



Compensatory feeding by lady beetles: enhanced biocontrol potential of *Harmonia axyridis* against caterpillars in salinity-affected agro-ecosystems

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Abstract The increasing salinization of agricultural land is a pressing problem, altering how plants interact with organisms across multiple trophic levels. While salinity-induced changes in plant chemistry are known to affect insect herbivores, it remains unclear how these changes shape predator responses. Here, we examined how prey quality (tomato fruitworm caterpillars—*Helicoverpa zea*), shaped by soil salinity influences the foraging and consumptive behavior of the generalist predatory Asian lady beetle (*Harmonia axyridis*). We tested how salt stress in host plants (tomato – *Solanum lycopersicum*) and "salty" *H. zea* caterpillars as prey shape predator attraction, feeding dynamics, and survival. Caterpillars reared

on salt-treated artificial diets showed reduced protein content and slower growth. Despite this potentially lower prey quality, *H. axyridis* consumed more of the "salty" prey than the "non-salty" prey, suggesting a compensatory feeding response. Petri dish dual-choice assays showed no consistent preference for prey type during initial behavioral stages (touch, bite, consumption), but total intake was significantly higher for the "salty" caterpillars. In Y-tube olfactometer choice assays, predators were equally attracted to non salt-stressed and salt-stressed plants, indicating that salinity did not disrupt olfactory cue-mediated predator recruitment. Together, these results suggest that *H. axyridis* may adjust its feeding behavior to compensate for likely reduced prey quality and enhance biocontrol potential in salinity-affected systems.

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Introduction

Soil salinity is a critical abiotic stressor that affects a wide range of agriculturally important crops (Munns and Tester 2008; Ashraf et al. 2015). In arid and poorly irrigated regions, it impacts photosynthesis, reducing plant growth and crop yields, thereby threatening food security (Cuartero and Fernández-Muñoz 1998). Insect herbivores further intensify this problem by damaging crops and lowering productivity (Oerke 2006). While salinity's impacts on plant physiology are well studied (Cuartero and Fernández-Muñoz 1998; Munns and Gilliam 2015), few studies have explored its cascading effects on insect herbivores (Quais et al. 2019; Dong et al. 2020), and even fewer on their natural enemies, including predators (Marroquin et al. 2023).

Salinity-induced changes to plant chemistry affect insect herbivore growth and development, and indirectly influence their natural enemies (Shikano et al. 2017; Rahman et al. 2023). For example, salinity-stressed rice plants reduced brown plant hopper populations, which in turn decreased the fitness of their predator, the green mirid bug (Ali et al. 2021). Such cascading effects may compromise the reliability of biological control agents such as predators. Effectiveness of predator-driven biological control relies on the ability of predators to locate herbivore-infested plants and consume nutritious prey (Jervis 2007; Pocius and Kersch-Becker 2024). Prey quality, particularly protein and lipid contents, is a key determinant of predator growth, survival, and reproductive success (Murahwi 2015; Ugine et al. 2021). When prey quality is low, predators may compensate by increasing their prey intake to meet nutritional requirements, a behavior known as “compensatory feeding” (Lawo et al. 2010; Kersch-Becker et al. 2017). This foraging plasticity enables predators to maintain fitness in nutritionally variable environments, which are especially relevant under abiotic stress conditions, such as salinity (Langerhans et al. 2021). Understanding how salinity affects prey quality and predatory feeding behaviors in response is essential to improving

biocontrol outcomes in stressed agro-ecosystems (Pocius and Kersch-Becker 2024).

The multicolored Asian lady beetle, *Harmonia axyridis* Pallas, is a generalist predator widely used in integrated pest management strategies. While it primarily targets aphids and scale insects, *H. axyridis* also preys on Lepidopteran pests such as the tomato fruitworm (*Helicoverpa zea*-laboratory observations) and fall armyworm (Di et al. 2021). A recent study has shown that salinity-treated tomato plants (*Solanum lycopersicum*) negatively impact *H. zea* caterpillars by reducing their growth and prolonging their development (Pawar et al. 2025). Building on these findings, we examined how salinity-mediated reductions in *H. zea* nutritional quality influenced *H. axyridis* predatory behavior. We hypothesize two outcomes: (1) that *H. axyridis* will preferentially consume high-quality caterpillars, and (2) that when constrained to lower quality prey, the predator will exhibit compensatory feeding by increasing its prey consumption rates. This dual hypothesis tests the adaptability of a biocontrol agent under abiotic stress and explores how salinity-induced changes to prey quality fluctuations might affect biocontrol efficiency.

Materials and methods

Study organisms

Tomato seeds (*Solanum lycopersicum* cv. Better Boy, Harris Seeds-Rochester, NY, USA) were planted in 8.9 cm cubic pots filled with Metromix 400 potting mix (Griffin Greenhouse and Nursery Supplies, MA, USA) and grown under greenhouse conditions (25 ± 2 °C, 60–70% RH, L:D 16:8 photoperiod). Plants at the four-leaf stage were used in all experiments.

The generalist predator, *H. axyridis*, was maintained in laboratory conditions (23 ± 2 °C, L:D 16:8 photoperiod) and supplemented with wild hand-collected individuals from the Penn State campus, USA each spring and fall. *H. axyridis* were fed corn leaf aphids (*Rhopalosiphum maidis* Fitch) reared on barley (*Hordeum vulgare*). Equal proportions of male and female adult *H. axyridis* (2–3 week old adults) were used in all the assays. However, differences in feeding responses of males vs. females were not quantified.

Tomato fruitworm (*H. zea*, Benzon Research Carlisle, PA, USA) were reared on artificial diet following Peiffer and Felton (2005). To simulate salt-stressed prey, caterpillars were reared on a salt-treated artificial diet, where control diet contained 875 mg kg^{-1} of Na^+ whereas salt-treated diet contained 4560 mg kg^{-1} of Na^+ . *H. zea* neonates were placed on their respective diets and used at the second larval instar which was suitable for predation by *H. axyridis*. We refer to control diet-fed caterpillars as “non-salty” caterpillars whereas larvae fed with salt-treated artificial diets are referred to as “salty” caterpillars. Size matching controlled for salinity-induced growth delays in “salty” caterpillars, though this may have introduced minor age variations between the treatments (“salty” prey can reach the 2nd instar a day later than “non-salty” prey) (Pawar et al. 2025).

Predator Y-tube olfactometer choice assay

No salt-treated (control) and salt-treated (stressed) tomato plants were prepared by watering with 200 ml of either 0 mM or 200 mM NaCl solution (prepared in DI water) for three days. Experiments were conducted in climate and light controlled growth chambers ($25 \pm 1^\circ \text{C}$ and 60–70% RH) using a Y-tube setup (Davidson-Lowe and Ali 2021). Plants were placed in glass chambers ($35 \times 15 \text{ cm}$) connected to a glass Y-tube (11 cm stem, 7.5 cm arms) via Teflon tubes with a charcoal-filtered airflow of 1.5 l min^{-1} . A single, 24-h starved *H. axyridis* adult was introduced into the base of the Y-tube and allowed to choose between odor sources. A choice was recorded when the beetle entered one arm and moved halfway up. A no-choice was recorded after 5 min of no response. Y-tube arms and Teflon tube connectors were rotated after every replicate; Y-tubes were replaced every six replicates, and plant sets every twelve. Each lady beetle was tested once ($n=20\text{--}90$). Y-tubes were rinsed with water, acetone, and hexane to remove traces of previous chemicals prior to their use.

For the herbivory treatments, 4th instar *H. zea* larvae were restricted to consume a 3.5 cm^2 area over 3 h, followed by unrestricted feeding during the choice assay. We compared no salt-treated vs. salt-treated plants under both undamaged and damaged conditions (Fig. 1). As positive controls, we looked at empty arm vs. no salt (undamaged, damaged), empty arm vs. salt

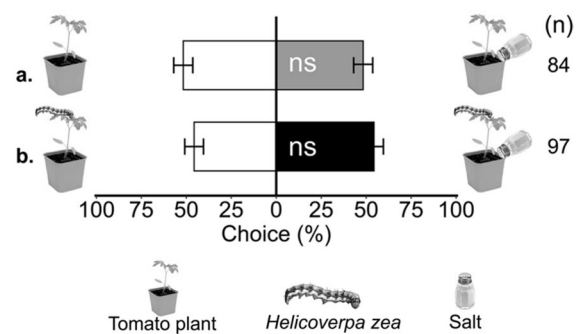


Fig. 1 Predator Y-tube olfactometer choice assay **a** *H. axyridis* preference when given a choice between undamaged no salt and salt-treated plants **b** *H. axyridis* preference when given a choice between herbivore-damaged no salt and salt-treated plants. Bars represent mean $\pm$ SE of the percentage of individuals choosing each odor source. Sample sizes (n) are indicated on the right. In each panel, the left bar represents the no salt plant choice, and the right bar represents the salt-treated plant choice. In **a**, the two treatments are shown in white (no salt + no herbivory) and light gray (salt-treated + no herbivory). In **b**, the two treatments are shown in white (no salt + herbivory) and black (salt-treated + herbivory). Non-responders (i.e., beetles making no choice within 5 min) were excluded from analysis. This occurred in 7.29% of trials ($n=7$) in the undamaged plant assay and 3.16% of trials ($n=3$) in the herbivore-damaged plant assay. “ns” indicates non-significant difference in choice ($P > 0.05$; logistic regression)

(undamaged, damaged), salt (undamaged vs. damaged), and no salt (undamaged vs. damaged) choices (Supplementary Fig. S1).

Quantifying caterpillar nutritional content (protein and Na^+ levels)

Second instar “non-salty” and “salty” caterpillars of similar sizes were pooled (ten larvae per sample), weighed, and flash frozen in liquid nitrogen. Caterpillars were homogenized using a metal bead, and larval protein content was estimated using a Bradford assay (Bradford 1976). Absorbance readings were converted to mg protein using a standard curve of bovine serum albumin (BSA) and normalized per mg tissue (Fig. 2). Seven replicates were used per treatment. For sodium analysis, pooled larval samples (ten larvae per sample) were sent to the Penn State Analytical laboratory, USA for quantification using ICP Emission Spectroscopy (Huang and Schulte 1985).

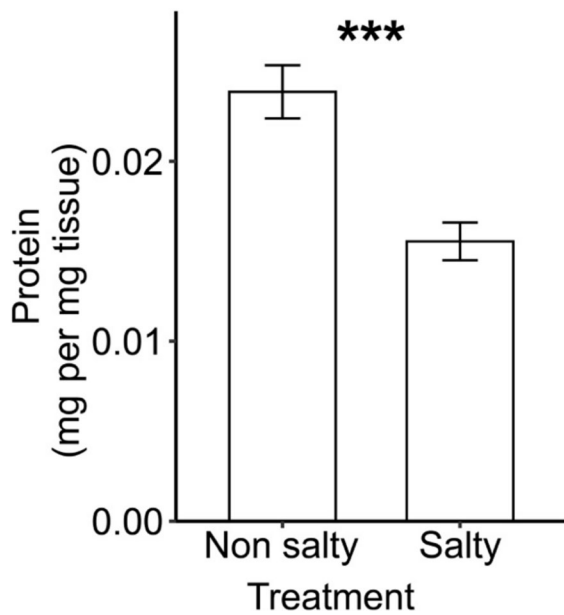


Fig. 2 Caterpillar nutritive content. Plot showing protein content (mean $\pm$ SE; mg mg^{-1} tissue) in *H. zea* larvae reared either on a control diet (non-salty; $n=7$) or a salt-treated diet (salty; $n=7$). Asterisks (***) indicate statistically significant differences between treatments ($P<0.001$)

Predator dual-choice assay

For each observation, one “non-salty” and one “salty” 2nd instar *H. zea* larva of similar sizes were placed at opposite ends of a Petri dish (35 $\times$ 15 mm). A two-day starved adult *H. axyridis* was introduced at the center, facing perpendicular to both caterpillars. We recorded the first larva touched (first touch; Supplementary Fig. S3a, 3b), bitten (first bite; Supplementary Fig. S3c, 3d), and completely consumed (first consume; Fig. 3a, 3b). A no-choice was recorded if no action occurred within 15 min ($n=90$). The experiment was conducted over nine separate days, with each day treated as an independent experimental session to account for temporal variability. See statistical analysis for more details.

Time course consumption assay

Ten “non-salty” and “salty” 2nd instar caterpillars each were placed in separate Petri dishes (35 $\times$ 15 mm) with a single, 24 h-starved adult *H. axyridis*. A wet cotton ball was included, and dishes were

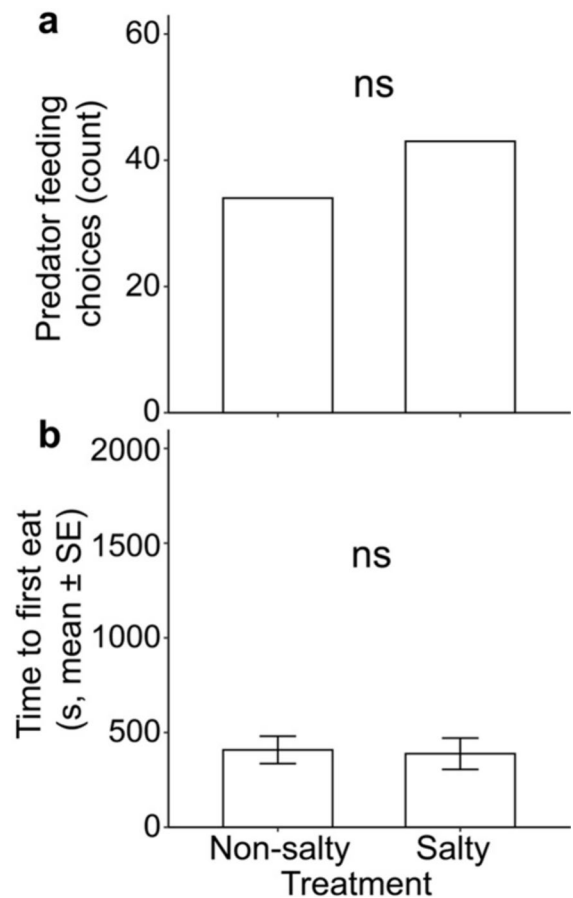


Fig. 3 Predator dual-choice assay **a** Frequency of *H. zea* larva completely consumed by *H. axyridis* adults, categorized by larval type: “non-salty” or “salty.” Bars represent the total number of choices observed for each outcome. “No choice” trials accounted for 37.6% of total responses and were excluded from the analysis. **b** Time required by *H. axyridis* adults to initiate consumption of either “non-salty” ($n=34$) or “salty” ($n=43$) *H. zea* larvae. “ns” indicates no significant differences between treatments ($P>0.05$)

sealed with parafilm. Caterpillar survival was monitored every 15 min for 8 h ($n=17$) (partially consumed caterpillars were marked as dead at the earliest time point that they were recorded). See statistical analysis for more details.

Total consumption assay

Twenty-five “non-salty” and “salty” 2nd instar caterpillars each were placed in separate Petri dishes (35 $\times$ 15 mm) with a single, 24 h-starved adult *H. axyridis*.

A wet cotton ball was included and dishes were sealed with parafilm. We allowed the ladybeetles to feed for 24 h and surviving caterpillars were counted (only complete consumption was considered and we did not observe regular partial caterpillar consumption) (Fig. 4b). One lady beetle corresponds to one replicate ($n=30$ per treatment). See statistical analysis for more details.

Statistical analysis

To determine whether *H. axyridis* preference is odor mediated, we conducted a predator Y-tube olfactometer choice assay. Each predators' choice between the two treatment arms (e.g., "no Salt" vs. "salt") was recorded as a binary response. Trials in which predators did not make a choice within 5 min ("no choice") were excluded from statistical analyses (4.9% of total observations per assay). Binomial generalized linear models (GLMs) with a logit link function were fitted separately for each assay. Model diagnostics (fit, dispersion, and residuals) were assessed using the DHARMa package (Hartig et al. 2024). All models met assumptions of binomial GLMs. The effect of

treatment was assessed using likelihood ratio tests, and results are reported with odds ratios and 95% confidence intervals to convey effect sizes.

Protein content (per mg tissue) was compared between the "non-salty" and "salty" larval treatments. Prior to analysis, distributional assumptions were assessed, where normality within each treatment group was tested using the Shapiro-Wilk test, using the package stats (R Core Team 2026), and equality of variances was assessed using Levene's test using package car (Fox and Weisberg 2018). The "non-salty" group passed the Shapiro-Wilk test for normality ($P=0.435$), while the "salty" group violated the assumption ($P=0.015$). Variance was not significantly different between the groups (Levene's tests; $P=0.24$). Therefore, we compared protein content between treatments using a two-sample Student's t-test assuming equal variances.

To assess whether *H. axyridis* prey choice differed across foraging stages (first touch, bite, and consumption), we conducted the predator dual-choice assays. We modeled prey selection (non-salty vs. salty) using a binomial generalized linear mixed-effects model (GLMM). The binary response variable (salty = 1,

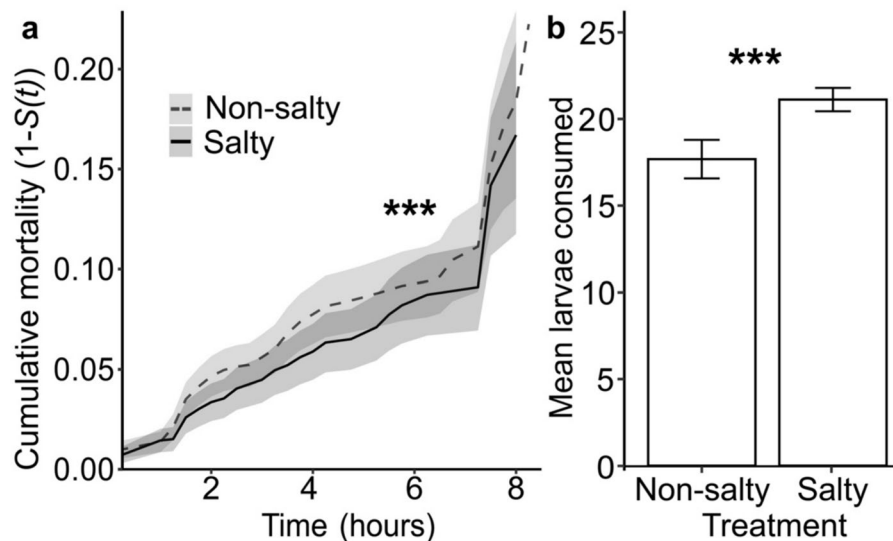


Fig. 4 Predator consumption dynamics across treatments. **a** Cumulative mortality over time for *H. zea* larvae under "non-salty" (gray dashed line; $n=17$) and "salty" (black solid line; $n=13$) treatments, expressed as $1 - S(t)$, where $S(t)$ denotes the Kaplan-Meier estimate of survival probability at time t . Estimates were based on individual-level time-to-death data; Shaded ribbons indicate 95% confidence intervals, and right-

censored observations were retained. **b** Mean number of larvae consumed ($\pm$ SE) by *H. axyridis* adults in 24-h total consumption assays for the "Non-salty" ($n=23$) and "Salty" ($n=24$) treatments, calculated as the total number consumed per replicate across trials. Asterisks (***) indicate a significant difference between treatments ($P < 0.001$)

non-salty=0) was modeled as a function of behavioral stage, with a random intercept for individual predator ID to account for repeated measures (glmmTMB(); package; Brooks et al. 2017). DHARMA residual diagnostics confirmed no overdispersion or violations of model assumptions (Hartig et al. 2024). The significance of stage was assessed using a likelihood ratio test, and estimated marginal means were obtained for each foraging stage using the emmeans package (Lenth and Piaskowski 2025) and conducted Tukey-adjusted post-hoc pairwise comparisons to test differences between stages. Effect sizes are reported as odds ratios with 95% confidence intervals, derived from the log-odds contrasts between stages.

To evaluate whether prey choice at each behavioral stage predicted the predator's timing profile, we initially fit a classical MANOVA with the three latency measures, i.e., latency to touch, latency to bite, and latency to consume prey (in seconds), as the multivariate response, and prey choice at each stage (touch, bite, consume) as categorical predictors. However, multivariate normality was violated (Mardia's test: skewness=865.7, $P<0.05$), and strong collinearity was observed between response variables ($r=0.92$ between touch and bite latencies). As a result, a robust MANOVA was conducted using Wilks' Lambda (Wilks.test(); rrcov package; Todorov and Filzmoser 2010) with prey type consumed ("salty" vs. "non-salty") as the grouping variable. Assays where no prey was consumed ("no choice") were excluded to retain biological relevance (30 assays (24.2%) at touch, 38 (30.6%) at bite, and 47 (37.9%) at consumption).

Our first predator consumption assay was the time course consumption assay. To evaluate how treatment influenced predation dynamics over time, we conducted two complementary analyses using the same individual-level time-to-death dataset. First, we modeled prey survival using a mixed effects Cox proportional hazards model (Therneau 2025), with treatment as a fixed effect. A random intercept for replicate nested within Petri dish accounted for hierarchical experimental design and non-independence of observations. This model retained full temporal and individual level resolution. Treatment effects were evaluated by likelihood ratio tests, while holding the random effects structure constant. Second, we performed Petri dish level survival analysis by summarizing individual level data into a single event per

dish (time-to-event format): the time at which any predation was observed, or right-censored if no predation occurred by the end of the observation period (0.25 h intervals). In this analysis, any predation occurring within a time interval was counted as a single event at the dish level. By summarizing the data to a single event per Petri dish, this analysis allowed us to ask a complementary question: whether treatment influenced the likelihood and timing of predation events, independent of individual survival patterns. We analyzed these Petri dish level data using a Cox proportional hazards model with treatment as a fixed effect. Visualizations of both analyses were produced using the survminer package (Kassambara et al. 2025), including survival and cumulative mortality curves.

We conducted a second predator consumption assay: the total consumption assay, in which experimental set consisted of multiple Petri dishes assayed together under the same conditions. A GLMM with a binomial distribution and logit link function was employed to model consumption as the total number of caterpillars consumed out of 25. Larval treatment was included as a fixed effect, and experimental Petri dish sets was treated as a random intercept (package glmmTMB; Brooks et al. 2017). The effect of treatment was assessed using a likelihood ratio test. Model assumptions (fit, dispersion, and residual distribution) across all GLMMs were evaluated using the DHARMA package, which evaluates model fit by simulating standardized residuals from the fitted model (Hartig et al. 2024). All figures were generated using the package ggplot2 (Wickham and Sievert 2009) and assembled using the package patchwork (Pedersen 2019). All statistical analyses were conducted in R (v4.3.3) (R Core Team 2026).

Results

Predator Y-tube olfactometer choice assay

H. axyridis showed no significant preference between no salt and salt-treated plants, regardless of whether both the plants were undamaged (Fig. 1a; $\chi^2=0.2023$, $df=1$, $P=0.653$; odds ratio=0.87, 95% CI [0.48, 1.57]) or herbivore-damaged (Fig. 1b; $\chi^2=1.393$, $df=1$, $P=0.238$; odds ratio=1.42, 95% CI [0.80, 2.54]). In the control assays to assess

baseline predator attraction to plants, *H. axyridis* adults preferred the odor of undamaged (no salt: $\chi^2=8.593$, $df=1$, $P=0.003$, Supplementary Fig. S1a; salt: $\chi^2=7.96$, $df=1$, $P=0.004$, Supplementary Fig. S1b, Table S1) or herbivore damaged (no salt: $\chi^2=12.55$, $df=1$, $P=0.004$, Supplementary Fig. S1c, Table S1; salt: $\chi^2=34.45$, $df=1$, $P<0.001$, Supplementary Fig. S1d, Table S1) plants over clean air (empty arms). *H. axyridis* lady beetles clearly preferred the odor of herbivore-damaged plants over undamaged plants in both no salt ($\chi^2=12.503$, $df=1$, $P=0.004$, Supplementary Fig. S1f, Table S1) and salt ($\chi^2=11.234$, $df=1$, $P=0.008$, Supplementary Fig. S1Table S1) treatments.

Caterpillar nutritional content

Larval protein content was significantly higher (Fig. 2; $t=4.59$, $df=12$, $P=0.0006$) in “non-salty” larvae (0.023 ± 0.001 mg/mg⁻¹ tissue) compared to “salty” larvae (0.015 ± 0.001 mg/mg⁻¹ tissue), indicating that salt treatment significantly reduced caterpillar protein levels. We selected ten caterpillars of similar sizes across treatments, ensuring similar total larval mass to facilitate reliable protein content comparisons (Supplementary Fig. S2; Student’s *t*-test of total larval mass, $t=0.394$, $df=12$, $P=0.701$). “Salty” caterpillars also accumulated roughly four times more salt in their tissues than “non-salty” caterpillars, with average Na⁺ levels of 647.5 mg kg⁻¹ and 160 mg kg⁻¹, respectively.

Predator dual-choice assay

The probability of selecting “salty” prey did not differ among foraging stages (touch, bite, consume; $\chi^2=2.54$, $df=2$, $P=0.28$; predicted probabilities shown in Supplementary Fig. S3a (touch), Supplementary Fig. S3c (bite), Fig. 3a (consume)). Estimated marginal means indicated that the likelihood of choosing “salty” prey increased from 48.2% at the touch stage to 69.1% at bite and 66.7% at consumption, though this trend was not statistically different. The odds of choosing “salty” prey at the bite stage were 0.42 times those at touch (OR=0.42, 95% CI [0.11, 1.65], $P=0.294$), and at the consumption stage were 0.47 times those at touch (OR=0.47, 95% CI [0.11, 1.92], $P=0.415$). The bite vs. consumption contrast yielded nearly equivalent odds (OR=1.12,

95% CI [0.27, 4.59], $P=0.981$). Robust MANOVA showed no significant difference in latency to touch, bite, or consume between predators that ultimately selected “non-salty” “salty” larvae (Wilks’ Lambda=0.983, $\chi^2=1.21$, $df=3$, $P=0.75$) (Fig. 3b; Supplementary Fig. S3b and Supplementary Fig. S3d). These results indicate that *H. axyridis* exhibits no strong or consistent preference for “non-salty” vs. “salty” *H. zea* larvae, either in prey selection or in the timing of behavioral interactions.

Time course consumption assay

In the time-to-death analysis, based on individual level survival data, caterpillars from the “salty” treatment had a significantly lower risk of predation compared to “non-salty” larvae (Fig. 4a; mixed-effects Cox proportional hazards model; $\chi^2=6.27$, $df=1$, $P=0.012$). A complementary Petri dish level analysis focusing on the timing of any predation event also revealed a significant difference between treatments (Supplementary Fig. S4; Cox proportional hazards model; $\chi^2=8.61$, $df=1$, $P<0.01$), with earlier and more frequent predation events occurring on Petri dishes with “non-salty” larvae than the “salty” larvae.

Total consumption assay

H. axyridis lady beetles consumed significantly more “salty” larvae (21.1 ± 0.6) than “non-salty” larvae (17.7 ± 1.1) (Fig. 4b; $\chi^2=35.14$, $df=1$, $P<0.001$).

Discussion

Salinity stress in plants can fundamentally alter plant chemistry with downstream effects on herbivores and their predators. Caterpillars feeding on salt-treated diets exhibited slower growth (Pawar et al. 2025) and reduced protein content. These physiological changes resulted in increased “salty” prey consumption by the generalist predator *H. axyridis*, suggesting a potential compensatory feeding strategy. By testing predator response to prey reared under contrasting salinity conditions, the study highlights how abiotic stress can propagate through trophic levels. Because *H. axyridis* is not a primary biocontrol agent for *H. zea* (Symondson et al. 2002), the observed increase in consumption of salt-affected prey underscores the importance

of nutritional dynamics in shaping predator-prey interactions and offers insight into potential applications for pest management under salinity stress.

Effective biocontrol relies on the ability of predators to locate and consume their prey (Ugine et al. 2021). In Y-tube olfactometer assays, *H. axyridis* exhibited equal attraction to no salt-treated and salt-treated plants, regardless of herbivory (Fig. 1). While salt treatment alters volatile emission profiles (Pawar et al. 2025), these changes apparently did not influence predator recruitment. Instead, consistent with the importance of herbivore-induced plant volatiles in guiding natural enemy behavior (Davidson-Lowe and Ali 2021), predator attraction increased in response to herbivore damage (Supplementary Fig. S1e, . S1f). This suggests that herbivore presence may override salinity-driven shifts in plant signaling in the context of predators making foraging decisions (Louthan et al. 2014).

We hypothesized that *H. axyridis* will preferentially consume high quality caterpillars. However, Petri dishbased dual-choice assays revealed complex predator behaviors prior to prey consumption (Fig. 3; Supplementary Fig. S3) (Provost et al. 2006). *H. axyridis* frequently investigated both prey types through touching and biting a caterpillar before consuming, and in some cases switched prey mid-assay (switching occurred from both “non-salty” to “salty” caterpillars and “salty” to “non-salty” caterpillars). Despite these behavioral complexities, no consistent preference emerged in the dual-choice assay for either prey type at the touch, bite, or consume stages. These behaviors imply a detailed assessment of prey quality and suggest that factors beyond initial contact influence consumption decisions.

Patterns of consumption across both consumption assays suggested that prey quality influenced feeding strategies of *H. axyridis*. In the time course consumption assay, predators consumed “non-salty” caterpillars early and more consistently (with more feeding events), while “salty” caterpillars were consumed in delayed, clustered bouts (with more caterpillars consumed per feeding event) (Fig. 4a; Supplementary Fig. S4). This implies that predators assess prey quality and adjust prey intakes over time (Pervez and Yadav 2018). We hypothesized that, when constrained to lower quality prey, *H. axyridis* would exhibit compensatory feeding by increasing its prey consumption rates. In the total consumption assay over 24 h,

H. axyridis consumed significantly higher numbers of “salty” caterpillars than “non-salty” caterpillars (Fig. 4b). Prey preferences of *H. axyridis* can be influenced by prey quality, size, and mobility (Kumar and Omkar 2023). However, since larval size was standardized (Supplementary Fig. S2) and no major differences in prey mobility were observed (laboratory observations), we rule out these factors as primary drivers of predator preference. Thus, *H. axyridis* might have compensated for the likely lower prey quality by increasing its prey consumption. Bradford assays confirmed that “salty” caterpillars contained significantly less protein than “non-salty” caterpillars (Fig. 2). Such compensatory feeding behavior has been documented across predator taxa when facing nutritionally imbalanced diets and may reflect a strategy to meet physiological demands when prey are nutritionally deficient (Schmidt et al. 2012; Kersch-Becker et al. 2017).

Similar outcomes have been reported in *Hippodamia convergens* Guérin-Méneville lady beetles, which showed increased predation on *H. zea* larvae feeding on Bt protein-incorporated artificial diet. This indicates complex relationships of sublethal toxins on prey-predator interactions, and pointing to potential trade-offs between immediate compensatory consumption and long-term fitness outcomes (Elkins et al. 2024). Elevated Na⁺ in “salty” caterpillars could pose sublethal risks to predators consuming them over multiple days (Ugine et al. 2021). Although *H. axyridis* may tolerate elevated salt levels, no evidence was found for active salt-seeking behaviors akin to mud-puddling butterflies or crickets (Simpson et al. 2006; Ravenscraft and Boggs 2016). We also did not observe any specific preference for water or salt-dipped cotton balls (unpublished data), suggesting that predator consumption might not be driven by salt cravings. Specifically, our data supports salt-induced reductions in protein content necessitated compensatory feeding. Nevertheless, alternative mechanisms involving osmotic or ionic effects on prey water/protein balance, or modifications to cuticular and volatile cues cannot be ruled out.

The diet of *H. axyridis* plays a central role in its biocontrol effectiveness as they optimize their feeding strategies to achieve nutritionally balanced diets (Verma and Mishra 2024). Although it primarily targets soft-bodied insects such as aphids and scale insects, its capacity to consume *H. zea* caterpillars expands its potential utility in salinity-affected agroecosystems.

Given its equal attraction to both plant treatments and its higher consumption of “salty” *H. zea* caterpillars in laboratory assays, *H. axyridis* may be effective where herbivores are nutritionally compromised. Furthermore, delayed development and increased dispersal of caterpillars under salt stress in search of more nutritious host plants may increase their exposure to predation, further enhancing the biocontrol potential of *H. axyridis* (Urban 2007). Finally, it is important to note that these predator-prey interactions are highly dependent upon specific predator-prey combinations, crop cultivars, and salinity stress levels. Future research should investigate the long-term impacts of consuming salt stressed prey on predator fecundity, survival, and behavior. Incorporating field-based trials and a multi-trophic assessment will be essential to evaluate whether compensatory consumption translates to improved pest control under real-world salinity conditions.

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Data availability Data to support the findings of this study are freely available upon request to the corresponding author.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

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