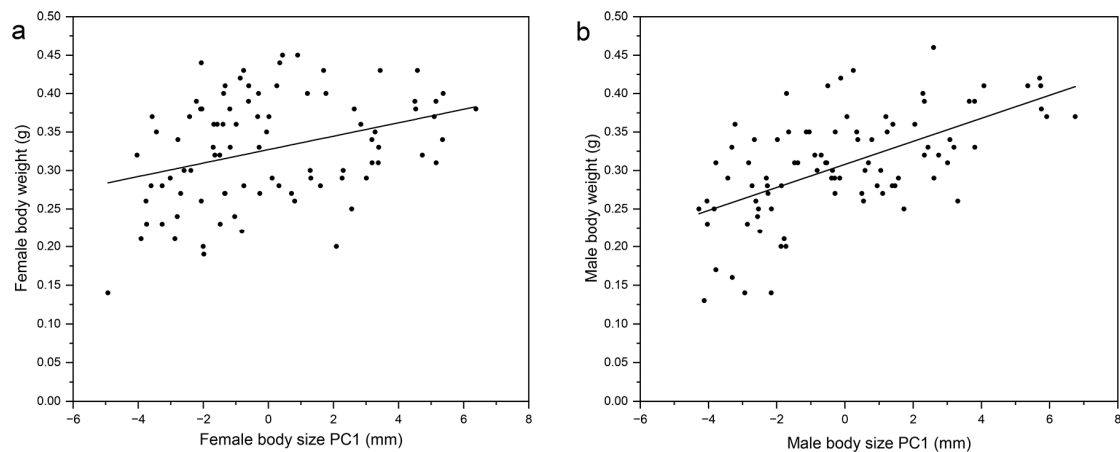


Figure 1. Correlations between female body size PC1 and female body weight (a) and between male body size PC1 and male body weight (b).

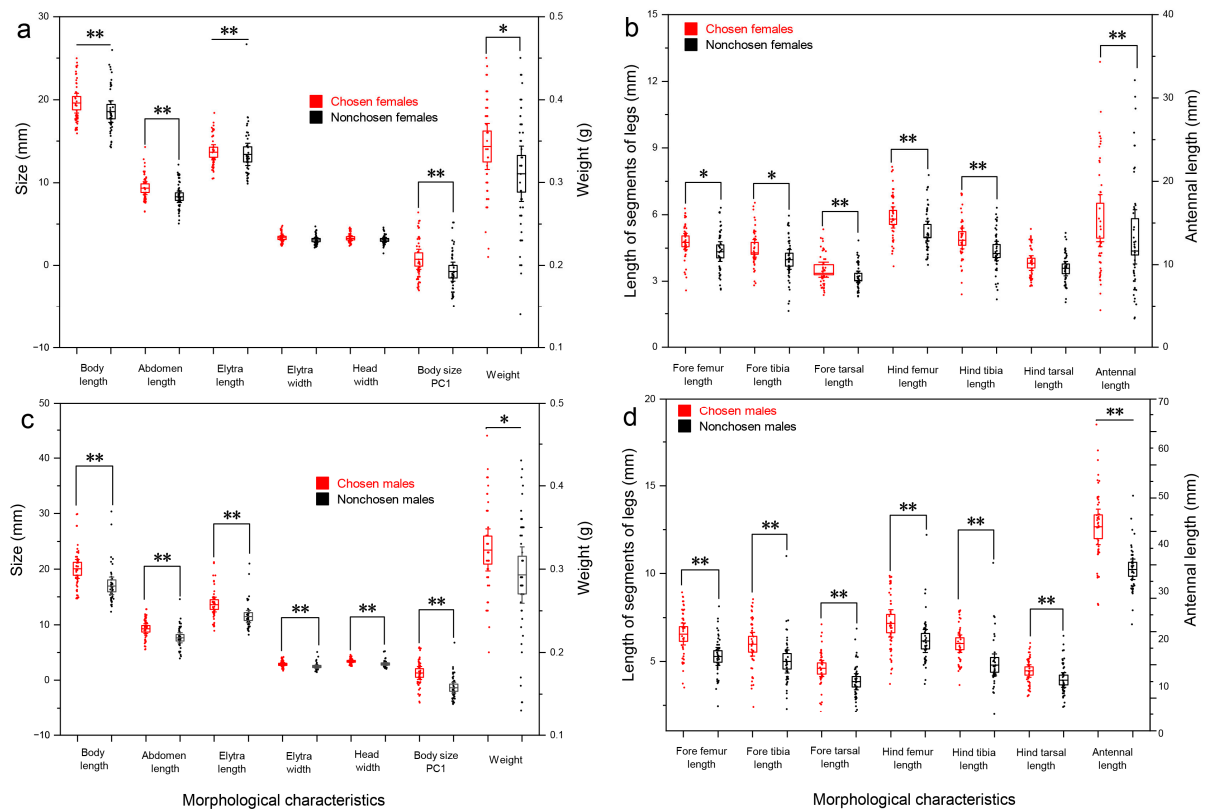


Figure 2. Comparison of morphological characteristics between females and males that successfully mated ($n = 45$) and failed to mate ($n = 45$). (a) Female weight and morphological characteristics, (b) female leg length and antennal length, (c) male weight and morphological characteristics, and (d) male leg length and antennal length. * $p < 0.05$; ** $p < 0.01$.

3.2. Sexual Selection on Male Traits

Mating was successful in all 45 replicates. Based on multicollinearity analysis, the VIF value for the body length (48.259) and elytra length (40.091) was more than 10 (Table 4), so we removed it [30]. Spearman correlation coefficients revealed positive correlations between the 11 traits measured. The correlation coefficient was highest for the relationship between abdomen length and foretarsal length (i.e., 0.781) (Table 5). The first principal component for males explained 79.775% of the total variance and was regarded as an index of the body size of males (Table 3). For males, body size PC1 = $0.486 \times \text{body length} +$

$0.485 \times \text{elytra length} + 0.451 \times \text{elytra width} + 0.462 \times \text{head width} + 0.334 \times \text{abdomen length}$. Male body weight and male body size were positively correlated ($r = 0.595$, $p < 0.01$, $n = 90$ males) (Figure 1b).

Table 4. Multicollinearity analysis for morphological traits in males.

	B	SE	Beta	t	p	VIF
Weight	4.595	1.862	0.337	2.468	0.016	1.969
Body length	−0.143	0.159	−0.609	−0.902	0.370	48.259
Antennal length	−0.020	0.019	−0.175	−1.057	0.294	2.899
Elytra length	0.091	0.198	0.284	0.462	0.646	40.091
Elytra width	0.383	0.291	0.287	1.317	0.192	5.003
Head width	0.534	0.303	0.365	1.762	0.082	4.546
Abdomen length	−0.023	0.089	−0.053	−0.258	0.797	4.402
Fore femur length	0.068	0.108	0.104	0.631	0.530	2.899
Fore tibia length	0.119	0.109	0.198	1.085	0.281	3.524
Fore tarsal length	−0.067	0.175	−0.079	−0.383	0.703	4.495
Hind femur length	−0.057	0.104	−0.102	−0.545	0.588	3.730
Hind tibia length	−0.007	0.121	−0.010	−0.055	0.956	3.519
Hind tarsal length	0.031	0.191	0.031	0.165	0.870	3.680

Table 5. Spearman correlation matrix for morphological traits in males (* $p < 0.05$; ** $p < 0.01$).

	Weight	Antennal Length	Elytra Width	Head Width	Abdomen Length	Fore Femur Length	Fore Tibia Length	Fore Tarsal Length	Hind Femur Length	Hind Tibia Length
Antennal length	0.551 **									
Elytra width	0.491 **	0.650 **								
Head width	0.611 **	0.736 **	0.732 **							
Abdomen length	0.415 **	0.498 **	0.295 **	0.457 **						
Fore femur length	0.249 *	0.476 **	0.292 **	0.381 **	0.678 **					
Fore tibia length	0.218 *	0.351 **	0.181 **	0.335 *	0.664 **	0.649 **				
Fore tarsal length	0.265 *	0.428 **	0.290 **	0.384 **	0.781 **	0.667 **	0.756 **			
Hind femur length	0.306 **	0.419 **	0.350 **	0.357 **	0.740 **	0.688 **	0.685 **	0.772 **		
Hind tibia length	0.229 *	0.472 **	0.404 **	0.399 **	0.587 **	0.649 **	0.623 **	0.683 **	0.618 **	
Hind tarsal length	0.215 *	0.411 **	0.385 **	0.381 **	0.748 **	0.675 **	0.630 **	0.754 **	0.743 **	0.670 **

Independent-sample t -tests showed that there were extremely significant differences in body length ($z = -4.305$, $p = 0.000$), body weight ($t = 2.127$, $p = 0.036$), antennal length ($t = 6.202$, $p = 0.000$), elytra width ($t = 3.120$, $p = 0.002$), abdomen length ($t = 3.960$, $p = 0.000$), fore femur length ($t = 4.738$, $p = 0.000$), fore tibia length ($t = 3.121$, $p = 0.002$), fore tarsal length ($t = 3.475$, $p = 0.001$), hind femur length ($t = 3.010$, $p = 0.003$), hind tarsal length ($t = 3.010$, $p = 0.003$) and body size PC1 ($t = 3.044$, $p = 0.004$) between chosen and nonchosen males (Figure 2c,d). Mann–Whitney U test revealed that extremely significant differences existed in head width ($z = -4.237$, $p = 0.000$), elytra length ($z = -3.240$, $p = 0.001$), and hind tibia length ($z = -2.825$, $p = 0.005$) between chosen and nonchosen males (Figure 2c,d).

4. Discussion

In the realm of sexual competition, female preference for high-quality mates takes precedence over quantity. The result is that females can exhibit both choosiness and competitiveness in their pursuit of mates [31–33]. Morphological characteristics in females also play an important role in mate selection and have been shaped by sexual selection [34–38]. In competition for access to males, larger females may be at an advantage because they are better able to dominate other females and possess higher reproductive fitness [36].

In the hollyhock weevil *Rhopalapion longirostre* (Olivier), individuals with large elytra are favored by the opposite sex. Prior to mounting, the prospective male *R. longirostre* seeks a large female with a long elytra, and females with a larger elytra enable males to crawl better and promote mating success [39], which is consistent with our results. The elytra length showed a significant positive correlation with the elytra width and other

morphological characteristics of females. In general, the larger the elytra, the larger the female traits. The larger body size of female insects appears to be attractive to males. This could be due to the male's ability to easily perceive them or to the possibility that larger females emit more pheromones [40]. Regardless, body size is a key characteristic that can provide insight into ecological, behavioral, and evolutionary patterns. In many insect species, females are larger than males, a phenomenon known as sexual dimorphism. Scientists believe this may be due to the fact that the females are responsible for egg production [40]. One popular theory, the fecundity advantage hypothesis, posits that larger females have higher fecundity rates. These insights help advance our understanding of the diverse and complex behaviors and adaptations of insects in the natural world [9].

In some insect species, the thickness of a female's abdomen is a dependable indicator of the quantity and growth stage of her eggs. Males can gain reproductive advantages by selecting females with thicker abdomens for mating and fertilizing their more developed eggs. This is a common occurrence in the animal kingdom, so the abdomen of the female may be an important indicator of fecundity, which makes her more attractive to males [37,38,41]. In the seed bug *Nysius huttoni* White [35], the cotton bollworm *Helicoverpa armigera* (Hübner) [41], the long-tailed dance fly *Rhamphomyia longicauda* Loew [37], and the *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) [42], a positive correlation exists between female abdominal size and lifetime reproductive output. Males in these species show a preference for larger abdomens in females as potential mates. These findings highlight the importance of female body size in reproductive success across different taxa. We found that the abdominal length of mated females differed significantly from that of unmated females (Figure 2a), and the abdominal length of females was significantly positively correlated with the elytra length and elytra width (Table 2). Therefore, mate selection based on female abdomen size in this species via male orientation can be attributed to the fact that this feature is a reliable indicator of the lifetime reproductive success of females.

Many morphological characteristics in males play an important role in mate selection and are sexually selected [10,34,35,43,44]. Morphological features can be used as weapons in male competition [43–50] or to attract females [51–54]. Insect precopulatory interactions involve frequent contact on the antenna and legs. In many species, males with larger body sizes [10,43,55], longer antennal [35,43] and legs [44], and longer wings [56] may have better opportunities to mate.

In addition, there is some evidence that larger males have better genes and a larger ejaculatory supply than those of smaller males [57–60]. In certain insect species, males exhibit a preference for mating with larger females due to their increased ability to dominate other females and higher reproductive fitness [61]. For instance, *Micrarchus hystriuleus* (Westwood), a sexually dimorphic stick insect species, displays a positive correlation between body size in female–male pairs collected in the field. In some species, larger male individuals have the opportunity to copulate with females of various sizes, while small males primarily mate with small females [62]. This can occur because large females do not choose to mate with small males, and large males may physically be unable to mate with small females. Alternatively, if mating occurs in a confined space, it is possible for the body size of both participants to be restricted [63]. Mating with larger males may result in the production of larger offspring for females, potentially leading to better reproductive success through their offspring. In the three species in the genus *Drosophila*, *D. bipectinata* (Duda), *D. rajasekari* (Joshi), and *D. nasuta* Lamb, females showed a preference for mating with large males, regardless of their own size. This highlights the advantage that large males have in intrasexual competition. Female selection criteria appeared to be based on relative size alone, favoring the larger males. These findings suggest that size plays an important role in mate selection among these species of fruit flies [64]. Further research indicates that male *Acheta domesticus* (L.) exhibit a preference for larger females, which may be due to the increased detection of pheromones emitted by these females [65]. The size of an insect's mate plays a crucial role in determining its reproductive success. Certain species exhibit selective behavior in choosing their mates, with large females having longer lifespans and

larger males having a higher likelihood of mating. In situations where larger females are in competition, larger males tend to emerge victorious and mate with them, leaving smaller males with the opportunity to mate with less contested, smaller females. These factors allow for variations in reproductive success within individual insect populations.

The secondary sexual characteristics of insects in the mating process are generally sexually dimorphic (i.e., they are generally larger in males than in females [42]). Many species of longicorn beetles (Coleoptera Cerambycidae) often display sexual dimorphism in their antennal length and in the ratio of antennal length/body size. Typically, males have longer antennal than females and a higher ratio of antennal length/body size [66–68]. Antennal is a major secondary sexual trait of *M. saltuarius*. The length or structural dimorphism of antennae is common in species that use air pheromones to find a mate [69]. Male antennal play an important role in female choice and competition between males. For males, the obvious selective advantage of longer antennal is the effect on mating opportunities [67]. For example, in *Cnephasia jactatana* Walker (Lepidoptera: Tortricidae), females significantly preferred males with longer antennal for mating [43]. Hanks et al. [67] found that larger males of *Phoracantha semipunctata* (Fabricius) (Cerambycidae) with longer antennal, were able to detect females more efficiently than smaller males due to their ability to sweep a larger area. Larger males were also more successful in aggressive contests for mating partners. Research regarding the antenna morphology of *Pseudomantis albofimbriata* (Stal) suggests that this may also affect the speed at which males are able to locate females [70]. In mating systems based on scramble competition, the ability to efficiently locate mates can greatly increase male mating success, with faster males potentially gaining an advantage over slower males in this regard [70]. Previous research has demonstrated the importance of male cricket antennal in initiating courtship behavior, facilitating copulation, and allowing for the ability to engage in mate guarding. These findings have implications for understanding the mating strategies of these insects [71,72]. According to Svensson [73], male moths with greater sensitivity to pheromones are more likely to find mates, implying that the length of their antennal is under significant sexual selection pressure. We detected a significant difference in the length of antennal between selected and unselected males (Figure 2c).

The male leg also contributes to insect mating. The harlequin beetle, *Acrocinus longimanus* (L.) have enlarged forelegs that flank females during mating and mate guarding. This is important to note as it contributes to the unique mating behavior of these beetles [74]. In some species, the hind leg plays an important role in mate selection; for example, in the ambush bug (Heteroptera: Reduviidae), sexual selection appears to act on the length of the male hind leg [75]. In *Pachyrhamma waitomoensis* Richards (Orthoptera: Rhaphidophoridae), males with the longest hind legs could accrue approximately triple the number *Phymata wolffii* Stal of copulations [76]. Female bean bugs *Riptortus pedestris* (Fabricius) prefer males with higher frequencies of courtship display and larger hind legs, which indicate better abilities to compete for mates. This information is important for understanding the reproductive behavior of *R. pedestris* [77]. During copulation, male *M. saltuarius* stroke their legs along the edges of the female elytra. This behavior is crucial for sperm precedence and paternity success, as previous research has shown that female perception of this leg-rubbing plays a key role. Overall, this information is part of a student assignment aimed at enhancing their understanding of reproductive behavior in *M. saltuarius*. For example, in *Tribolium castaneum* (Herbst), when females mate with two males, leg amputation in males reduces the number of offspring significantly [78]. Sexual dimorphism in *R. longirostre* is attributed to the interplay of two forces: natural selection, favoring larger females, and sexual selection, which stabilizes the size of male hind legs. This pattern has been observed and studied in this species [39]. In *Nicrophorus orbicollis* Say, the length of the male tarsus (especially the fore tarsus) is selected by females [79]. Kelly et al. [80] showed that females of *Deinacrida rugosa* Buller tend to choose males with smaller body sizes and longer legs, as this phenotype clearly has an advantage with respect to competition for mates. In many species of insects, legs have evolved to carry individuals through their surroundings, but in

certain instances, leg length is also a subject of sexual selection [81]. Our observations show that to mate successfully, three pairs of legs behind the female are needed to ensure that the female is firmly grasped and that the male genitalia are inserted appropriately. This also prevents the male from falling off during the mating process, resulting in interrupted mating [26]. Therefore, male *M. saltuarius* with longer legs may be more capable of grasping females, which may explain our observation that leg length is significantly related to mating success.

Our results indicate that differences in the female abdomen size and male antenna length, as well as other traits, may reliably reflect variance in reproductive fitness in *M. saltuarius*. These traits differed significantly between selected and unselected individuals and may have evolved under sexual selection. The differences in key traits among species suggest that sexual selection acts on different traits in different species, probably due to diverse mating systems [82].

5. Conclusions

M. saltuarius is a pest that causes significant damage to pine forests in temperate regions of China, and the losses associated with this species are expected to increase in the near future. We studied mate selection behavior in *M. saltuarius* and the effects of various morphological characteristics on mating preferences. We detected positive correlations between female and male morphological characteristics. Furthermore, we observed significant differences in most morphological characteristics between selected and unselected females and males. The differences between selected and unselected males were significant in all the morphological characters measured, and we refer to previous research to demonstrate the role of body size, elytra length, antennal length, and leg length in insect mating. The differences between selected and unselected females were significant in the morphological characteristics of the abdomen and the leg, and we also refer to previous research to demonstrate the role of the abdomen and the leg in the mating of insects. We also refer to previous research to demonstrate the role of abdominal length and leg length in insect mating.

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