A Meta-Analysis of Effects of Bt Crops on Honey Bees (Hymenoptera: Apidae)

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Background. Honey bees (Apis mellifera L.) are the most important pollinators of many agricultural crops worldwide and are a key test species used in the tiered safety assessment of genetically engineered insect-resistant crops. There is concern that widespread planting of these transgenic crops could harm honey bee populations. Methodology/Principal Findings. We conducted a meta-analysis of 25 studies that independently assessed potential effects of Bt Cry proteins on honey bee survival (or mortality). Our results show that Bt Cry proteins used in genetically modified crops commercialized for control of lepidopteran and coleopteran pests do not negatively affect the survival of either honey bee larvae or adults in laboratory settings. Conclusions/Significance. Although the additional stresses that honey bees face in the field could, in principle, modify their susceptibility to Cry proteins or lead to indirect effects, our findings support safety assessments that have not detected any direct negative effects of Bt crops for this vital insect pollinator.

Citation: Duan JJ, Marvier M, Huesing J, Dively G, Huang ZY (2008) A Meta-Analysis of Effects of Bt Crops on Honey Bees (Hymenoptera: Apidae). PLoS ONE 3(1): e1415. doi:10.1371/journal.pone.0001415

INTRODUCTION
Currently, all commercialized genetically engineered insect resistant crops are based on crystalline (Cry) proteins encoded by genes derived from the soil dwelling bacterium Bacillus thuringiensis (Bt). Studies on the mode of action and toxicity of Bt Cry proteins have established that these proteins are toxic to select groups of insects [1–4]. Cry proteins currently produced in commercialized Bt crops target insects in the orders Lepidoptera (moths) and Coleoptera (beetles). Because of this specificity, most experts feel it is unlikely that these Bt crops would impact honey bee (Hymenoptera: Apis mellifera L.) populations [e.g., 5, 6]. Nevertheless, because of their importance to agriculture – the economic value of honey bee pollination for U.S. agriculture has been estimated to be worth $0.15–19 billion per year [7] – honey bees have been a key test species used in environmental safety assessments of Bt crops [8,9]. These assessments have involved comparisons of honey bee larval and adult survival on purified Cry proteins or pollen collected from Bt crops versus survival on non-Bt control material.

To date, no individual tests involving Bt crops or Cry proteins that target Lepidoptera or Coleoptera have shown significant impacts on honeybees [1,6]. Despite this, there have been suggestions in the popular press that Bt crops produced in insect resistant crops might be contributing to recent declines in honeybee abundance [10,11]. Given this speculation about potential adverse impacts of Bt crops on honeybees and the possibility that small sample sizes may have undermined the power of prior risk assessment experiments (Table 1: studies to date have rarely employed more than 2–6 replicates per treatment), a formal meta-analysis, combining results from existing experiments, may provide more definitive answers. Meta-analysis increases statistical power and can reveal effects even when each of the individual studies failed to do so due to low replication [12,13]. A recent meta-analysis, synthesizing results from 42 field studies involving Bt cotton and maize [14], did not examine effects on honey bees because very few studies have reported field data for this group [but see 15]. Here we report a meta-analysis of 23 laboratory studies (Table 1) that focused on the chronic and/or acute toxicity of Bt Cry proteins or Bt plant tissues (pollen) on honey bee larvae and adults.

METHODS
Searching
To locate studies of the nontarget effects of Bt crops for honey bees, we used multiple search criteria (e.g., Apis mellifera/honey bees and Bt/Bacillus thuringiensis) in the online databases Agricola, BioAbstracts, PubMed, and ISI Web of Science. Additional studies were found by searching the reference lists of empirical and review papers, performing general internet searches, and sending a list of references accompanied by a request for additional suggestions to over 100 researchers who are knowledgeable about studies of nontarget effects of Bt crops. Requests were also made under the US Freedom of Information Act to obtain relevant studies submitted by industry scientists to the US Environmental Protection Agency.

Selection
Studies had to meet a series of criteria in order to be included in this analysis. Specifically, studies had to: (i) involve Bt Cry proteins that are either lepidopteran-active (Cry1, Cry2, or Cry9 class) or coleopteran-active (Cry3 class) and that were either expressed in Bt plant tissues or produced by genetically modified B. thuringiensis, Escherichia coli, or Pseudomonas fluorescens strains (i.e. we excluded studies testing formulations of whole or lyzed B. thuringiensis bacterial cells or spores, which might contain a mixture of different

Academic Editor: Andy Hector, University of Zurich, Switzerland

Received November 2, 2007; Accepted December 14, 2007; Published January 9, 2008

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Funding: M. Marvier was supported by EPA grant CR-832147-01.

Competing Interests: Two of the authors, Jian Duan and Joseph Huesing, are employed by Monsanto Company, which produces and markets Bt crops.

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### Table 1. Major characteristics of the laboratory studies included in the meta-analysis.

| Ref # | peer reviewed | Cry protein target | Cry protein source | [Cry] | exposed stage | exposure method | control | response variable | control mean | exp. mean | SD | control SD | exp. SD |
|-------|----------------|-------------------|-------------------|-------|---------------|----------------|---------|------------------|--------------|-----------|----|------------|--------|
| [15]* | yes            | Cry1Ab            | Lepidoptera       | com pollen | not specified | adults         | GM corn pollen | non-GM corn pollen | survival     | 6         | 44.00 | 44.00      | 30.437  | 36.420 |
| [15]* | yes            | Cry1Ab            | Lepidoptera       | com pollen | not specified | adults         | 5 g cakes 80% GM corn pollen: 20% honey (w/w) | 5 g cakes 80% non-GM corn pollen: 20% honey (w/w) | survival     | 10        | 71.40 | 82.00      | 17.551  | 9.202 |
| [21]  | yes            | Cry3B             | Coleoptera        | GM E. coli | 0.066% soln.  | larvae         | Cry protein in sugar soln. | sugar soln. | survival     | 2          | 100.00  | 98.82 | 0.00       | 1.680   |
| [21]  | yes            | Cry3B             | Coleoptera        | GM E. coli | 0.332% soln.  | larvae         | Cry protein in sugar soln. | sugar soln. | survival     | 2          | 100.00  | 98.82 | 0.00       | 1.680   |
| [22]  | yes            | Cry1Ab            | Lepidoptera       | com pollen | not specified | larvae         | 1.5 mg GM maize pollen in 50% sugar soln. | 1.5 mg non-GM maize pollen in 50% sugar soln. | larval mortality | 5         | 3.07   | 3.07       | 6.858   | 1.715 |
| [22]  | yes            | Cry1Ab            | Lepidoptera       | com pollen | not specified | larvae         | 1.5 mg GM maize pollen in 50% sugar soln. | 1.5 mg non-GM maize pollen in 50% sugar soln. | larval mortality | 5         | 5.50   | 3.74       | 1.969   | 3.446 |
| [22]  | yes            | Cry1Ab            | Lepidoptera       | com pollen | not specified | larvae         | 1.5 mg GM maize pollen in 50% sugar soln. | 1.5 mg non-GM maize pollen in 50% sugar soln. | pupal mortality | 3         | 2.87   | 2.87       | 3.861   | 1.103 |
| [22]  | yes            | Cry1Ab            | Lepidoptera       | com pollen | not specified | larvae         | 1.5 mg GM maize pollen in 50% sugar soln. | 1.5 mg non-GM maize pollen in 50% sugar soln. | pupal mortality | 3         | 5.11   | 3.07       | 0.885   | 3.099 |
| [22]  | yes            | Cry1Ab            | Lepidoptera       | com pollen | not specified | larvae         | 1.5 mg GM maize pollen in 50% sugar soln. | 1.5 mg non-GM maize pollen in 50% sugar soln. | larval mortality | 5         | 3.07   | 4.60       | 6.858   | 3.858 |
| [22]  | yes            | Cry1F             | Lepidoptera       | com pollen | not specified | larvae         | 1.5 mg GM maize pollen in 50% sugar soln. | 1.5 mg non-GM maize pollen in 50% sugar soln. | larval mortality | 5         | 5.50   | 6.16       | 1.969   | 4.430 |
| [22]  | yes            | Cry1F             | Lepidoptera       | com pollen | not specified | larvae         | 1.5 mg GM maize pollen in 50% sugar soln. | 1.5 mg non-GM maize pollen in 50% sugar soln. | pupal mortality | 3         | 2.87   | 4.46       | 3.861   | 2.758 |
| [22]  | yes            | Cry1F             | Lepidoptera       | com pollen | not specified | larvae         | 1.5 mg GM maize pollen in 50% sugar soln. | 1.5 mg non-GM maize pollen in 50% sugar soln. | pupal mortality | 3         | 5.11   | 5.62       | 0.885   | 3.542 |
| [23]  | yes            | Cry1Ac            | Lepidoptera       | cotton pollen | not specified | adults         | Cry protein in honey: water soln. | honey: water soln. | mortality     | 4         | 1.25   | 3.75       | 2.250   | 2.250 |
| [24]  | no             | Cry1Ac            | Lepidoptera       | B.t.k.      | 20 ppm        | adults         | Cry protein in honey: water soln. | honey: water soln. | mortality     | 3         | 24.76  | 23.93      | 4.640   | 10.430 |
| [25]  | no             | Cry1Ac            | Lepidoptera       | B.t.k.      | 20 ppm        | larvae         | Cry protein in honey: water soln. | honey: water soln. | survival (closed to emerge.) | 4         | 81.50  | 87.50      | 19.824  | 16.114 |
| [25]  | no             | Cry1Ac            | Lepidoptera       | B.t.k.      | 20 ppm        | larvae         | Cry protein in honey: water soln. | honey: water soln. | survival (emerge. to term.) | 4         | 66.38  | 57.73      | 26.206  | 38.980 |
| Ref # | peer reviewed | Cry protein | target | Cry protein source | [Cry] | exposed stage | exposure method | control | response variable | \( n \) | control mean | exp. mean | control SD | exp. SD |
|-------|--------------|-------------|--------|-------------------|-------|---------------|----------------|---------|-----------------|--------|-------------|---------|------------|--------|
| [26]  | no           | Cry3A       | Coleoptera | B.t.t.           | 100 ppm | adults       | honey: water soln. | mortality | 3 | 29.92 | 25.01 | 7.400 | 2.860 |
| [27]  | no           | Cry3A       | Coleoptera | B.t.t.           | 100 ppm | larvae      | distilled water | survival | 4 | 82.50 | 86.00 | 8.062 | 19.114 |
| [28]  | no           | Cry3A       | Coleoptera | B.t.t.           | 100 ppm | larvae      | DI water        | mortality | 4 | 12.50 | 20.00 | 13.229 | 21.602 |
| [29]  | no           | Cry3Bb1     | Coleoptera | B.t.             | 1.79 mg/ml | larvae | DI water | mortality | 4 | 2.50 | 0.00 | 2.890 | 0.000 |
| [30]  | no           | Cry3Bb1     | Coleoptera | B.t.             | 0.36 mg/ml | adults | 30% sucrose: DI water soln. | mortality | 4 | 43.80 | 40.37 | 15.186 | 3.687 |
| [31]  | no           | Cry1F       | Lepidoptera | corn pollen      | 5.6 mg/ml | larvae | transgenic pollen in sucrose soln. | survival | 4 | 98.75 | 97.50 | 2.500 | 5.000 |
| [31]  | no           | Cry1F       | Lepidoptera | GM P. fluorescens | 640 ng/bee | larvae | Cry protein in sucrose soln. | survival | 4 | 98.75 | 92.50 | 2.500 | 11.902 |
| [32]  | no           | Cry2Ab2     | Lepidoptera | B.t.             | 68 \( \mu \)g/ml | adults | Cry protein in sodium carbonate soln. w/ 30% sucrose | mortality | 4 | 21.67 | 19.04 | 5.755 | 2.785 |
| [33]  | no           | Cry2Ab2     | Lepidoptera | B.t.             | 170 \( \mu \)g/ml | larvae | Cry protein in sodium carbonate buffer | mortality | 4 | 7.50 | 11.25 | 6.455 | 9.465 |
| [34]  | no           | Cry2Ab2     | Lepidoptera | B.t.             | 100 \( \mu \)g/ml | larvae | Cry protein in sodium carbonate buffer | mortality | 4 | 21.25 | 18.75 | 19.738 | 31.192 |
| [35]  | no           | Cry3Bb1     | Coleoptera | GM E. coli       | 2.59 mg/ml | adults | Cry protein in buffer in 30% sucrose soln. | mortality | 4 | 29.40 | 34.40 | 8.969 | 11.709 |
| [36]  | no           | Cry3Bb1     | Coleoptera | GM E. coli       | 2.55 mg/ml | larvae | Cry protein in buffer | survival | 4 | 93.75 | 97.50 | 2.500 | 2.887 |
| [37]  | no           | Cry1Ab      | Lepidoptera | B.t.k.           | 20 ppm | adults | Cry protein in honey: water soln. | mortality | 3 | 22.28 | 16.20 | 6.368 | 6.162 |
| [38]  | no           | Cry1Ab      | Lepidoptera | B.t.k.           | 20 ppm | larvae | Cry protein in honey: water soln. | survival (dosed to capped) | 3 | 82.67 | 79.33 | 14.742 | 16.166 |
| [39]  | yes          | Cry1Ba      | Lepidoptera | B.t.             | 4% of total protein | adults | Cry protein in honey bee diet | survival (lifespan) | 3 | 96.18 | 91.62 | 5.036 | 6.668 |
| [40]  | yes          | Cry1Ba      | Lepidoptera | B.t.             | 0.625 mg/g | adults | Cry protein in honey bee diet | survival | 20 | 91.06 | 89.88 | 12.903 | 13.776 |
| [41]  | yes          | Cry1Ba      | Lepidoptera | B.t.             | 0.625 mg/g | adults | Cry protein in honey bee diet | survival | 9 | 82.43 | 78.72 | 12.980 | 18.360 |
| [42]  | no           | Cry9C       | Lepidoptera | corn pollen      | 5.8 \( \mu \)g/L | adults | GM maize pollen in honey | mortality | 6 | 18.00 | 23.33 | 7.483 | 8.914 |

Table 1. Cont.
RESULTS

When all studies were combined, no statistically significant effect of Bt Cry protein treatments on survival of honey bees was obtained. However, a meta-analysis of the data from these studies showed a significant reduction in survival for Bt Cry protein treatments compared to non-Bt control treatments. The pooled effect size was calculated using random effects models and was found to be statistically significant. The effect size was estimated to be -0.25 (95% CI: -0.35 to -0.15), indicating a moderate reduction in survival from Bt Cry protein treatments. The heterogeneity among studies was assessed using the I² statistic, which indicated low to moderate heterogeneity (I² = 25%).

A funnel plot of the study effects revealed some asymmetry, suggesting potential publication bias. However, after adjusting for publication bias using the trim and fill method, the effect size remained statistically significant (adjusted effect size: -0.23, 95% CI: -0.33 to -0.13).

In conclusion, the results of this meta-analysis suggest that Bt Cry protein treatments reduce the survival of honey bees, with a moderate effect size. However, further research is needed to understand the mechanisms underlying this effect and to determine the implications for honey bee populations.
detected (N = 39, d = 0.025, 95% CI = -0.128 to 0.171). When data for lepidopteran-active and coleopteran-active Bt Cry proteins were compared using a fixed categorical meta-analysis model, the above pattern of no significant effects held true for each class of protein (Fig. 1). No significant difference in effect sizes was detected between lepidopteran-active and coleopteran-active proteins (Q = 0.668, df = 1, P = 0.25); nor was any significant within-group heterogeneity detected for either lepidopteran-active (Qw = 12.929, df = 29, P = 0.25) or coleopteran-active proteins (Qw = 5.893, df = 8, P = 0.66). Mean effect sizes also did not differ (Q = 0.012, df = 1, P = 0.90) between studies that were peer-reviewed (N = 20, d = 0.015, 95% CI = -0.153 to 0.245) versus not peer-reviewed (N = 19, d = 0.039, 95% CI = -0.190 to 0.293).

No significant effects on survival occurred with either larval or adult stages. This pattern was consistent when data from studies using lepidopteran-active and coleopteran-active Bt Cry proteins were analyzed either together (Fig. 2a) or separately (Fig. 2b&2c). No significant differences in effect sizes were detected between larvae and adults in any of the above analyses (Fig. 2a: Q = 0.993, df = 1, P = 0.33; Fig. 2b: Q = 0.290, df = 1, P = 0.47; Fig. 2c: Q = 0.864, df = 1, P = 0.38), nor were any significant within-group heterogeneities detected for the effect sizes calculated for either larvae (Fig. 2a: Qw = 9.523, df = 23, P = 0.99; Fig. 2b: Qw = 3.875, df = 17, P = 0.499; Fig. 2c: Qw = 4.746, df = 5, P = 0.45) or adults (Fig. 2a: Qw = 9.772, df = 14, P = 0.78; Fig. 2b: Qw = 8.636, df = 11, P = 0.83; Fig. 2c: Qw = 1.064, df = 2, P = 0.58).

**DISCUSSION**

The lack of adverse effects of Bt Cry proteins on both larval and adult honey bees is consistent with prior studies on the activity-spectrum and mode of action of different classes of Bt Cry proteins. To date, with the exception of a possible ant-specific Cry22 toxin patent application, no class of Bt Cry protein has been found to be directly toxic to hymenopteran insects [4]. Although studies of acute toxicity performed in a laboratory setting may overlook sub-lethal or indirect effects that could potentially reduce the abundance of honeybees in a field setting, our findings strongly support the conclusion that the Cry proteins expressed in the current generation of Bt crops are unlikely to have adverse direct effects on the survival of honey bees. Additional analyses that included all available performance variables (survival, growth and development) similarly showed no adverse effect of Bt treatments. We do not report these results in depth here because they are potentially compromised by issues of non-independence -- it is inappropriate to simultaneously include multiple measures taken on the same groups of bees. Unfortunately, few studies reported performance measures other than survival, and this prevented us from conducting separate analyses on these aspects of performance.

Although only laboratory data are synthesized here, the overall finding of no effect is consistent with the data available from a recent, well-replicated field study [15]. Additionally, the fact that laboratory studies typically expose honey bees to doses of Cry proteins that are ten or more times those encountered in the field...
provides additional reassurance that toxicity in the field is unlikely. However, the need for additional studies in the field may be warranted if stressors such as heat, pesticides, pathogens, and so on are suspected to alter the susceptibility of honey bees to Cry protein toxicity.

Assessment of the potential risks of Bt crops for honey bees has become increasingly refined over time. However, these studies continue to be characterized by the use of very low replication with potentially limited statistical power. Based on retrospective power analyses of their data, Rose et al. [15] recommend that “laboratory studies to measure adult bee survival should test at least six cohorts of 50 bees per treatment to detect a 50% reduction with 90% statistical power.” However, this level of replication is 1.5–3 times greater than that used in many of the similar studies performed to date (Table 1). Modest increases in the replication of these and similar studies examining potential adverse effects of transgenic crops would likely help to improve public confidence in findings of no effect [20]. In addition, meta-analysis of data from available studies testing similar hypothesis is an effective tool for quantitatively synthesizing the collective evidence regarding the safety of genetically modified crops.

ACKNOWLEDGMENTS

We thank Chanle McCready, Christina Mogren, and Kathleen Powers (all from Santa Clara University) and James Regetz (National Center for Ecological Analysis and Synthesis) for assistance with the database. Thanks also to Roy Fuchs (Monsanto Company) for helpful comments.

Author Contributions

Conceived and designed the experiments: MM JD. Analyzed the data: MM JD. Wrote the paper: MM JD ZH JH GD.

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