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Inheritance Pattern and Cross-Resistance Assessment of Flonicamid Resistance in the Biological Control Agent *Chrysoperla carnea* (Neuroptera: Chrysopidae)

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ABSTRACT

A field-collected laboratory population of *Chrysoperla carnea*, a polyphagous predator important in integrated pest management, was subjected to flonicamid selection pressure for three generations using a micro-droplet topical bioassay. Following selection, the flonicamid-selected strain exhibited 6.83-fold resistance (LC50 = 260,730 ppm; 95% FL = 148,090–1,561,600 ppm) compared with the unselected strain (LC50 = 38,122 ppm; 95% FL = 23,259–138,440 ppm). Reciprocal crosses between resistant and susceptible parents produced overlapping 95% FLs, demonstrating autosomal inheritance with no detectable maternal or sex-linked effects. Dominance metrics indicated incomplete to partial dominance of resistance (DLC = 0.60 for F1; DLC = 0.55 for F2). Effective dominance estimates at four diagnostic doses (27,875; 62,500; 125,000; 272,000 ppm) yielded ED values of 0.53, 0.79, 0.91, and 0.88, respectively, showing increased dominance at higher doses. Chi-square goodness-of-fit tests rejected the null hypothesis of monogenic inheritance ($p < 0.05$), confirming a polygenic resistance model. Cross-resistance bioassays further revealed substantial co-selection effects, with resistance ratios of 24.35-fold for acetamiprid, 23.58-fold for triazophos, and 15.17-fold for deltamethrin, comparing initial and final LC50 values that showed non-overlapping 95% FLs. These results indicate that flonicamid resistance in *C. carnea* is a polygenic, autosomal, and incompletely to partially dominant trait. The findings provide genetic foresight for incorporating resistant predator populations into insecticide-compatible IPM programs and highlight the importance of mode-of-action-based chemical rotation to mitigate resistance co-selection in beneficial predator populations.

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INTRODUCTION

Chrysoperla carnea (Stephens) (Neuroptera: Chrysopidae), commonly known as the green lacewing, is among the most widely utilized and ecologically resilient generalist predators in agroecosystems. It plays a vital role in conservation and augmentative biological control, preying on a broad spectrum of soft-bodied pests, including

aphids, whiteflies, jassids, mealybugs, and the eggs of several lepidopteran species. Lacewing larvae exhibit voracious predatory activity across three instars, whereas adults are palyno-glycophagous, relying on nectar, pollen, and honeydew for reproduction. Under increasing prey density, *C. carnea* shows a type-II functional response, a characteristic that enhances its regulatory potential against homopteran pest outbreaks. Individual field and laboratory studies have reported larval consumption exceeding several hundred aphids or whiteflies prior to pupation, underlining its capacity for pest suppression at high prey densities.

Despite its importance, predator populations often face indirect and direct exposure to insecticides applied for rapid pest knockdown, particularly in systems dominated by chemical-based protection. Intensive and continuous use of insecticides has led to widespread resistance in pest populations, thereby shifting the ecological balance between chemical and biological control tactics. Importantly, several natural enemies, including lacewings and other predators, have demonstrated the capacity to evolve resistance under targeted selection pressure, either through direct contact or by consuming prey that has been previously exposed to toxicants. Resistance evolution in natural enemies remains a double-edged phenomenon. While resistance may allow predator persistence in sprayed fields—preserving predation services—co-selection for resistance across multiple chemistries can inadvertently reduce insecticide selectivity, constrain future chemical compatibility, and promote multidrug resistance syndromes in beneficial predator guilds.

Flonicamid is a nicotinamide-based insecticide that disrupts chordotonal stretch receptor signaling, targeting insect feeding and motor coordination without the acute knockdown mortality typically associated with nerve poisons. First commercialized in Japan in 2003 under the trade name Ulala®, flonicamid later entered international markets including Europe, the Americas, Brazil, and East Asia. It is generally considered to have low toxicity to vertebrates and pollinators, and is frequently categorized as compatible for sucking pest control in IPM programs. However, even compounds regarded as selective can drive resistance when applied under persistent directional selection, particularly in insects with metabolically flexible detoxification systems, such as cytochrome P450s, esterases, and glutathione S-transferases.

Genetic dissection of an evolved resistance trait in predators is essential for predicting its stability, dose-response dominance, and potential deployment in insecticide-compatible IPM frameworks. Unlike monogenic resistance, which follows predictable Mendelian segregation, polygenic resistance involves multiple loci with additive or interactive effects, potentially conferring broader stability under fluctuating selection; however, it also increases the probability of cross-resistance when metabolic pathways overlap. Although flonicamid resistance inheritance has been genetically characterized in pest species such as *Musca domestica*, *Tuta absoluta*, and *Bemisia tabaci*, inheritance architecture and cross-resistance potential following flonicamid selection remain unreported in beneficial predator *C. carnea*. This knowledge gap is significant for IPM programs aiming to conserve or intentionally deploy resistant natural enemy populations in conjunction with soft insecticide chemistries.

Therefore, this study was conducted to characterize: (1) the inheritance pattern of flonicamid resistance in a selected *C. carnea* laboratory strain, (2) the degree and effective dominance of resistance expression across diagnostic doses, and (3) the co-selection of cross-resistance to unrelated but commonly applied insecticides—acetamiprid (neonicotinoid), triazophos (organophosphate), and deltamethrin (pyrethroid). Understanding these genetic

resistance parameters will guide future IPM designs that strategically balance predator survival with insecticide compatibility and resistance management principles, particularly through the use of chemical rotation across non-overlapping modes of action.

MATERIALS AND METHODS

1. Rearing of *Chrysoperla carnea:*

The adult population of *C. carnea* was collected from the Agricultural field at Bahauddin Zakariya University (BZU), Multan, and brought to the Toxicology Laboratory of the Faculty of Agriculture, Department of Entomology. The adult has been transferred to cages for adult rearing whose dimension was (38 × 23 × 38 cm). They contain tiny holes on both sides for ventilation. The captured adults were reared on an artificial diet consisting of a mixture of 20 mL of water (H_2O), 2 mL of cereal, 2g of sugar, and 1g of honey. A wet cotton swab is placed in a rearing cage as a source of moisture and water. For egg laying, a black, glossy sheet was used in the cage, and the eggs were removed daily. The collected eggs have been transferred into gelatin capsules with the help of a camel hairbrush. After three days, the egg hatched, and the larvae were fed on pest eggs of *S. cerealella* and placed there until the start of pupation. The pupae had been shifted on tissue paper inside the cage. The collected population was designated as Field-Pop. The susceptible population (Lap-Pop) was unexposed to insecticide for 14 generations. The laboratory conditions were maintained at 28 ± 2℃, 60 ± 5% relative humidity, and a 14:10 hours L :D photoperiod (Mansoor & Shad, 2020).

2. Rearing of host *Sitotroga cerealella*

The Angoumois grain moth, *S. cerealella*, is a common host used in the rearing of *C. carnea* in the IR Lab. For that purpose, wheat was washed and placed under sunlight for 2-3 days. After drying, wheat was placed in metallic trays, and eggs of *S. cerealella* were sprinkled on each tray at a ratio of 1kg of wheat to 1 gram of eggs. The trays were then placed in a rearing chamber. The S. cerevisiae adults were collected in plastic bags using small pieces of off-white cloth, which were spread on trays and then transferred to plastic jars with a fine sieve attached to the bottom. The jars were placed on small plastic plates with starch on their surface, serving as an egg-laying medium for moths. The eggs are collected regularly by sieving the starch through a fine sieve. The sieved eggs were placed in a small petri dish and kept in a freezer for one day. These frozen eggs of the moth have been used as a diet for *C. carnea* larvae.

3. Insecticide:

The formulated insecticide flonicamid (Ulala® 50Df ICI) was used in this experiment.

3.1 Selection:

The collected field population of the biological control agent *C. carnea* is further divided into two sub-groups. One was known as the Unselected (Un-Sel) population, which had been left unexposed to insecticide, and the other, continuously selected with flonicamid insecticide for three generations (54^{th} to 57^{th}), was called the Flonica-Selected population of *Chrysoperla carnea*. For determining the dose of selection, an Initial bioassay was conducted using four different doses. Selection was always performed at $^{\text{the second}}$ instar of larvae. After the bioassay, the selected dose of flonicamid was applied to second-instar larvae of *C. carnea* using a microapplicator. After treatment with insecticide, eggs of *S. cerealella* were provided to *C. carnea* larvae. All experiments were conducted at 28 ± 2 °C, 60 ± 5% relative humidity, and a 14:10 hours L :D photoperiod. Data on selection were recorded after 72 hours to assess mortality.

3.2 Bioassays:

Four concentrations (272 k, 125 k, 62,500, and 27,875 ppm) of flonicamid were prepared in distilled water. For each concentration, 30 larvae were treated, and for control purposes, 30 larvae were treated with pure distilled water. In a single bioassay, 150 *C. carnea* larvae, including the

control, were used in the experiment. The bioassay was performed on second-instar larvae. These four concentrations of flonicamid were applied to the thorax of second instar larvae using a micro applicator. After treatment with insecticide, eggs of *S. cerealella* were provided to *C. carnea* larvae. All experiments were conducted at 28 ± 2℃, 60 ± 5% relative humidity, and a 14:10 hours L :D photoperiod. For checking the mortality percentage data of the bioassay, which was recorded after 72 hours.

3.3 Genetic Cross:

Reciprocal crosses were made to determine the inheritance of flonicamid resistance. The male and female Flonica-Sel and Unsel populations were crossed. To obtain C_1 progeny, 30 males of Flonica-Sel were crossed with 30 females of Unsel. The C_2 was obtained by crossing 30 females of Flonica-Sel with 30 males of Unsel. For the backcross (BC), males of F_1 were crossed with females of Unsel.

3.4 Degree of dominance:

The value of dominance of flonicamid resistance was obtained using the formula by Bourguet *et al.* (2000). For completely recessive D_{LC} =0, and for completely dominant D_{LC} =1

D_{LC} = (log LC_{RS}- log LC_S) / (log L_{CR} – log LC_S)

Where log LC_{RS}, log LC_S, and log LC_R are logs of LC_{50} of F_1/F_2, Unsel, and Flonica-SEL strains.

3.5 Cross-resistance analysis:

Four serial concentrations of deltamethrin, acetamiprid, triazophos, and alphacypermethrin were prepared in distilled water, and each concentration was replicated three times (Mansoor & Shad, 2020). A bioassay was performed on second-instar larvae. These serial concentrations were applied to the thorax of C. *carnea* larvae using a handheld micro applicator. Thirty *C. carnea* larvae were treated in each concentration with three replications (each replication containing 10 larvae) (Shah & Shad, 2020). Each bioassay contains a total of 150 *C. carnea* larvae, including the control. Treated larvae of *C. carnea* were placed one by one in gelatin capsules, which provided the *S. cerevisiae* eggs as the larval diet.

3.6 Data analysis:

Polo Plus software was used for analyzing toxicity data. Different parameters, such as LC_{50}, 95% Fiducial limits (FLS), slope with standard errors, and chi-square (χ2) values for each tested insecticide, were analyzed using Polo Plus software. The resistance ratio (RR) was calculated by dividing the LC_{50} of the respective strain by the LC_{50} of the Unsel population (Robertson, Currie *et al.*, 2003). Statistically, if the 95% FLS of the two LC_{50} values overlapped, then they were considered similar (Litchfield & Wilcoxon, 1949).

The following formula calculates cross resistance (CR):

CR= LC_{50} of final bioassay/ LC_{50} of initial bioassay

3.7 Statistical analysis:

Probit analysis was performed using the POLYPLUS software. This analysis produced the median lethal concentration (LC_{50}), 95% fiducial limits (FLs), standard error, slope value, degree of freedom, and chi-square value.

RESULTS AND DISCUSSION

Results

1. Flonicamid toxicity in *Chrysoperla carnea* strains

Flonicamid applied continuously exerted selection pressure from 27875 to 272K ppm until the 56th generation for the Flonica-Sel strain. After 56 generations of selection with flonicamid on *C. carnea*, resistance to flonicamid developed 6.83-fold compared to Unsel. The LC_{50} of Flonica-SEL was 260730 ppm, and that of Unsel was 38122ppm. The response of *C. carnea* was presented in Table 1. The resistance ratios of the Flonica-Sel population *of C. carnea*, F_1, F2, and backcross were 6.83, 0.46, 0.91, and 1.09, respectively.

Table 1. Toxicity of flonicamid in various *Chrysoperla carnea*

Strain	LC_{50}	FL (95%)	Slope ±SE	χ^2	df	P	RR	DL_c
Unsel	38122	23259-138440	1.08± 0.36	0.4	4	0.98		
Flonica-SEL	260730	148090-1561600	1.09±0.35	0.09	4	0.99	6.83	
F_1	121580	80080-222800	1.32± 0.34	0.67	4	0.95	0.46	0.60
F_2	110980	73867-188320	1.37± 0.34	0.51	4	0.97	0.91	0.55
BC	121580	80080-222800	1.32 ±0.34	0.64	4	0.95	1.09	

2. Maternal effect

The LC_{50} values of reciprocal crosses F_1 and F_2 were 121580 ppm and 110980 ppm, respectively, and did not differ significantly (95% FLs of F_1 and F_2 overlapped), indicating that resistance was autosomal and not sex-linked in the Flonica-Sel strain.

a. Monogenic Model of Flonicamid Resistance:

Backcrosses were examined using chi-square analysis to verify the null hypothesis of monogenic inheritance of flonicamid resistance following the Sokal and Rohlf (1981) method:

$$X^2 = (\boldsymbol{F - pn})\mathbf{2} / \boldsymbol{pqn}$$

In this equation, observed mortality is denoted by F, the tested concentration in backcross, n, the total number of larvae of *C.carnea* that are exposed to the tested concentration, p = the proportion of responses that are expected, and q=1-p. The null hypothesis of monogenic flonicamid resistance in *C. carnea* is rejected if the difference between the observed and expected mortality rates exceeds 50% of the experimental concentration. Chi-square analysis of the monogenic hypothesis for flonicamid resistance inheritance suggested that all four concentrations of flonicamid exhibited significant deviations between the expected and observed mortality rates ($p < 0.05$). This data showed us resistance evolution in Flonica-Sel was polygenic and controlled by more than one gene (Fig.1)

b. Level of dominance

The values of the degree of dominance were 0.60 and 0.55 for F_1 and F_2, respectively, which suggested an incompletely dominant nature of flonicamid resistance in *C. carnea.*

c. Effective dominance of Flonicamid resistance:

The effective dominance (ED) of the Flonica-Sel strain at four concentrations was 27,875, 62,500, 125,000, and 272,000 mg/L, with corresponding values of 0.53, 0.79, 0.91, and 0.88, respectively, indicating a partially dominant nature of resistance. An inverse relationship was present between the ED value and the concentration of Flonicamid; as the concentration value decreased, the ED value increased (Fig. 2).

Selection of the Flonica-Sel population with flonicamid resulted in the development of cross-resistance against acetamiprid, triazophos, and deltamethrin with RR values of 24.35, 23.58, and 15.17-fold, respectively. The initial and final bioassays were not similar, as the 95% FLs did not overlap, which confirms the development of cross-resistance in the Flonica-Sel population (Table 2).

Table 2. Cross-resistance to different insecticides in flonicamid-selected *Chrysoperla carnea*

Strain	Insecticide	LC50	(95% FL)	Slope(± SE)	X2	df	p	CR
Flonica G1	Acetamaprid	33.83	(24.52-55.11)	1.74(± o.39)	0.66	4	0.95616857	
Flonica G57	Acetamaprid	823.91	(520.96-2505.03)	1.20(± 0.37	0.26	4	0.99224784	24.3544192
Flonica G1	triazophas	261.63	(175.52-363.38)	1.72(±0.38)	1.35	4	0.852837	
flonica G57	Triazophas	6170.7	(3916.5-18424)	1.21(± 0.37	1.6	4	0.80879214	23.585598
flonica G1	deltamethrin	18.45	(15.40-22.140	0.09(±0.01)	0.51	4	0.9725202	
Flonica G 57	Deltamethrin	279.89	(168.22-1326.56)	1.13(± 0.37)	0.09	4	0.99901737	15.1701897

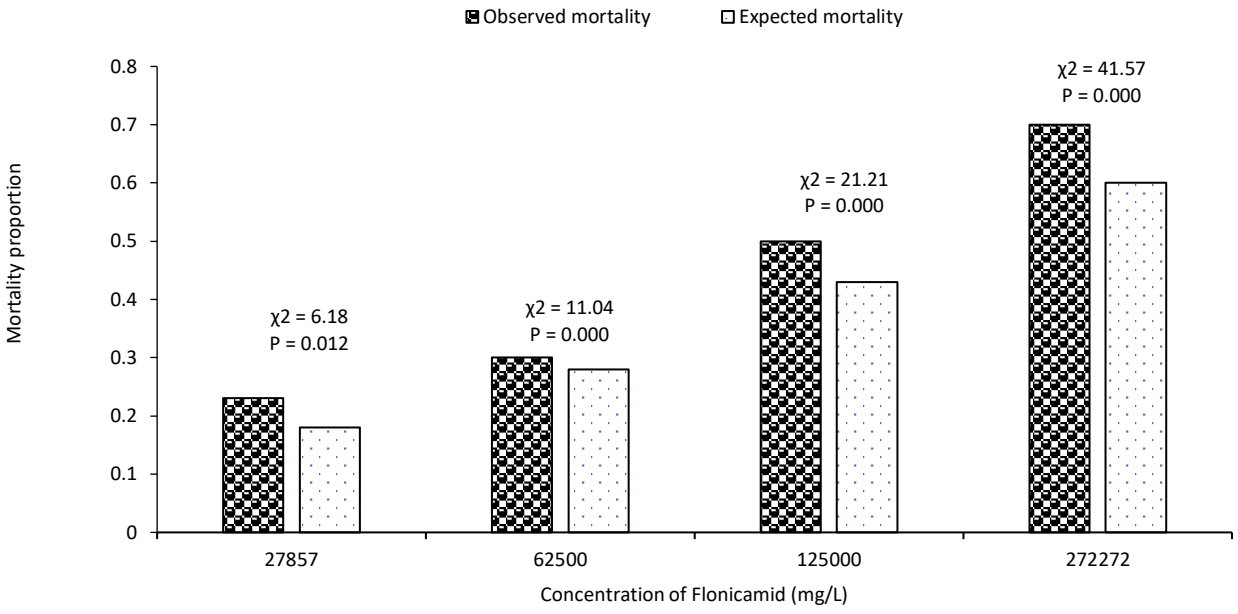


Figure 2. The Chi-square analysis for determining the monogenic or polygenic mode of inheritance of Flonicamid resistance by comparing mortality in *C. Carnea*

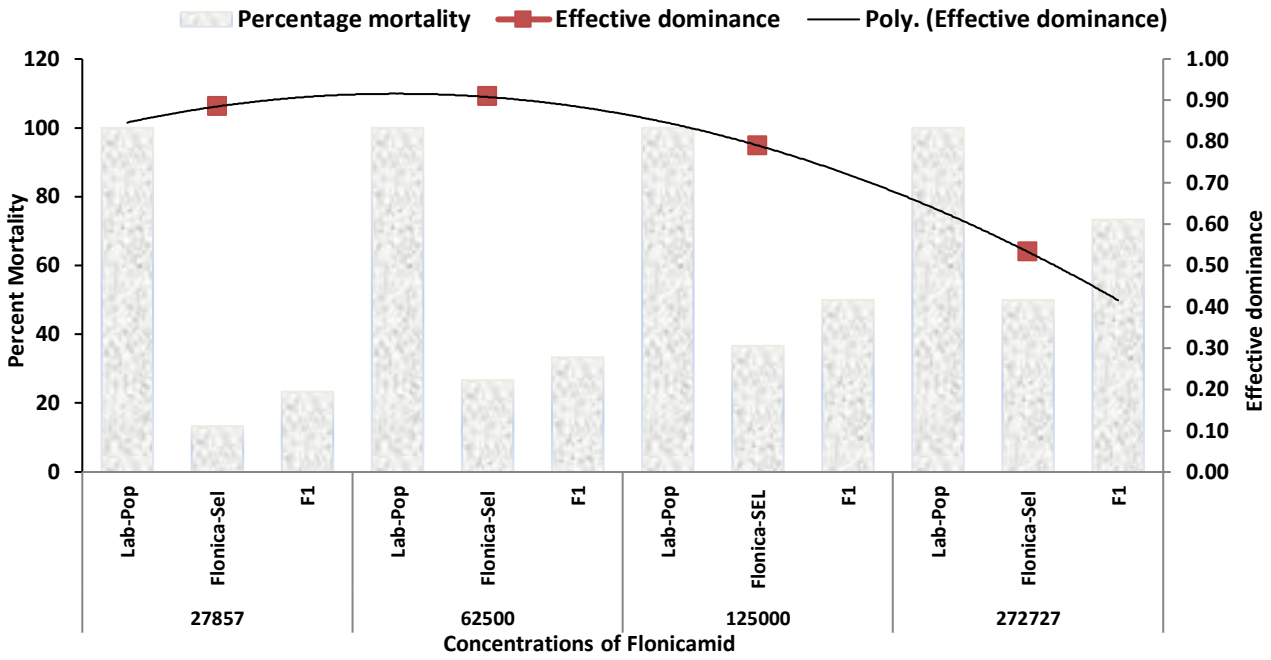


Figure 3. The Effective dominance (ED) of Flonicamid resistance in *C. carnea*

Discussion

The development of resistance to Flonicamid in *C. carnea* following 56 generations of continuous selection represents a significant shift in susceptibility, with the selected strain showing a 6.83-fold increase in resistance relative to the unselected population. The LC_{50} values for Flonica-SEL and Unsel were 260,730 ppm and 38,122 ppm, respectively, suggesting that extended exposure to flonicamid exerted intense selection pressure on *C. carnea* populations, promoting the survival of resistant phenotypes.

Such findings align with previous research indicating that insect predators, including lacewings, can develop tolerance to certain insecticides over successive generations (Desneux *et al.*, 2007). While Flonicamid is often regarded as a selective insecticide with reduced toxicity towards beneficial arthropods, the data from this study suggest that under prolonged and targeted selection, resistance can still evolve. This emphasizes the plasticity of insect detoxification and metabolic systems, and raises questions about the long-term sustainability of using even relatively safe chemicals in integrated pest management. (IPM) programs.

Interestingly, the relatively high LC_{50} value of the Unsel strain (38,122 ppm) also suggests that *C. carnea* possesses a baseline level of tolerance to flonicamid. This may reflect innate defence mechanisms or lower cuticular penetration in the species, factors previously reported in neuropteran resistance studies (Devine & Furlong, 2007). However, the more than sixfold increase in LC_{50} following selection pressure cannot be attributed to natural variability alone and is likely due to the upregulation of detoxifying enzymes, such as cytochrome P450 monooxygenases, glutathione S-transferases, or esterases, mechanisms commonly implicated in insecticide resistance (Li *et al.*, 2007).

The Evolution of resistance in a beneficial predator, such as *C. Carnea*, presents both challenges and opportunities. On one hand, it may allow these predators to survive in environments where flonicamid is applied, thus preserving biological control functions. Resistance

management strategies, such as rotating insecticides with different modes of action, employing refuges, and enhancing biological control, must be integrated into pest control programs to prevent the buildup of resistance in both pests and their natural enemies.

The analysis of LC_{50} values from reciprocal F_1 and F_2 crosses provides important insights into the genetic basis of resistance in the studied population. The observed LC_{50} values for the reciprocal F_1 crosses and the F_2 generations were not significantly different, as indicated by overlapping 95% fiducial limits. This lack of significant difference suggests that maternal effects are not influencing resistance and that the resistance trait is likely inherited in an autosomal fashion.

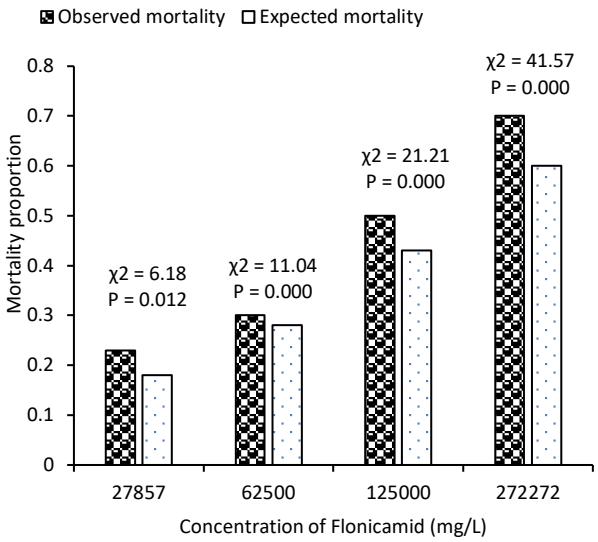
Maternal effects, which occur when the phenotype of an individual is influenced by the genotype or environment of the mother, can be identified when reciprocal crosses yield significantly different responses (Wolf & Wade, 2009). In this study, however, the reciprocal F_1 progeny showed similar LC_{50} values regardless of the direction of the crosses, suggesting that the maternal genotype does not affect the expression of resistance. If resistance were linked to sex chromosomes or influenced by cytoplasmic inheritance (e.g., mitochondrial DNA), significant differences in LC_{50} values between reciprocal crosses would be expected (Carrière, 2003).

Furthermore, the similar LC_{50} values between F_1 and F_2 generations imply that resistance is not autosomal but also likely governed by incompletely dominant or polygenic inheritance. However, further segregation analysis would be required to confirm the exact mood. Autosomal inheritance refers to the fact that the genes responsible for resistance are located on one of the non-sex chromosomes, allowing for equal expression in both sexes and independence from parental origin (Tabashnik *et al*., 1992).

The degree of dominance is a critical genetic parameter for characterizing the mode of inheritance of resistance traits in insect populations. In the present study, the values of the degree of dominance were calculated as 0.60 for the F_1 generation and 0.55 for the F_2 generation of *C. carnea* exposed to flonicamid, suggesting that resistance has an incompletely dominant nature. According to the criteria established by Stone (1968), a degree of dominance(D) value close to 1.0 suggests complete dominance, values near 0.5 indicate incomplete dominance, and values approaching 0 imply recessiveness. The values observed in this study fall within the range typical of incompletely dominant resistance.

Incomplete dominance in insecticide resistance has important implications for resistance management. In such cases, heterozygous individuals exhibit intermediate susceptibility between the resistant and susceptible homozygotes, which can slow the rate of resistance evolution under moderate selection pressure (Roush & McKenzie, 1987). However, under continuous and high selection pressure, even incomplete dominance can lead to a relatively rapid increase in the frequency of the resistance allele, especially if the resistance confers a significant survival advantage without affecting fitness (Tabashnik *et al*., 1992).

The observed pattern aligns with previous studies on other insect species, where flonicamid resistance has also been shown to be partial (Ullah et al., 2021). Given *C. Carnea*'s ecological role as a beneficial predator in integrated pest management systems (IPM systems), the emergence of resistance to flonicamid could affect both direct pest control and conservation biological control strategies. Therefore, the findings underscore the need for rotational use of insecticides with differing modes of action and implementation of resistance management strategies, such as refugia and dose optimization.



CONCLUSION

Flonicamid resistance in Chrysoperla carnea is inherited as a polygenic, autosomal, and incompletely to partially dominant trait with no measurable maternal or sex-linked influence. Flonicamid selection also co-selects for strong cross-resistance to acetamiprid, triazophos, and deltamethrin. These genetic parameters provide essential knowledge for forecasting resistance and designing insecticide-compatible, yet resistance-managed, IPM deployment strategies involving green lacewings. However, the observed cross-resistance spectrum highlights the importance of deliberate mode-of-action and detoxification-pathway-based chemical rotation to preserve long-term selectivity for beneficial predator populations.

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Arbaz Khan: Writing – original draft, Visualization,

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Data will be made available on request.

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