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小翅稻蝗的精子竞争及交配行为的适应意义

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摘要:许多昆虫有多次交配行为,因多次交配而引起不同雄虫的精子竞争,提供雌虫一种有效的性选择方式。小翅稻蝗(*Oxya yezoensis* Shiraki)具多次交配行为,雌雄交配时间长,且交配后常伴有长时间的抱对行为。利用近缘种的种间交配,对小翅稻蝗的精子竞争、交配后抱对行为的适应意义进行了探讨。结果表明,小翅稻蝗的 P_2 值(最后交配雄虫子代的比例)达 94.3%±5.3%,说明最后交配雄虫的精子优先用于卵子的受精,交配时存在着精子置换。长时间的交配后抱对行为是为了阻止雌虫与不同雄虫个体的再交配,保护精子免被置换。

关键词:精子竞争;精子优先;P_2 值;交配后抱对行为;小翅稻蝗

Sperm competition and adaptive significance of prolonged post-copulatory mounting in *Oxya yezoensis* (Orthoptera: Catantopidae)

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Abstract: Females copulate with multiple males in almost all insect species. This behavior allows different males to compete for fertilization and gives females the opportunity to mediate this competition. The eggs are typically fertilized by sperm from only one male, either the female's last mate or an earlier mate. The rice grasshopper, *Oxya yezoensis* Shiraki, shows not only multiple copulation, but also prolonged copulation and prolonged post-copulatory mounting between males and females. In this paper, sperm competition, measured by the P_2-value, (i.e., the proportion of offspring sired by the last male to mate) and the adaptive significance of prolonged post-copulatory mounting were studied by employing interspecific crosses.

Females of *O. yezoensis* were mated once with a male and were allowed to deposit up to four egg pods. The egg pods all had a high hatching success and hatching remained almost constant over the four successive egg pods. The results indicated that the rice grasshopper, like many other insects, store the sperms received from a male, which are then gradually released for fertilizing eggs efficaciously.

To determine the P_2-value of *O. yezoensis*, the female was mated with a male of *O. yezoensis* or *O. chinensis formosana* first and was allowed to lay one egg pod. It was then mated with a male of *O. chinensis formosana* or *O. yezoensis* and was allowed to lay two egg pods. Remated females all showed high P_2-values and no significant difference was found in P_2-value between the two tests sequence, indicating that sperms from the two species can fertilize eggs equally well. The average P_2-value of *O. yezoensis* was 94.3%±5.3% (mean±SD). Other females were each allowed to mate with three males, i.e., mated with a male of *O. yezoensis* or *O. chinensis formosana* first, then with *O. chinensis* formosana or *O. yezoensis*, and then remated with the first mated male. In all the crosses, high P_2-values (>90%) were also found. Those results indicated the sperm precedence of last male to mate and suggested the existence of sperm displacement in *O. yezoensis*.

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To measure the lengths of copulation and post-copulatory mounting, females and males paired in separate cages were observed every hour over three consecutive days. The mean lengths of copulation and post-copulatory mounting were 5.6±4.3 h and 6.5±5.5h (mean±SD), respectively, showing not only prolonged copulation, but also prolonged post-copulatory mounting. Considering the relatively high P_2-value, prolonged post-copulatory mounting may be regarded as mate guarding. A male's staying with his mate as post-copulatory mounting increases the number of eggs that he fertilizes because he prevents his partner from remating.

Key words: sperm competition; sperm precedence; P_2-value; post-copulatory mounting; *Oxya yezoensis*

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许多昆虫有多次交配行为[1~3],交配后不同雄虫个体的精子被较长时间地贮存在雌虫的受精囊内,这样,雌虫卵子受精时,就会发生不同雄虫的精子竞争(sperm competition),精子竞争也是雌虫一种主要而有效的性选择方式[4]。在多次交配的昆虫中,由于某种机制的存在,不同雄虫精子的受精机率并不相同,精子竞争的差异一般用 P_2 值(最后交配雄虫子代的比例)来表示[4,5]。根据 P_2 值可把多次交配昆虫的精子竞争分为 3 种类型:(1)最先雄虫精子优先(first male sperm precedence),卵子与最先交配雄虫精子受精的比例显著偏高,而后来交配雄虫的精子几乎或完全不受精(P_2 值很低),如一种姬蜂 *Diadromus pulchellus*[6];(2)最后雄虫精子优先(last male sperm precedence),卵子与最后交配雄虫精子受精的比例很高,P_2 值一般为 88%~100%[7],如一种蜻蜓 *Nanophya pygmaea*,P_2 值为 97.9%[8],一种果蝇 *Drosophila ananassae*,P_2 值为 91%~94%[3];(3)无雄虫精子优先(no male sperm precedence),精子与卵子的受精与雄虫交配次序无关,如 *Acromyrmex versicolor*[9]。大多数的昆虫表现为最后雄虫精子优先,Gwynne[10]统计了 37 种昆虫精子的竞争,发现 72.9%的种类为最后雄虫精子优先,18.9%的种类为最先雄虫精子优先,8.2%的种类无雄虫精子优先。

抱对行为在许多昆虫中能观察到,如直翅目的长额负蝗 *Atractomorpha lata*[11],半翅目的一种猎蝽 *Triatoma phyllosoma*[12],鞘翅目的柳沙天牛 *Semanotus japonicus*[13]等。抱对行为可分为交配前抱对(precopulatory mounting)和交配后抱对(post-copulatory mounting)。交配前抱对行为一般认为是为了获得潜在的交配对象[7],Zhu and Tanaka[14]发现飞蝗 *Locusta migratoria* 的长时间交配前抱对行为具有延长交配时间,增加 P_2 值的功能。交配后抱对行为一般认为是一种交配后保护行为[2,7]。

小翅稻蝗(*Oxya yezoensis* Shiraki)频繁而长时间地进行交配,交配后常伴有长时间的交配后抱对行为[15]。小翅稻蝗与中华稻蝗台湾亚种(*Oxya chinensis formosana* Shiraki)亲缘关系很近[16],交配后能如种内交配一样顺利实现精子传送[17],并能产生形态介于两种之间的杂种后代。杂种可通过雌成虫腹部第 3 节背板后侧角的小刺突和雄成虫交配器的形态加以判别,杂种的孵化率、羽化率与种内交配也无显著差异[15]。本研究利用近缘种的种间杂交,调查了小翅稻蝗的精子竞争及交配行为,并对其长时间的交配和交配后抱对行为的适应意义进行了探讨。

1　材料与方法

1.1　材料

小翅稻蝗越冬卵于 1994 年 11 月采自日本弘前市郊外水田。中华稻蝗台湾亚种成虫于 1993 年 12 月采自日本冲绳岛水田。然后于实验室按 Zhu and Ando[18]和朱道弘[19]的方法进行累代饲养。所有试验昆虫均用玻璃圆筒(直径 11cm,高 18cm)饲养于光照培养箱,每天更换新鲜饲料 1 次。饲养条件为温度 25±1℃,光周期 LD 14:10h。成虫羽化后,雌、雄成虫分别饲养于不同的容器。性成熟后(小翅稻蝗约 15d,中华稻蝗台湾亚种约 25d)[17]进行各种交配实验。

1.2　1次交配雌虫卵块的孵化

性成熟的小翅稻蝗雌雄成虫配对饲养,每 2h 观察 1 次,交配确认后 24h 移去雄虫,让每雌产 4 卵块,分别调查其孵化率,检测小翅稻蝗 1 次交配的射精量及精子受精的有效期间。

1.3　精子竞争试验

为调查小翅稻蝗的精子竞争,进行了两组实验。(1)小翅稻蝗雌成虫与小翅稻蝗雄成虫或中华稻蝗台湾亚种雄成虫配对饲养,交配确认后 24h 分别移去雄虫,产下 1 卵块后,与小翅稻蝗雄虫交配的雌虫再与中华稻蝗台湾亚种雄虫、反之与小翅稻蝗雄虫配对饲养,交配确认后 24h 分别移去雄虫,每雌分别获取 2 卵块。幼虫孵化后,饲养至成虫羽化,进行形态观察,统计杂种后代和小翅稻蝗的比例。检测小翅稻蝗的 P_2 值。(2)小翅稻蝗雌成虫与小翅稻蝗雄成虫或中华稻蝗台湾亚种雄成虫配对饲养,交配确认后 24h 分别移去雄虫,产下 1 卵块后,与小翅稻蝗雄虫交配的雌虫再与中华稻蝗台湾亚种雄虫、反之与小翅稻蝗雄虫配对饲养,交配确认后 24h 分别移去雄虫,每雌分别获取 2 卵块后,再按上述方法让雌虫分别与第一次交配同种的雄虫再交配一次,每雌获取 2 卵块。幼虫孵化后,饲养至成虫羽化,进行形态观察,统计杂种后代和小翅稻蝗的比例。检测小翅稻蝗的 P_2 值的变化

情况。

1.4 交配行为观察

成虫羽化后，雌雄虫分别饲养，性成熟后配对(32 对)于玻璃圆筒，调查小翅稻蝗的交配和交配后抱对行为的时间。试验进行 3d，每小时观察 1 次，记录交配和交配后抱对行为开始及结束的时间。

2 结果与分析

2.1 1 次交配雌虫卵块的孵化

小翅稻蝗 1 次交配后，所产 4 卵块的孵化率均保持在 80%以上，卵块间的孵化率并无显著差异(Kruskal-Wallis test；$n=6$；$P>0.05$)(图 1)。说明一次成功交配的射精量足以保证 4 卵块以上卵的受精，并且交配后至产下 4 卵块或更长的期间内，对贮存于雌虫受精囊内的精子活力无显著影响。

2.2 小翅稻蝗的 P_2 值

小翅稻蝗两次交配后的 P_2 值如表 1 所示。小翅稻蝗♀×小翅稻蝗♂产下 1 卵块，证实孵化率正常，表明已正常受精后，再与中华稻蝗台湾亚种雄虫交配，则子代有 87.2～100%的个体为杂种，平均 P_2 值为 94.8%±4.9%(平均±SD，下同)。小翅稻蝗♀×中华稻蝗台湾亚种♂产下 1 卵块，证实孵化率正常，表明已正常受精后，再与小翅稻蝗雄虫交配，则子代有 85.7%～100%的个体为小翅稻蝗，平均 P_2 值为 93.9%±5.4%。将两组处理的数据进行统计分析，二者间无显著差异(Mann-Whitney U test；$P>0.05$)，说明两种稻蝗雄虫与小翅稻蝗雌虫交配的先后秩序，不造成 P_2 值的变动。将两组数据平均，小翅稻蝗的平均 P_2 值为 94.3%±5.3%。以上结果说明，多次交配的小翅稻蝗绝大多数的卵与最后交配雄虫的精子受精，换言之，最后交配雄虫的精子优先。

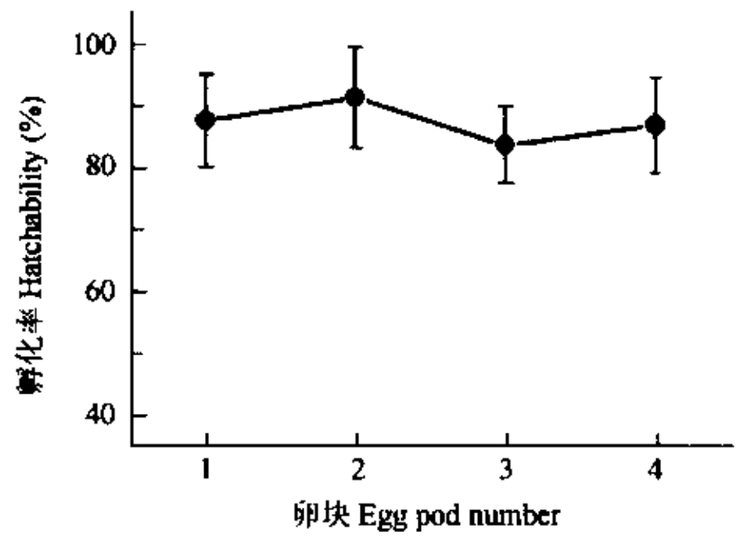

图 1 小翅稻蝗 1 次交配后 1～4 卵块的孵化率

各卵块的孵化率无显著差异(Kruskal-wallis test；$n=6$；$p>0.05$)

Fig. 1 Hachalings of first to fourth egg pod in *O. yezoensis*

Each female was mated once with a male；The hatchability of first to fourth was no significant difference (Kruskal-wallis test：$n=6$；$p>0.05$)

小翅稻蝗雌虫与两种稻蝗雄虫进行 3 次交配后，P_2 值也与上述试验结果相符合(图 2，图 3)。小翅稻蝗♀×小翅稻蝗♂产下 1 卵块，再与中华稻蝗台湾亚种雄虫交配，2 卵块分别有 95.7%±4.1%、97.1%±4.6%($n=6$，下同)的子代为杂种，同一雌虫再一次与小翅稻蝗雄虫交配，则 2 卵块仅有 5.9%±5.3%、2.6%±3.2%的子代为杂种，其余都是最后交配的小翅稻蝗雄虫的子代(图 2)。小翅稻蝗♀×中华稻蝗台湾亚种♂产下 1 杂种卵块后，再与小翅稻蝗雄虫交配，则子代几乎都是小翅稻蝗，杂种后代为 3.4%±4.0%、5.5±6.1，同一雌虫再一次与中华稻蝗台湾亚种雄虫交配，则子代又几乎都是最后交配的中华稻蝗台湾亚种雄虫的后代，分别为 98.2%±5.7%、93.9%±6.0%。上述结果更明确地证明了多次交配的小翅稻蝗，最后交配雄虫的精子被雌虫优先用于受精。

表 1 小翅稻蝗多次交配后的 P_2 值

Table 1 P_2 values after remating in different crosses

杂交② Crosses	孵化率(%) Hatchability	羽化率(%) Percentage of emergence	$P_2^{①}$(%)	P_2 范围(%) Range of P_2	杂交雌数 No. of crossed female
Oy×Oy×Ocf	89.0±9.8③	79.1±9.9	94.8±4.9	87.2～100	6
Oy×Ocf×Oy	90.1±6.8	79.3±8.1	93.9±5.4	85.7～100	7

①最后交配雄虫子代的比例 The proportion of offspring sired by the last male to mate；②Oy 小翅稻蝗 *O. yezoensis*，Ocf 中华稻蝗台湾亚种 *O. chinensis formosana*；③平均±SD Mean±SD

2.3 交配及交配后抱对行为的时间

为调查小翅稻蝗一次交配所需时间及交配后抱对行为时间的长短，32 对雌雄被配对饲养，每小时 1 次进行了 3d 观察，结果如图 4 所示。3 日间的交配率为 83%，抱对/交配的比例为 44%，近一半的交配伴随着抱对行为的发生(由于是 1h 观察 1 次，结果未包括短于 1h 的交配后抱对行为)。完成 1 次交配的时间变异较大，为 1～19h，平均(±SD)为 5.6±4.3h。交配后抱对行为的时间是 1～17h，平均为 6.5±5.5h。小翅稻蝗不仅进行长时间的交配，而且交配后常伴有抱对行为的发生。

3 讨论

小翅稻蝗 1 次成功交配的射精量足以保证 4 卵块以上卵的受精，并且交配后至产下 4 卵块或更长的期间内，贮存于雌虫受

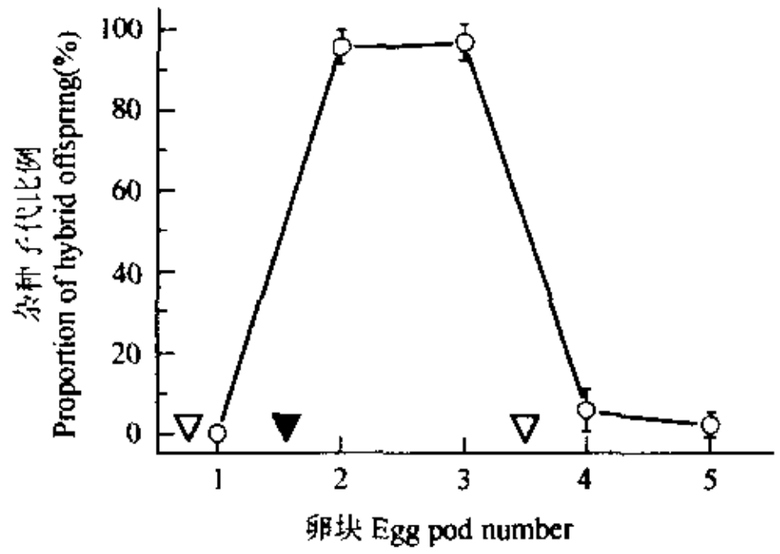

图 2　小翅稻蝗雌虫与小翅稻蝗雄虫交配(空心三角)，再与中华稻蝗台湾亚种(实心三角)及小翅稻蝗雄虫交配后杂种子代比例的变化情况($n=6$)；显示平均及 SD

Fig. 2　Changes in proportion of hybrid offspring produced by *O. yezoensis* females($n=6$) which were first mated with a male of *O. yezoensis*(open triangle), second with *O. chinensis formosana* (closed triangle) and then with *O. yezoensis*; Mean and SD are given

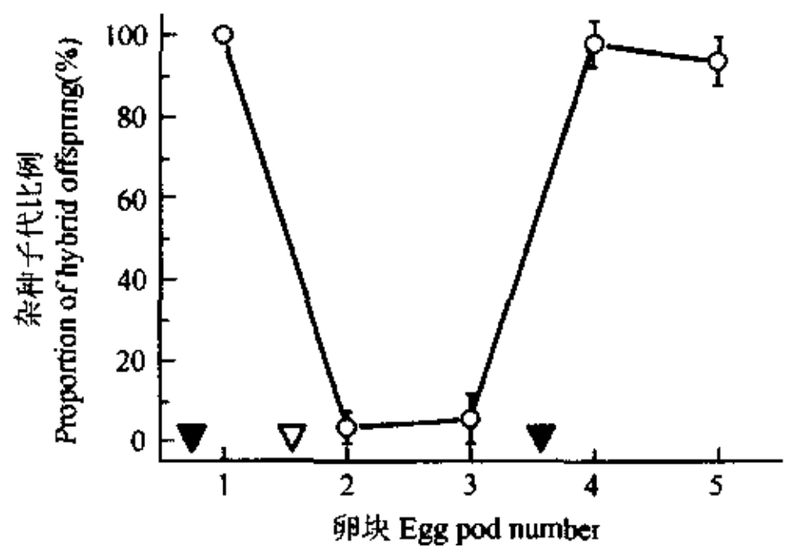

图 3　小翅稻蝗雌虫与中华稻蝗台湾亚种雄虫交配(实心三角)，再与小翅稻蝗(空心三角)及中华稻蝗台湾亚种雄虫交配后杂种子代比例的变化情况($n=6$)；显示平均及 SD

Fig. 3　Changes in proportion of hybrid offspring produced by *O. yezoensis* females($n=6$) which were first mated with a male of *O. chinensis formosana*(closed triangle), second with *O. yezoensis* (open triangle) and then with *O. chinensis formosana*. Mean and SD are given

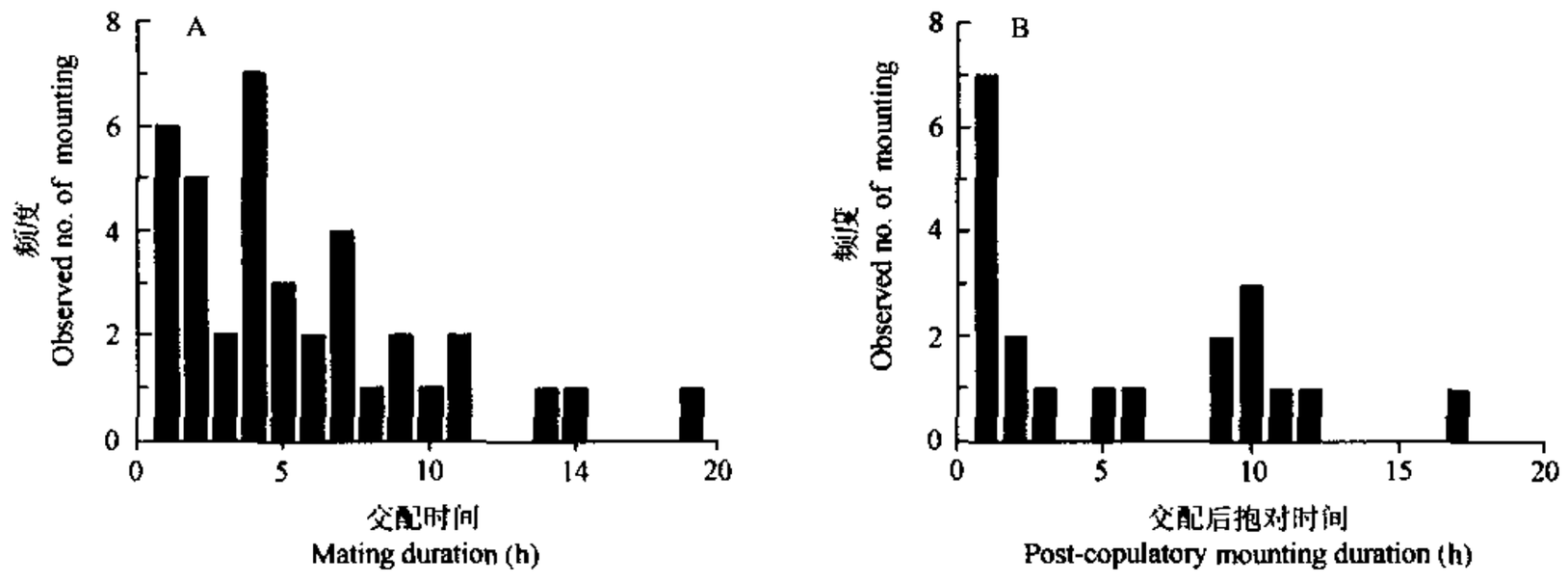

图 4　小翅稻蝗交配(A)和交配后抱对行为(B)时间的频度分布($n=36$)

Fig. 4　Frequency distribution of mating duration(A) and post-copulatory mounting duration(B) in *O. yezoensis* ($n=36$)

精囊内的精子活力无显著影响。这样，多次交配后，围绕着与雌虫卵子的受精，不同雄虫则发生精子竞争。近缘种间的杂交试验证明，2 次交配或 3 次交配后总是最后交配雄虫的精子优先，平均 P_2 值达 94.3%(表 1，图 2，图 3)。说明最后交配雄虫的精子将先前交配雄虫的精子以某种机制加以了置换。最后雄虫精子优先的精子竞争机制因种类不同而不同，主要有机械置换、层化置换[20]，如 *Calopteryx maculata*[21]、菜叶蜂 *Athalia rosae*[22]使用其特殊的交配器，在射精前将受精囊内先前交配雄虫的精子移出，一种蟋蟀 *Truljalia hibinonis*[23]自弯曲阴茎的先端喷射强力的精液，挤压出先前交配雄虫的精子，*Lestex vigilax*[24]使用阴茎将对手的精子移动到受精囊的一角。Price 等[25]通过标记精子的 DAPI 染色，证实一种果蝇 *Drosophila melanogaster* 具有物理置换和精子失效两种精子竞争机制。Zhu and Tanaka[14]的研究结果表明飞蝗 *L. migratoria* 在不同的交配阶段分别发生精子置换、精子混合、精子喷射。说明同一种昆虫可能具有多种精子竞争机制。虽然一些多次交配昆虫种类已证实其精子优先，但多数昆虫的精子竞争机制并不清楚。小翅稻蝗是以何种机制实现精子的置换，将是一项令人感兴趣的研究。

与雌虫交配的次数越多，雄虫有可能留下越多的子代，因而，交配次数的增加会使雄虫的适应度呈直线增长。长时间的抱对行为以及长时间的交配，由于可能失去与其它雌虫交配的机会，对雄虫来说无疑是一种消耗(cost)[26]。而且这种行为会给雄虫带来一定的环境压力，因为在抱对和交配时，雄虫不能取食，也不能快速飞行以逃避天敌的攻击。然而，小翅稻蝗 1 次交配的时间长达 5.6±4.3h(平均±SD)(最长的交配时间达 19h)，并且交配后常伴有长时间的抱对行为(6.5±5.5h)(最长的交配后抱对达 17h)。一些直翅目的昆虫交配时间越长雌虫获得的精子量越大[14,27,28]。可以推测小翅稻蝗长时间交配的作用之一是为了让雌虫获取更多的精子。精子竞争试验的结果表明，小翅稻蝗的 P_2 值为 94.3%，最后交配雄虫的子代占绝大多数。根据实验观

察，其它雄虫个体很难与交配中或抱对中的雌虫实现交配。可以认为小翅稻蝗交配后长时间的抱对是一种交配后保护行为，目的是阻止其它雄虫与雌虫的再交配，以保护自己的精子不被置换。有意思的是同为直翅目的飞蝗 *L. migratoria* 主要进行交配前抱对[29,14]，飞蝗 *L. migratoria* 的交配前抱对行为具有延长交配时间、增加 P_2 值的功能，而交配后抱对行为不能给抱对雄虫带来更大的利益，因为 P_2 值仅为 52.5%[14]。两种蝗虫的 P_2 值和抱对行为很好地说明了昆虫行为和功能的统一性。

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