

草地贪夜蛾和棉铃虫种间竞争行为表现*

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摘要 【目的】草地贪夜蛾 *Spodoptera frugiperda* (J.E. Smith) 和棉铃虫 *Helicoverpa armigera* (Hübner) 是玉米穗期的重要害虫, 均具有自相残杀行为, 且存在对食物及空间资源的竞争。研究草地贪夜蛾和棉铃虫种内和种间的攻击和防御行为, 为明确二者田间条件下的种间关系提供参考。【方法】在室内有食物条件下, 设置草地贪夜蛾 4-6 龄幼虫和棉铃虫 4-6 龄幼虫 15 个龄期组合, 观察竞争行为出现的频率, 并记录 20 min 内草地贪夜蛾和棉铃虫攻击和防御行为的类型及次数; 24 h 后记录幼虫存活情况, 并计算幼虫死亡率。【结果】棉铃虫种内竞争主要表现为攻击行为, 在 5 龄和 6 龄幼虫竞争时最明显, 其中 5 龄幼虫头部接触行为和 6 龄幼虫猛击行为出现的频率最高, 分别占各自竞争行为总数的 46.1%±3.1% 和 51.0%±2.3%。草地贪夜蛾和棉铃虫种间竞争行为都主要表现为攻击行为, 同龄期草地贪夜蛾与棉铃虫竞争时, 4 龄草地贪夜蛾猛击行为出现的频率显著高于棉铃虫, 5 龄棉铃虫头部接触行为出现的频率显著高于草地贪夜蛾, 而 6 龄幼虫各行行为出现频率均无显著差异。不同龄期的草地贪夜蛾和棉铃虫竞争时, 6 龄幼虫头部接触行为出现的频率显著高于 5 龄, 同龄期竞争时草地贪夜蛾与棉铃虫的存活率无显著差异, 草地贪夜蛾 4-6 龄幼虫的存活率依次为 83.3%、86.6%、80.0%, 棉铃虫 4-6 龄幼虫的存活率分别为 76.7%、73.3%、63.3%。不同龄期幼虫竞争时, 5 龄草地贪夜蛾和 5 龄棉铃虫幼虫存活率分别为 80.0% 和 56.7%, 均显著低于 6 龄棉铃虫和 6 龄草地贪夜蛾幼虫存活率 (100%)。【结论】草地贪夜蛾和棉铃虫幼虫种间竞争激烈, 同一龄期幼虫竞争时, 草地贪夜蛾竞争优势不明显, 而 5 龄和 6 龄幼虫竞争时, 6 龄草地贪夜蛾幼虫的竞争优势更明显。

关键词 草地贪夜蛾; 棉铃虫; 攻击行为; 防御行为; 存活率

Intra and interspecific competition in *Spodoptera frugiperda* and *Helicoverpa armigera*

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Abstract 【Objectives】To investigate intra and interspecific attack and defensive behaviors of the fall armyworm, *Spodoptera frugiperda* (J. E. Smith) and the corn earworm, *Helicoverpa armigera* (Hübner), important maize pests that engage in cannibalistic behavior and compete for food and habitat, and thereby further understanding of interspecific relationships between these species in the field. 【Methods】Under indoor food conditions, 15 instar combinations of 4-6 instar larvae of *S. frugiperda* and 4-6 instar larvae of *H. armigera* were set up, the frequency of competitive behavior was observed, and the types and times of attack and defense behaviors of *S. frugiperda* and *H. armigera* were recorded within 20 min. 【Results】Attack behavior was the predominant form of intraspecific competition in *H. armigera*, and was more obvious in competition between 5th and 6th instar larvae. The frequency of head touching in 5th instar larvae, and the frequency of strike behavior in 6th instar larvae, were the highest, accounting for 46.1% ± 3.1 % and 51.0% ± 2.3%, respectively, of all competitive behaviors. Both species displayed attack behavior during interspecific competition. The frequency of strike behavior was significantly higher, and recoil behavior significantly lower, in 4th instar *S. frugiperda* larvae than in 4th instar *H. armigera* larvae. The frequency

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of head touching was significantly higher, and the frequency of recoil and retreat behavior significantly lower, in *H. armigera* during competition between 5th instar *S. frugiperda* and 5th instar *H. armigera* larvae. There were no significant differences in the frequencies of competitive behaviors between 6th instar *S. frugiperda* and *H. armigera* larvae. The frequency of head touching was significantly higher in 6th instar larvae than in 5th instar larvae, but the frequency of recoil and retreat behavior was significantly lower, both for *S. frugiperda* and *H. armigera*. Fourth to 6th instar larvae of *S. frugiperda* had similar survival rates (83.3%, 86.6% and 80.0%, respectively) in competition with the same instar of *H. armigera* (76.7%, 73.3% and 63.3%, respectively). Survival of 5th instar *S. frugiperda* and *H. armigera* larvae was 80% and 56.7%, respectively, which is significantly lower than the survival of 6th instar larvae, which was 100% for both species. **[Conclusion]** Interspecific competition between *S. frugiperda* and *H. armigera* can be intense. *S. frugiperda* had no obvious competitive advantage in competition with *H. armigera* larvae of the same instar, but 6th instar *S. frugiperda* larvae were competitively superior to 5th instar *H. armigera* larvae.

Key words *Spodoptera frugiperda*; *Helicoverpa armigera*; attack behavior; defensive behavior; survival rate

草地贪夜蛾 *Spodoptera frugiperda* (J. E. Smith) (鳞翅目 Lepidoptera, 夜蛾科 Noctuidae) 自 2019 年入侵我国以来, 凭借强大的迁飞能力、环境适应能力和繁殖能力等特点, 迅速成为我国玉米生产的头号一类害虫 (郭井菲等, 2019; 陈辉等, 2020; 高祖鹏等, 2020; 王磊和陆永跃, 2020)。棉铃虫 *Helicoverpa armigera* (Hübner), 原本是棉花上的重要害虫, 近年来随着黄淮海地区棉花种植面积的减少, 在玉米田发生面积逐年上升, 成为了重要的玉米穗期害虫之一 (王振营和王晓鸣, 2019)。草地贪夜蛾幼虫虽然可为害玉米雄穗、茎及叶等多个组织部位, 但在玉米中后期主要以 4 龄及以上龄期幼虫集中在雌穗上为害 (栗圣博等, 2022), 而棉铃虫在玉米灌浆期只分布在雌穗上 (陈浩等, 2016), 因此这 2 种害虫在玉米灌浆期会混合发生 (陈琦等, 2020), 在生存空间及食物资源上存在强烈的种间竞争。

害虫种内和种间竞争关系是决定不同物种地理分布、种群丰富度和多样性的关键因素 (Denno *et al.*, 1995)。竞争行为表现对害虫在种间竞争环境下能够正常存活、完成生长发育、将基因顺利传递给下一代至关重要 (Ongaratto *et al.*, 2021)。对于入侵害虫来说, 优越的竞争能力是其成功入侵和定殖的关键。草地贪夜蛾在我国入侵扩散的过程中也表现出了强大的竞争能力, 在 2019-2020 年对河南主要玉米种植区的调查发现草地贪夜蛾已成为部分地区秋玉米上的优势害虫 (徐永伟等, 2021)。在对草地贪夜

蛾和亚洲玉米螟 *Ostrinia furnacalis* (Guenée) 竞争行为和存活率的研究中也发现草地贪夜蛾占据竞争优势 (施建琴等, 2021)。草地贪夜蛾和棉铃虫都具有自相残杀和种间捕食行为, 那么当草地贪夜蛾遇到同样具有攻击性的棉铃虫, 二者的种间竞争行为是怎么样? 是否能占据优势?

玉米田调查发现, 一般一个玉米雌穗上只有 1-2 头高龄草地贪夜蛾或棉铃虫幼虫 (李贤嘉等, 2021), 那么高龄幼虫的种间竞争行为的胜负直接影响着二者的种群动态。因此, 本研究在室内条件下, 从二者个体竞争行为表现方面分析其竞争关系, 为田间草地贪夜蛾和棉铃虫幼虫种群动态规律与预测预报提供理论依据。

1 材料与方法

1.1 供试虫源

供试的草地贪夜蛾和棉铃虫饲养于中国农业科学院植物保护研究所, 初孵幼虫采用玉米叶片饲养至 4-6 龄幼虫供试验所用, 试验条件为温度 (28±1) °C, 湿度 75%±5%, 光周期 L:D=16:8。

1.2 试验方法

试验统一选取蜕皮 4-12 h 后的 4-6 龄幼虫进行试验, 根据表 1 设置不同处理组合。将 1 粒新鲜的灌浆期的玉米籽粒放置培养皿 (d=60 mm, 高 15 mm) 中间, 2 头棉铃虫接于籽粒两侧, 或 1 头草地贪夜蛾和 1 头棉铃虫接于籽粒两侧。

20 min 内观察幼虫攻击和防御行为, 攻击和防御行为标准按照表 2 进行记录。每组处理设置 4 次重复, 每个重复 5 对幼虫, 每头幼虫只观察一次。试验 24 h 后记录死亡虫数。同龄期幼虫个体大小基本一致 (表 3), 并提前进行 4 h 饥饿处理。

1.3 数据处理

用 Microsoft Excel 对试验原始数据进行处
理, 每种行为出现的频率=(不同行为表现次数/

总行为次数)×100。结果用平均值 (Mean) ±标准误 (SE) 来表示。棉铃虫种内竞争中各龄期处理间攻防行为出现的频率采用 Tukey 氏检验进行差异显著性检验 (P=0.05)。草地贪夜蛾与棉铃虫各龄期处理组合的种间攻防行为出现的频率采用 t 检验进行差异显著性分析。幼虫存活率用卡平方检验比较 (P=0.05)。数据分析前进行正态性检验和方差齐性检验, 所有统计分析均用 SAS 软件进行。

表 1 草地贪夜蛾和棉铃虫种内及种间竞争组合设置
Table 1 Intraspecific and interspecific competitive combinations of *Spodoptera frugiperda* and *Helicoverpa armigera*

棉铃虫 (vs.棉铃虫) <i>H. armigera</i> (vs. <i>H. armigera</i>)	草地贪夜蛾 (vs.棉铃虫) <i>S. frugiperda</i> (vs. <i>H. armigera</i>)	棉铃虫 (vs.草地贪夜蛾) <i>H. armigera</i> (vs. <i>S. frugiperda</i>)
4 龄 (vs. 4 龄) 4th (vs. 4th)	4 龄 (vs. 4 龄) 4th (vs. 4th)	4 龄 (vs. 4 龄) 4th (vs. 4th)
5 龄 (vs. 5 龄) 5th (vs. 5th)	5 龄 (vs. 5 龄) 5th (vs. 5th)	5 龄 (vs. 5 龄) 5th (vs. 5th)
6 龄 (vs. 6 龄) 6th (vs. 6th)	6 龄 (vs. 6 龄) 6th (vs. 6th)	6 龄 (vs. 6 龄) 6th (vs. 6th)
5 龄 (vs. 6 龄) 5th (vs. 6th)	5 龄 (vs. 6 龄) 5th (vs. 6th)	5 龄 (vs. 6 龄) 5th (vs. 6th)
6 龄 (vs. 5 龄) 6th (vs. 5th)	6 龄 (vs. 5 龄) 6th (vs. 5th)	6 龄 (vs. 5 龄) 6th (vs. 5th)

记录列表中括号外试虫行为表现。
Record the behavior of the larvae outside parentheses in the list.

表 2 草地贪夜蛾和棉铃虫竞争中攻击和防御的行为特征
Table 2 Behavioral characteristics of attack and defense in the competition between *Spodoptera frugiperda* and *Helicoverpa armigera*

行为 Behavior	特征描述 Behavior description
攻击行为 Attack	
头部接触 Head touching	试虫遇到对方时将其头部和前胸突然快速的向一侧或两侧摆动, 定为进攻行为
猛击 Strike	试虫突然朝对方头部咬去或猛击, 包括接触和不接触, 定为最强烈的进攻行为
防御行为 Defense	
畏缩 Recoil	试虫面对对方攻击时仅虫体部分表现出退却回避反应, 定为防御行为
离开 Move away	试虫通过爬行离开来躲避对方的攻击, 定为防御行为

攻击和防御的行为特征参考 Bentivenha 等 (2016 年) 及施建琴等 (2021 年) 的描述。
Behavioral characteristics of attack and defense refer to the description of Bentivenha *et al.* (2016) and Shi *et al.* (2021).

表 3 草地贪夜蛾和棉铃虫幼虫体长和体重
Table 3 Length and body weight of *Spodoptera frugiperda* and *Helicoverpa armigera* larvae

	龄期 Instar	体长 (mm) Length (mm)	体重 (mg) Weight (mg)
草地贪夜蛾 <i>S. frugiperda</i>	4 龄 4 stage	11.0±0.49	14.0±0.01
	5 龄 5 stage	17.6±0.50	68.1±0.03
	6 龄 6 stage	24.1±0.40	168.5±0.06
棉铃虫 <i>H. armigera</i>	4 龄 4 stage	14.84±0.57	13.2±0.03
	5 龄 5 stage	21.24±0.61	65.1±0.03
	6 龄 6 stage	28.28±1.33	156.3±0.04

2 结果与分析

2.1 棉铃虫种内竞争的行为表现

棉铃虫种内竞争行为主要表现为以头部接触和猛击为代表的攻击行为, 其中头部接触行为出现的频率在各龄期处理组合中没有显著差异 (P>0.05), 而猛击行为在 6 龄 (vs. 5 龄) 幼虫竞争中表现最强烈, 占其竞争总行为的 51.0%±2.3%, 且显著高于其在 4 龄 (vs. 4 龄) 和 5 龄

(vs. 6 龄) 出现的频率 ($F=27.93$, $P<0.001$) (表 4)。棉铃虫的离开和畏缩行为出现频率较低,最高仅为 $16.8\%\pm 3.3\%$ 和 $14.0\%\pm 2.6\%$ (表 4)。从存活率上看,同龄幼虫竞争,可导致 25%-40% 的幼虫死亡,不同龄期幼虫竞争时,较高龄期幼虫可以 100%存活,而较低龄期幼虫仅 50%存活 (表 4)。

2.2 相同龄期草地贪夜蛾和棉铃虫种间竞争行为表现

同一龄期草地贪夜蛾和棉铃虫幼虫竞争时,二者都主要表现为以头部接触和猛击行为为代表的攻击行为 (图 1: A-C)。在攻击行为中,4 龄草地贪夜蛾幼虫的猛击行为频率 ($34.9\%\pm 0.09\%$) 显著高于同龄棉铃虫幼虫猛击行为频率

表 4 棉铃虫幼虫在种内竞争时的行为比例 (%) 及存活率 (%)
Table 4 Percentage of intraspecific competition behaviors of *Helicoverpa armigera* larvae and their survival rates (%)

行为 Behavior	龄期组合 Stage combinations				
	4 龄 (vs. 4 龄) 4th (vs. 4th)	5 龄 (vs. 5 龄) 5th (vs. 5th)	6 龄 (vs. 6 龄) 6th (vs. 6th)	5 龄 (vs. 6 龄) 5th (vs. 6th)	6 龄 (vs. 5 龄) 6th (vs. 5th)
头部接触 Head touching	35.2±5.9 aA	36.2±3.5 aA	38.8±3.5 aA	46.1±3.1 aA	39.2±1.2 aA
猛击 Strike	34.0±5.4 aB	41.4±3.4 aAB	41.5±1.6 aAB	38.7±3.5 aB	51.0±2.3 bA
畏缩 Recoil	16.8±3.3 bA	13.8±2.0 bAB	9.4±1.5 bBC	7.8±2.2 bBC	5.5±1.2 cC
离开 Move away	14.0±2.6 bA	8.6±2.6 bAB	10.3±2.6 bAB	7.4±3.1 bAB	4.4±1.9 cB
存活率 (%) Survival rate (%)	75.0	72.5	60.0	50.0	100.0

表中数据为平均值±标准误, 同列数据后标有不同小写字母表示差异显著, 同行数据后标有不同大写字母表示差异显著 ($P<0.05$, Tukey 氏检验)。
Date in the table are mean ±SE, and followed by the different uppercase letters in the same column indicate significant differences, while followed by the different lowercase letters in the same raw indicate significant differences ($P<0.05$, Tukey's test).

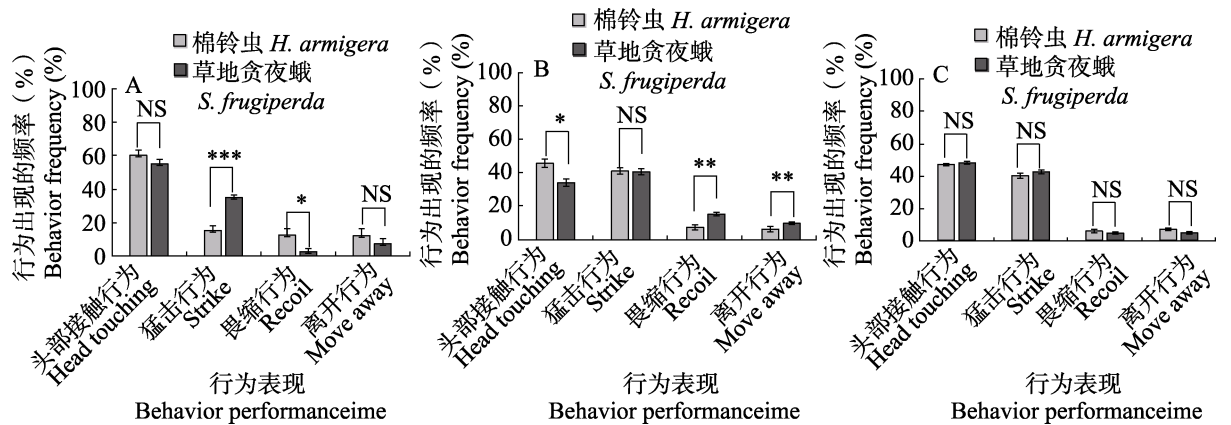


图 1 相同龄期草地贪夜蛾和棉铃虫幼虫种间竞争行为表现
Fig. 1 Behavior of interspecific competition between *Spodoptera frugiperda* and *Helicoverpa armigera* larvae at the same instar

A. 4 龄棉铃虫与 4 龄草地贪夜蛾竞争; B. 5 龄棉铃虫与 5 龄草地贪夜蛾竞争; C. 6 龄棉铃虫与 6 龄草地贪夜蛾竞争。
图中数据均以平均值±标准误表示。柱上星号表示经 t -test 检验存在显著性差异, ($* P<0.05$, $** P<0.01$, $*** P<0.001$), NS 表示没有显著性差异 ($P>0.05$)。下同。
A. 4th *H. armigera* vs 4th-*S. frugiperda*; B. 5th *H. armigera* vs 5th *S. frugiperda*; C. 6th *H. armigera* vs 6th *S. frugiperda*.
Data are mean±SE. Histograms with asterisk indicate significant differences ($* P<0.05$, $** P<0.01$, $*** P<0.001$) by t -test, while NS shows no significant difference. The same as below.

($15.2\% \pm 0.11\%$) ($t = -5.92, P < 0.001$), 5 龄草地贪夜蛾幼虫头部接触出现的频率 ($34.1\% \pm 0.09\%$) 显著低于同龄棉铃虫幼虫头部接触出现的频率 ($45.7\% \pm 0.1\%$) ($t = 3.46, P < 0.05$)。在防御行为中, 4 龄草地贪夜蛾幼虫畏缩行为出现的频率 ($2.6\% \pm 0.08\%$) 显著低于棉铃虫的畏缩行为频率 ($12.5\% \pm 0.16\%$) ($t = -5.92, P < 0.001$), 5 龄草地贪夜蛾畏缩 ($15.4\% \pm 0.04\%$) 和离开行为 ($9.9\% \pm 0.03\%$) 出现的频率显著高于这两种行为在棉铃虫上出现的频率 (畏缩: $7.4\% \pm 0.06\%$, $t = -4.23, P < 0.01$; 离开: $6.3\% \pm 0.06\%$, $t = -2.65, P < 0.01$)。其他攻击和防御行为在各个处理之间均无显著差异 ($P > 0.05$)。

2.3 不同龄期草地贪夜蛾和棉铃虫种间竞争行为表现

不同龄期的草地贪夜蛾和棉铃虫竞争时, 二者都主要表现为头部接触和猛击行为(图 2: A, B)。5 龄草地贪夜蛾幼虫头部接触和猛击行为出现的频率分别为 ($44.3\% \pm 0.07\%$) 和 ($36.3\% \pm 0.23\%$), 均显著低于这两种行为 (头部接触: $t = -3.32, P < 0.05$; 猛击行为: $t = -3.30, P < 0.05$) 在 6 龄棉铃虫幼虫上出现的频率 (图 2: A), 6 龄草地贪夜蛾幼虫头部接触行为出现的频率为 $56.1\% \pm 0.34\%$, 显著高于 5 龄棉铃虫头部接触行为出现的频率 ($t = -3.30, P < 0.05$), 但猛击行

为出现的频率在二者间差异不显著 ($P > 0.05$) (图 2: B)。在两个龄期组合中, 低龄幼虫的畏缩行为出现的频率均显著高于高龄幼虫 ($P < 0.05$) (图 2: A, B)。

2.4 草地贪夜蛾和棉铃虫在竞争后的存活率

在相同龄期的草地贪夜蛾和棉铃虫的种间竞争中, 4-6 龄的草地贪夜蛾的幼虫存活率分别为 83.3%、86.6% 和 80.0%, 与同一龄期的棉铃虫相比, 均无显著差异 ($P > 0.05$)。不同龄期竞争时, 5 龄草地贪夜蛾存活率为 80.0%, 显著低于 6 龄棉铃虫的存活率 (100%) ($\chi^2 = 16.6, P < 0.01$), 5 龄棉铃虫的存活率为 56.7%, 也显著低于 6 龄草地贪夜蛾的存活率 (100%) ($\chi^2 = 6.67, P < 0.01$) (表 5)。

3 讨论

入侵害虫草地贪夜蛾和本土害虫棉铃虫都是我国玉米上重要害虫, 对我国玉米的品质和产量造成严重威胁。二者在玉米灌浆期都主要为害玉米雌穗, 2 个生态位相似的物种, 通常产生种间竞争, 而种间竞争最激烈的结果就是竞争取代。2019 年在云南冬季甜玉米上的调查结果显示, 草地贪夜蛾田间为害明显重于棉铃虫。草地贪夜蛾与棉铃虫的种间关系以及其是否会取代棉铃虫引起了研究人员的重点关注。

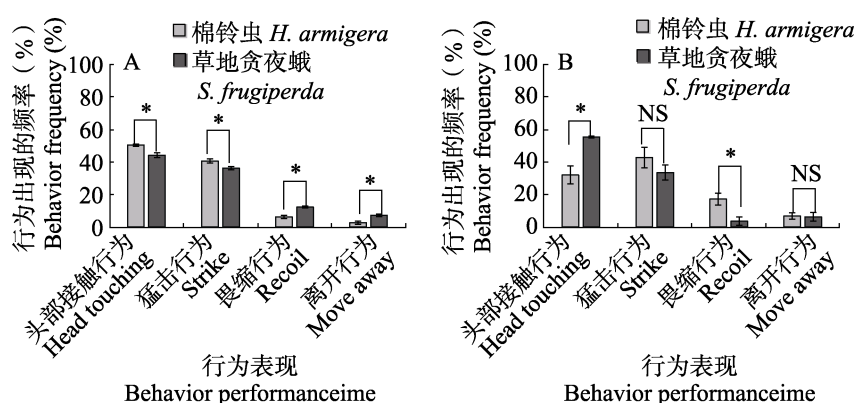


图 2 不同龄期草地贪夜蛾和棉铃虫幼虫种间竞争行为表现

Fig. 2 Behavior of interspecific competition between *Helicoverpa armigera* and *Spodoptera frugiperda* larvae at different instars

A. 6 龄棉铃虫与 5 龄草地贪夜蛾竞争; B. 5 龄棉铃虫与 6 龄草地贪夜蛾竞争。

A. 6th *H. armigera* vs 5th *S. frugiperda*; B. 5th *H. armigera* vs 6th *S. frugiperda*.

表 5 种间竞争中草地贪夜蛾与棉铃虫存活率 (%)

Table 5 Survival rate (%) of *Spodoptera frugiperda* and *Helicoverpa armigera* in interspecific competition

龄期 Instar	草地贪夜蛾 <i>S. frugiperda</i>	棉铃虫 <i>H. armigera</i>	χ^2	<i>P</i>
4 龄 (vs. 4 龄) 4th (vs. 4th)	83.3	76.7	0.42	0.52
5 龄 (vs. 5 龄) 5th (vs. 5th)	86.6	73.3	1.66	0.19
6 龄 (vs. 6 龄) 6th (vs. 6th)	80.0	63.3	2.05	0.15
5 龄 (vs. 6 龄) 5th (vs. 6th)	80.0	100.0	16.60	<0.01
6 龄 (vs. 5 龄) 6th (vs. 5th)	100.0	56.7	6.67	<0.01

括号外为草地贪夜蛾, 括号里为棉铃虫。

In the first column, the insect outside parentheses is *S. frugiperda*, and the insect in parenthesis is *H. armigera*.

草地贪夜蛾和棉铃虫都具有自相残杀特性, 攻击性明显 (李哲等, 2006; 王道通等, 2019), 因此, 二者相遇时的竞争行为表现对其争夺有限的空间和食物资源至关重要。本研究结果显示同一龄期的草地贪夜蛾与棉铃虫竞争时, 双方均表现出猛烈的进攻行为, 但从攻击频率和存活率上看, 草地贪夜蛾略占优势 (图 1, 表 5)。不同龄期的草地贪夜蛾和棉铃虫相遇时, 较高龄幼虫占据绝对优势。这与 Kakimoto 等 (2003) 及 Kristensen 等 (2009) 研究结果一致, 即不同龄期组成的种群中, 被残杀的对象都趋向于低龄幼虫。Bentivenha 等 (2016) 在 2 龄和 4 龄的草地贪夜蛾与美洲棉铃虫 *Helicoverpa zea* 和棉铃虫的种间竞争行为中发现, 草地贪夜蛾在与同一龄期的或者与较低龄期的美洲棉铃虫、棉铃虫竞争中优势明显, 这与本实验结果互为补充 (Bentivenha *et al.*, 2017), 进一步说明龄期是决定草地贪夜蛾和棉铃虫竞争行为表现的重要因素。那么, 草地贪夜蛾和棉铃虫在玉米田发生的先后顺序以及二者的生长发育速率是决定二者竞争行为表现的关键, 谁先发生, 谁先发育到高龄幼虫, 谁就会在竞争中占据优势 (Bentivenha *et al.*, 2016)。

本研究仅在环境可控的室内条件下从竞争行为这一昆虫个体生物学角度明确了高龄草地贪夜蛾与高龄棉铃虫之间的竞争关系, 虽然二者相遇时均表现出激烈的攻击行为, 但不会发生一方完全被取食的现象, 即使是 5 龄棉铃虫与 6 龄草地贪夜蛾竞争时, 棉铃虫仍然有 50% 的个体可以存活。此外, 草地贪夜蛾与棉铃虫的种间竞争

关系复杂, 会受到寄主植物、温湿度、天敌、药剂多种外在因子的影响, 因此 需要在考虑上述多种外在影响因素影响的前提下, 进一步研究二者在田间的种间竞争关系。

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