Social information use in herbivore prey can influence the success of biological control

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HIGHLIGHTS

- Predators often induce costly trait responses in prey (i.e., risk-related effects)
- Consequences of copying other conspecifics' antipredator response were modelled.
- Inadvertent social information (ISI) use reduced total prey consumption.
- This effect was independent of detection ranges and prey social organisation.
- ISI use may contribute to herbivore control via its influence on prey behaviour.

ABSTRACT

Predation-risk effects (PEs), i.e. costly consequences of antipredator trait responses in prey, have been the focus of many theoretical and applied studies on predator–prey systems, but we still have limited knowledge on how prey functional traits – such as the ability to acquire and use inadvertent social information (ISI) – influence the susceptibility to strong PEs. In this study, I used an individual-based model to explore how ISI use alters the relative importance of consumptive and predation-risk effects on herbivore prey abundance and total consumption, a proxy for plant damage. I found that ISI use contributed to higher prey abundance by lowering predation-related mortality, but it also decreased prey total consumption through PE irrespective of the relation between prey and predator detection ranges and the type of prey social organisation. Moreover, due to its stronger effect on the non-consumptive component of the total predation effect, ISI use contributed to an overall reduction in prey feeding performance. The estimated strengths of different predator effect components were also comparable to previous experimental findings. These findings provide strong support for the idea that the access to and use of risk-related social information not only result in more prey individuals exhibiting the antipredator response but also leads to strong behavioural PEs with substantial consequences on prey consumption.

1. Introduction

Predation-risk effects (PEs; also referred to as 'non-consumptive effects' or NCEs; Lima 1998; Peckarsky et al. 2008) are those effects that predators exert on their prey populations in addition to direct consumption, such as altering prey behaviour, physiology, or life history traits (Peacor et al. 2020). From the prey's perspective, these are plastic responses to predation threats that incur costs to produce but enhance fitness in risky environments (DeWitt and Scheiner 2004; Pigliucci 2001). Trait plasticity often induces cascading trait-mediated indirect interactions between species at multiple trophic levels (Werner and Peacor 2003, Peacor and Werner 2008; Bestion et al. 2015), but

evidence suggests that risk-induced trait responses in prey rarely translate to changes in prey population size (Say-Sallaz et al. 2019; Sheriff et al. 2020) due to accompanying compensatory physiological and behavioural responses (McPeek 2004; Thaler et al. 2012; Kaplan et al. 2014) or because of little associated costs (Creel et al. 2014; Peacor et al. 2013). Nevertheless, PEs are generally regarded as having the potential to affect various aspects of prey population dynamics thanks to those predator–prey systems where manipulated predation risk (i.e., the presence of predator cues or predators without the ability to attack prey) has been linked to reduced survival (McCauley et al. 2011), growth rate (Nelson et al. 2004; Scrosati 2021) or reproductive output in prey (Sheriff et al. 2009; Zanette et al. 2011). In a recent paper, Peacor et al.

(2020) introduced a conceptual framework and standardized terminology of predation-risk effects that can facilitate the communication of insights and methodologies across study systems and highlighted those terms that should be used to describe different levels of predation-risk effects. I apply the terminology corresponding to those recommendations throughout the text (for more details, see Peacor et al. 2020).

PEs can be utilised in biological control by introducing predators or predator cues into agro-habitats, so herbivore pest species alter their behaviour to avoid areas where predation threats are perceived (Ninkovic et al. 2013; Harrison and Preisser 2016; Sendoya and Oliveira 2015), reduce their feeding rate (Hermann and Thaler 2014; Thaler and Griffin 2008) and decrease the transmission of plant pathogens (Elderd 2019; Tholt et al. 2018). In cultivated plants, especially those with a relatively short growing season, the aim is not necessarily to lower the equilibrium population size of pests *per se* but to reach the maximal marketable yield by reducing pests' damage to plants. This can be achieved by increasing predators' consumptive effects and/or PEs related to prey feeding rate and efficiency. Previous experiments indicate that the magnitude of PEs on prey feeding can be equally or more important than predators' direct consumption. For example, the leaf consumption of tobacco hornworm caterpillar, *Manduca sexta* was shown to decrease by 30–40% when exposed to predation risk (i.e., the presence of sham predators) (Thaler et al., 2012, 2014). Jandricic et al. (2016) found that by interrupting the feeding of western flower thrips (*Frankliniella occidentalis*), *Neoseiulus cucumeris* predatory mite attacks reduced leaf damage by 38–51%. Plant damage by adult Colorado beetles, *Leptinotarsa decemlineata* was also reduced by 63.9% when pests were exposed to predation risk in open-field tests (Hermann and Thaler 2018). Despite the growing evidence for high levels of plant damage reduction due to predators' PE in various herbivore-predator interactions, however, we still have limited knowledge about the conditions that favour strong PEs in agrarian (and non-agricultural) ecosystems (Hermann and Landis 2017).

Previous studies indicate that the magnitude of PEs is often context-dependent and may vary with temperature, resource growth rates, the ontogeny, foraging mode and density of prey, and prey–competitor density (Peacor and Werner 2008; Veselý et al. 2017; Pessarrodona et al. 2019; Mestre et al. 2020). Theoretical works also proved that strong PEs can be expected if the benefit of reduced predation exceeds the high cost of trait plasticity and the predation level is high in the absence of induced trait change (Peacor et al. 2013). Furthermore, PE was shown to promote the persistence of prey metapopulations by facilitating colonization (Orrock et al. 2008), and to allow the invasion and persistence of a competitor on a shared resource (Larsen 2012). While such works provided crucial information about the emergence and community-level consequences of multiple predator effects, we do not know if prey functional traits – such as the ability to acquire and use inadvertent social information – can also modulate the susceptibility to strong PEs. Inadvertent social information (ISI) is a form of biological information that is conveyed by the presence or the behaviour of others, or the product of their behaviour such as scent marks, excretions or food remnants, all of which may provide relevant updates about current environmental conditions. ISI use is known to occur in many ecological contexts, including predator avoidance (Danchin et al. 2004; Gil et al. 2018). In group-living prey, predation risk-related social information can be transmitted among group members, leading to changes in the behaviour and physiology of the entire group (Lima, 1991; Firth 2020; Brandl et al. 2022). Consequently, ISI use can be expected to increase the magnitude of PE in prey species where social cohesion maintains a local density that generates opportunities for the acquisition of social information. However, ISI use is also known to facilitate population abundance and stability under high predation pressure (e.g., Gil et al. 2018) and thus may diminish the benefits of PEs if it results in a reduced feeding rate but at a larger equilibrium population size. Moreover, recent theoretical advancements suggest that temporary local densities in non-grouping organisms also allow information diffusion about predation threats among conspecifics that may facilitate population stability and persistence (Tóth et al. 2020; Tóth 2021; Tóth and Csöppü 2022). Examples of ISI use in herbivore pests in foraging or predator avoidance contexts are currently lacking, however. There are a few agriculturally relevant insect species, where social information use is extensively studied (e.g., bumblebees [Leadbeater and Chittka 2005], honeybees [Grüter et al. 2013], ants [Detrain and Deneubourg 2008], and fruit flies [Sarin and Dukas 2009]), but previous works examined this phenomenon in detail predominantly in vertebrates. The lack of relevant examples is due to that biocontrol studies usually do not clarify what rules and modalities are used for predator avoidance as only overall behavioural and/or life history responses are measured (in accordance with the focus of such investigations). That knowledge gap, on the other hand, does not necessarily mean that ISI use is not present in agricultural pests, where it can also fundamentally influence predator–prey interactions and prey population dynamics.

In this study, I built a tentative individual-based model to elucidate how ISI use alters the relative importance of consumptive and predation-risk effects on prey abundance and feeding performance. For that, I took the dynamic state variable model of Gil et al. (2017) as a basis. In their work, the authors investigated the effects of social information about food and predators on prey grouping behaviour and individual fitness and showed that social information use in itself can promote group formation up to a threshold group size and enhances fitness substantially across various ecological scenarios. I customized this model by restricting the simulations to the predation avoidance context and incorporating individual-level interactions and tradeoffs regarding movement, ISI use, vigilance and feeding. With the applied changes, I could estimate how ISI use and related parameters such as detection range and social organisation influence the magnitude of PE in differently characterized herbivore prey.

2. Materials & methods

2.1. Model specifications

As the model of Gil et al. (2017), the constructed individual-based model simulate a single diel period of foraging activity in prey, set to be 20 time steps in length (*T*). In each time step, a prey has an energy level ($E_{j,t}$), which could be a maximum of 30 (E_{max}) and if it becomes lower than 1, the individual's death by starvation was assumed. To represent general physiological constraints, each prey may consume a maximum of 3 units of energy per time step (which is 10% of the maximum energy level), while also using up 1 unit of energy.

The model includes two entities, prey and predators, that do not differ in sex or age. Prey form groups whenever parameter *m* (i.e., the threshold above which a group splits into smaller groups during movement) is set to greater than one. Group-living prey includes, for example, those gregarious herbivore species that feed in groups through some of the ontogenetic stages – either with kin like the larvae of some species of Lepidoptera (Reader and Hochuli 2003) or with unrelated individuals like bark beetles (Grégoire 1988), fruit flies (Rooke et al. 2020), treehoppers (Cocroft 2005) or cockroaches (Lihoreau et al. 2010). Non-grouping prey are those solitary species that feed individually as nymphs and adults (e.g., most leafhoppers; Dietrich 2004) or have eggs in clusters but larvae disperse before feeding (e.g., caterpillars in many Lepidopterans [Hunter 2000]). In non-grouping prey, *m* is set to one as individuals do not maintain spatial proximity with conspecifics but follow independent movement paths. Non-grouping prey individuals and predators exhibit correlated random walks that consider short-term correlations between successive step orientations and have often been regarded as a null model for non-orientated animal movement (Benhamou 2006; Fagan and Calabrese 2014; Reynolds 2014). In group-living prey, individuals move toward the closest conspecific if any are within their detection range (r_{prey}). Once the given individual gets near to others (i.e., within attraction range, r_{social}), it becomes part of the group;

groups move under the same rule as non-grouping individuals. If the group size becomes higher than the parameter m, the group splits into several smaller groups, with the membership assigned randomly. The number of newly generated groups is given by the smallest integer greater than or equal to the value of group size divided by m plus one. If a group-living prey has no conspecifics within its detection range, it also moves according to the rules of correlated random walks. During movement, each individual's movement distance is randomly selected from a Weibull distribution (shape $= d_{\text{prey}}/2$ and scale $= d_{\text{prey}}$, respectively). Turning angles are determined by random deviates drawn from wrapped Cauchy circular distribution with $\mu = 0$ and $\rho = 0.8$.

Vigilance and feeding were modelled as mutually exclusive activities to represent the trade-off between food and safety observed in most animal systems (Brown and Kotler 2004; McNamara and Houston 1987; Lima and Dill 1990). In general, vigilance involves the termination of ongoing activities and monitoring the surroundings for predation threats, although the presence of actively scanning for danger is elusive in many prey organisms. For example, leafhoppers considerably delay their feeding and feed much less often in the presence of a spider, implying that the potential predator is detected by the leafhopper (Beleznai et al. 2015; Tholt et al. 2018), but the exact mechanism and modalities involved are not known. Nevertheless, the modelled phenomenon meets the three assumptions of vigilance proposed by Treves (2000): it is costly, increasing vigilance improves predator detection, and it can decrease risk with increasing group size (this is achieved through ISI use). Prey could detect predators that are within r_{prey} distance with a probability given by the equation:

$$P_{detect} = 3 \times E_{j,t}/100$$

where $E_{j,t}$ denotes the energy level of individual j in time step t. This means that a prey with an energy level of 1 detects predators with a probability of 0.03 (reflecting its dire need of feeding), a prey with an energy level of 15 (i.e., half of the maximum energy level) exhibits vigilance behaviour with a probability of 0.45, whereas a prey with an energy level of 30 scans for predators with a probability of 0.9. Whether or not a prey becomes alarmed and hides (i.e., and thus undetectable to predators) is determined by individual Bernoulli trials with the calculated P_{detect} probability. Prey can also detect conspecifics and copy their antipredator behaviour within r_{prey} distance with a probability given by P_{isi} (also determined by individual Bernoulli trials). Alarmed individuals do not feed. If prey remains unalarmed, its consumption (1, 2 or 3 energetic units) depends on its energetic state and is given by:

$$X \ Binomial(3, 1 - P_{detect})$$

The initial energy level is selected randomly for each prey between 5 and 10. Predators attack a maximum of five unalarmed prey within their detection range, which is defined as a distance r_{P} from the predator's position in any direction. Hunting success is set to 25 per cent (being consumed is determined by individual Bernoulli trials [i.e., random experiments in probability whose possible outcomes are only of two types, 'success' or 'failure', with each trial outcome being independent of the other] for the attacked prey). I assumed generalist predators that exert a constant predation pressure on prey, its level being directly proportional to the constant number of predators that appear in the simulated landscape.

Individuals can detect and copy the adaptive antipredator behaviour of others (i.e., thus exploit social cues when present) in each time step. To track the emerging pattern of ISI use among prey (i.e., the diffusion of social information), temporary detection networks are constructed based on individuals' location and detection range. The rationale for the use and a detailed description of these networks can be found in Tóth et al. (2020) and Tóth and Csöppü (2022). Briefly, the networks consist of nodes representing individuals and edges denote spatial proximity (i. e., being within each other's detection range). The probability of information acquisition from one node to another is given by w^{k}, where w

is the edge weight (specified by the parameter P_{isi} in the model), and k is the number of steps on the shortest path between the two nodes. According to the applied settings, an individual can receive information from a maximum of ten of its neighbours that were a maximum of two steps away (i.e., $k_{\text{max}} = 2$ and $n \leq 5$ at each k step). If there are more than five individuals at k step to a focal individual, five are randomly selected. For each node in the network, I used the inclusion–exclusion principle to calculate the overall probability of receiving information from its detected neighbours (Allenby and Slomson 2010). The model does not incorporate any decision-making rule that individuals would follow in the presence of conflicting information, so prey always performs the antipredator behaviour even if it detects only a single demonstrator conspecific. Such a rule is not uncommon in evasion and predator avoidance contexts (e.g., Rosenthal et al. 2015, Quinn & Cresswell 2005), and it is unknown whether or not other rules are more relevant under predation risk in biocontrol systems.

I simulated a homogeneous, continuous 2D landscape with an extent of 100×100 spatial units. Habitats of this type are characterised by uniform resource distribution similar to grasslands, beaches, plantations and crops (Byers 2001). When crossing the landscape edge, entities move to the opposite side of the landscape and continue moving (i.e., torus landscape with no boundaries). Entities can also detect hetero- and conspecifics through the edges within their detection range. At initialisation, 1000 prey and 100 predators are placed randomly on the simulated landscape with random orientation. To provide time to form groups when $m > 1$, prey moved ten times before the start of a simulation run. Each run consists of 20 time steps. At the start of a time step, prey moves on the landscape, and predators appear randomly. Then, the detection of predators and conspecifics exhibiting antipredator behaviour by prey, prey feeding and predator hunting occurs as described above. This cycle (from prey moving to predator hunting) is then repeated 20 times in a simulation run. State variables and parameters of the model are listed in Table 1.

2.2. Analysis of model outputs

All simulations and calculations were performed in R 4.2.2 (R Core Team 2022). Instead of using frequentist hypothesis testing, I evaluated the magnitude of differences between simulation runs with different parameter settings (White et al. 2014). The analysed output measures included the final prey number, i.e., the number of prey individuals at the end of the 20th time step and total consumption, i.e., the sum of energy units that prey individuals acquired during all the 20 time steps; this latter was regarded as a proxy for the damage herbivore prey exerts on its host plant. Additionally, I also examined the dynamics of per capita prey consumption, i.e. the energy units that prey individuals acquired in a given time step and prey energetic state, i.e., the initial energetic condition of prey in a given time step. In all parameter settings, the number of iterations was set to 100. R scripts for model construction and data supporting the results are archived and available at Figshare (doi: 10.6084/m9.figshare.23267708).

I used Morris's "OAT" elementary effects screening method (Morris 1991) with the extension introduced by Campolongo et al. (2007) as a global sensitivity analysis to rank the model parameters according to their impact on the final prey number and total consumption. This method produces results comparable to more complex procedures (Confalonieri et al. 2010) and can be applied to individual-based models as well (Imron et al. 2012; Beaudouin et al. 2015; Ten Broeke et al. 2016). The mean of the absolute value of the elementary effect (μ^{*}_{i}) provides a measure for the overall influence of each input variable on the model output, and the standard deviation of the elementary effect (σ_{i}) indicates possible non-linear effects or interactions among variables (Iooss and Lemaître 2015). I also ranked the model parameters using a global index (GI) (Ciric et al. 2012) calculated as follows:

Table 1

Model parameters, state variables and their range for the global sensitivity analysis. The values for parameters $E_{j,t}$, E_{max}, and T were obtained from the original model of Gil et al. (2017), P_{ISI} had the same value as in Tóth and Csöppü (2022), parameters m and d_{prey} had the same values as in Tóth et al. (under review), whereas the values for parameters r_{social}, r_{prey}, and r_P, were chosen arbitrarily (with the rule of $r_{social} < r_{prey}$). The value of parameter P_s reflects a conservative estimation of the hunting success of a generalist predator (for examples of higher success rates, see Beleznai et al. 2015, Michálek et al. 2017).

Symbol	Description	Nominal value	Unit/ scale	Range
n	Spatial extent of the simulated 2D landscape (in both × and y directions)	100 (constant)	–	–
N_{prey}	Number of prey at the start of a simulation cycle	1000 (constant)	–	–
N_P	Number of predators that appears on the landscape in each time step	100 (constant)	–	–
m	Group size threshold above which a group splits into smaller groups during movement	1 (non-grouping) or 15 (group-living)	2	1–15
d_{prey}	Parameter related to prey movementdistance (determines the shape and scale parameters of the Weibull distribution from which movement distances are randomly drawn)	10	1	6–15
r_{social}	Range of social cohesion, i.e. within which group-members maintain spatial proximity	2 (only if $m >$ 1)	–	–
r_{prey}	Prey detection range	3 or 5	1	2–6
r_P	Predator hunting range	4 (constant)	–	–
P_s	Probability of success when a predator attacks prey	0 (only PE*) or 0.25 (both CE and PE)	0.25	0–0.25
P_{ISI}	Probability of prey ISI use (i.e., copying the defensive behaviour of others); determined by individual Bernoulli trials	0.5	0.1	0–0.9
$E_{j,t}$	Energy level of an individual (j) in a time step (t)	0–30	–	–
E_{max}	Number of energy units an individual could store	30 (constant)	–	–
T	Number of time steps in a single diel period of prey foraging activity	20 (constant)	–	–

* for the biological relevance of the 'only PE' setting, seeJandricic et al. 2016.

$$GI = \sqrt{(\mu_i^*)^2 + (\sigma_i)^2}$$

For the space-filling sampling strategy proposed by Campolongo et al. (2007), I generated $r_2 = 1000$ Morris trajectories and then retained $r_1 = 100$ with the highest 'spread' in the input space to calculate the elementary effect for each model parameter.

I explored a major part of the parameter space by visualising the interactive effects of the following parameters on the final prey number and total consumption: prey type (group-living prey with m set to 15 ['GL'] and non-grouping prey with m set to 1 ['NG']), detection range (i. e., the relation between prey detection range and that of the predators; '$r_{prey} < r_P$' or '$r_{prey} > r_P$') and predator effects with or without ISI use ('Only PE', 'Both CE & PE', 'Only PE with ISI use', 'Both CE & PE with ISI use'). For each parameter combination, I calculated the per cent changes compared to an identical setting with no predators present, allowing me to compare the estimated effects to published *meta*-analysis results. Furthermore, I visually explored the changes in the per capita prey consumption and prey energetic state during simulation runs in different combinations of the above model parameters to gain insights into how prey behaviour is shaped by both predation risk and energetic demands. All other parameters were set to their nominal values (Table 1).

Finally, I examined which combinations of prey traits and predator effects led to the greatest decrease in the measured outputs using parallel coordinate plots ('ggpcp' R package; Ge and Hofmann 2023). These plots display multiple *y*-axes and show the observations across several dimensions as lines. By scrutinising which settings resulted in observations belonging to the first quartile of the output distributions, I could generate predictions under what conditions one may expect strong PEs within the examined parameter set.

3. Results

3.1. Final prey number

The sensitivity analysis showed that parameters r_{prey}, P_{ISI} and P_s had strong influences with non-linear and/or interaction effects on the final prey number (as their σ_i and μ^*_i values have the same order of magnitude; Fig. 1a). Prey detection range was the most influential among the examined model parameters, indicating that larger prey detection ranges (with r_P being fixed to a constant value; Table 1) contributed to higher probabilities of escaping predation. P_{ISI} also had a strong influence on this model output, confirming that social information use can affect prey population abundance under high predation pressure. Not surprisingly, the presence or absence of predators' consumptive effect, P_s, also contributed substantially to the dispersion of the final number of prey, and its small σ values indicated that the elementary effect had lower variations on the support of this input than in the case of the previous two parameters. Parameters d_{prey} and m had considerably less influence on the final prey number, suggesting that movement decisions affected the final prey number to a much lesser extent.

When predators' detection range exceeded that of the prey and predators exerted only PE on the prey, the final prey number was almost identical to the setting where no predators were present, irrespective of the presence or absence of ISI use in prey (Fig. 2a). Thus, PE did not affect prey abundance in itself. When predators also consumed prey, the final prey number decreased by 70.17–81.24% in the two prey types. As PE had a negligible effect on prey abundance, these substantial reductions in prey number are attributable to predators' consumptive effect. In this scenario, the presence of ISI use increased the number of prey by 34.61% in GL and by 7.97% in NG prey, suggesting that social information use could effectively lower predation-related mortality, notably in group-living prey. When prey detection range exceeded that of predators, PE did not affect prey abundance in itself but the presence of ISI use resulted in substantially lower final prey numbers (28.97% decrease in GL and 50.83% decrease in NG prey, respectively). When predators exerted multiple effects on their prey without ISI use, CE greatly reduced the final prey number in both prey types (66.12–75.83%). ISI use increased prey abundance in the presence of multiple predator effects in this scenario as well (increased by 25.59% in GL and by 5.62% in NG prey). This difference can be attributed to the larger negative impact of ISI use on PE in NG prey, however; the effect of ISI use on CE (i.e., the consumption-related component of the total predator effect) was similar irrespective of prey social organisation (a reduction of 54.56% in GL and 56.45% in NG prey, respectively).

Observations in the first quartile of the final prey number distribution (equivalent to a 70.23–84.4% decrease in prey number compared to the corresponding 'no predator' setting) occurred mostly in non-grouping prey and in both r_{prey}-r_P detection range relations, but only when predators' consumption was not restricted to zero (Fig. 3a). While the previous results showed that behavioural PE might contribute to a reduced prey population size in itself in some parameter settings, this pattern indicates that predators' consumptive effect is pivotal for substantial population dynamic consequences in prey.

3.2. Total consumption

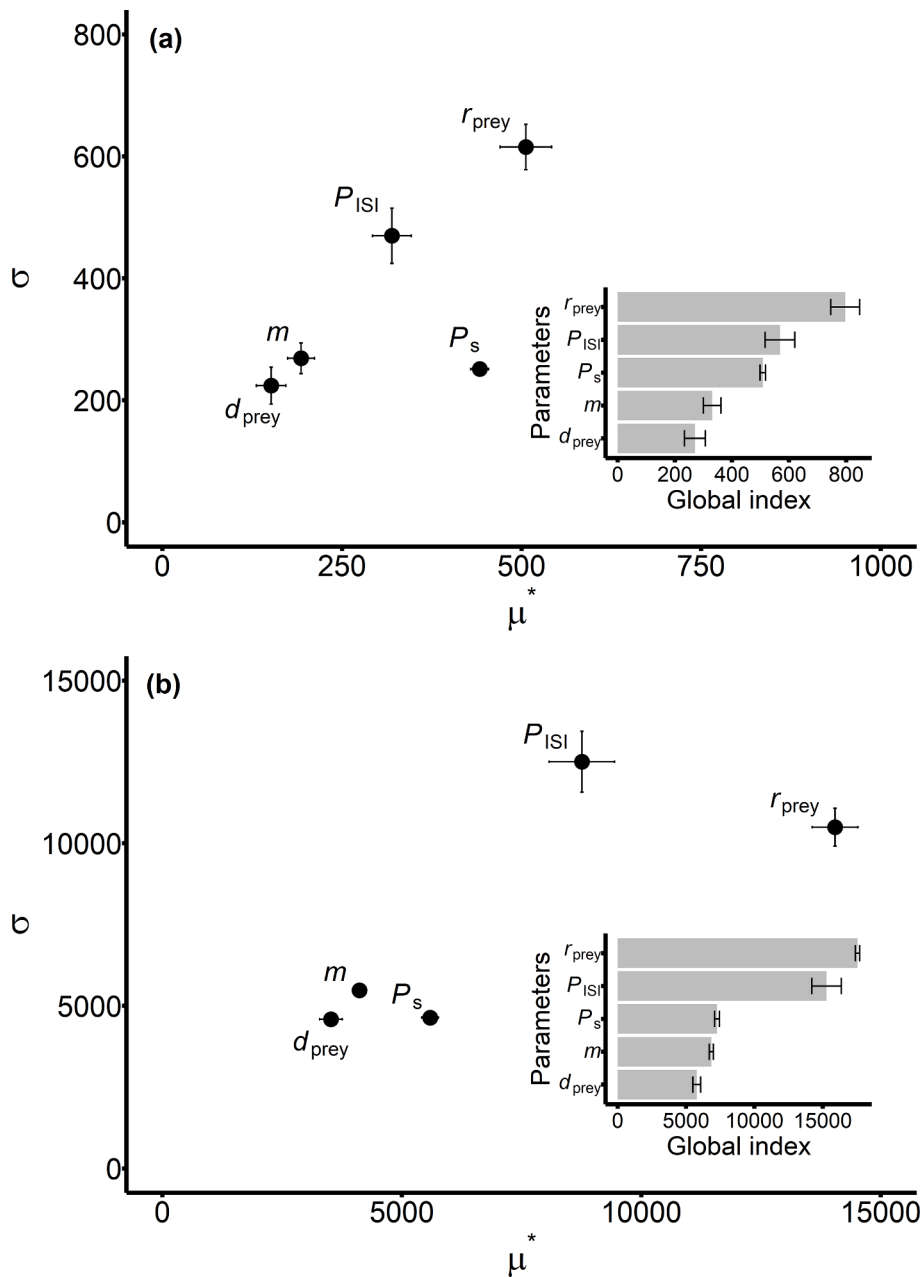The sensitivity analysis for total consumption showed a similar

Fig. 1. Results of the global sensitivity analysis (SA) depicting the impact of each model parameter on the mean (*x*-axis) and standard deviation (*y*-axis) of final prey number (a) and total consumption (b). Mean ± SD values for each parameter were calculated from five independent SA runs. Inset shows the model parameters ordered according to their overall influence on the model output.

pattern to that of the final prey number, except a much smaller influence of P_s (Fig. 1b). The two most influential parameters were r_{prey} and P_{ISI}, indicating that the emergence and spread of induced antipredator responses can have a fundamental effect on prey resource consumption. The relation between the magnitude of σ_i and μ^*_i implies that model inputs had non-linear effects, or interacted with at least one other variable. Parameters d_{prey}, m and P_s had considerably less influence on the dispersion of this model output.

When predators' detection range exceeded that of the prey, PE in itself had a small effect on total consumption (4.88% decrease in GL and 4.91% decrease in NG prey; Fig. 2b), whereas CE and PE together caused a 38.88% reduction in this output in GL prey and a 48.71% reduction in NG prey. This result suggests that CE had an 8–10 times larger effect on prey feeding than PE in the two prey types in the absence of ISI use. ISI use decreased prey total consumption when only PE was present

(18.93% decrease in GL prey and 16.54% decrease in NG prey) but had an opposite weak effect when predators exerted both CE and PE on the prey (6.9% increase in GL and 4.07% in NG prey). When prey detection range exceeded that of predators, PE in itself caused a 10.71% reduction in total consumption in GL prey, and a 10.63% reduction in NG prey. When both CE and PE were present, the total consumption of prey decreased extensively in both prey types (40.78% in GL and 48.65% in NG prey), illustrating a 4–5 times larger effect of CE than PE on this output measure in the absence of ISI use. The presence of ISI use substantially lowered prey total consumption when predators exerted only PE on the prey (53.23% decrease in GL and 67.17% decrease in NG prey), and did not change positively the magnitude of reduction in the presence of CE either (further decreased by 2.29% in GL and by 0.84% in NG prey). Thus, the effect of ISI use on CE could not completely compensate for the substantial reduction in total consumption due to the
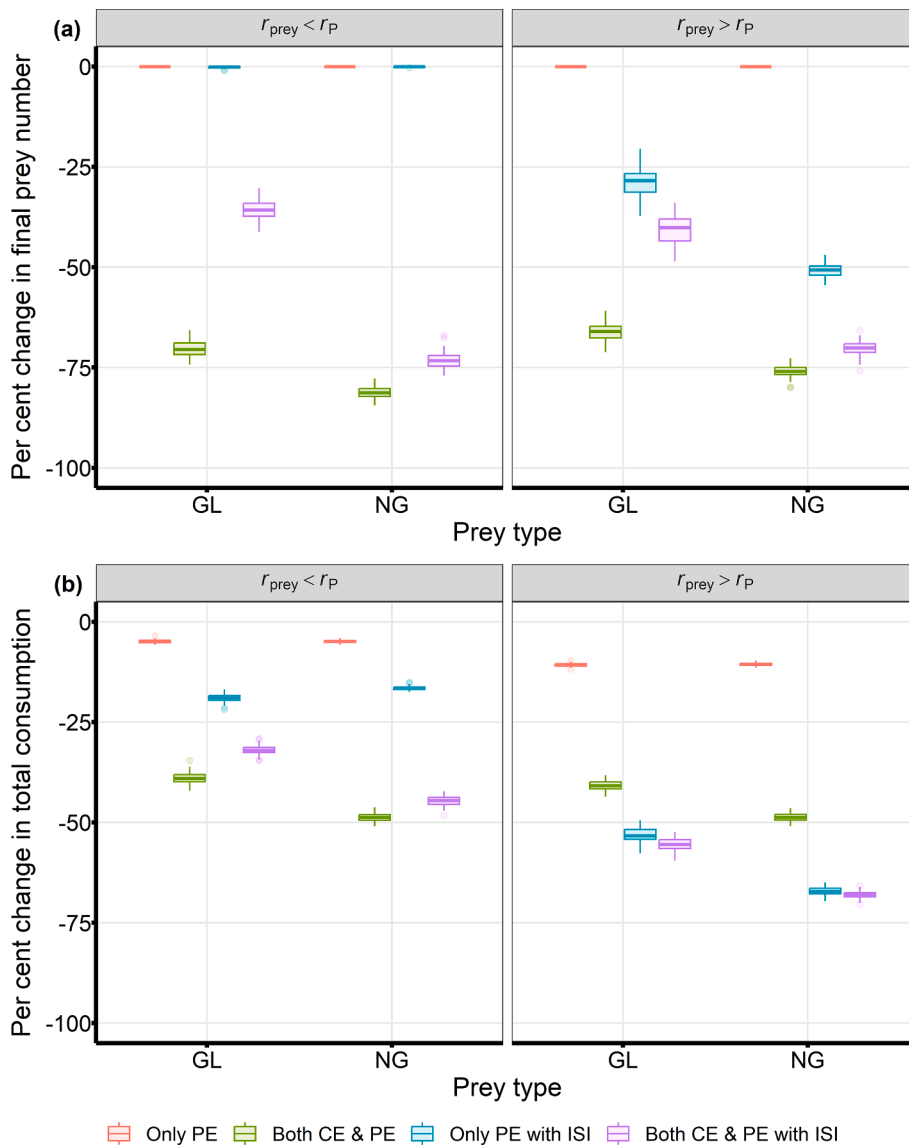
Fig. 2. Per cent changes in final prey number (a) and total consumption (b) in the explored parameter settings compared to corresponding 'no predator' scenarios. Prey type denotes the social organisation of prey (GL: group-living, NG: non-grouping), predator effects indicate the effects that predators exert on the prey population (only PE or both CE & PE) with or without ISI use, and detection range indicates the relation between prey detection range (r_{prey}) and the detection range of predators (r_P). Boxplots show the median and interquartile range, whiskers show values within 1.5-fold of the interquartile range, and dots indicate outliers.

effect of ISI use on PE. This finding demonstrates that PE in itself can successfully reduce prey feeding particularly if individuals share information about predation risk with spatially close conspecifics.

As total consumption is heavily influenced by prey population size, the per capita consumption of prey can provide a better understanding of the effects of predation risk on prey feeding behaviour. However, this measure was found to change dynamically during the 20 time steps (Fig. S1). When predators' detection range exceeded that of the prey, this measure showed an asymptotic decrease in all parameter combinations as the energetic state of prey increased in parallel within the simulation runs (Fig. S2). Nevertheless, the presence of ISI use resulted in lower starting values of per capita consumption in both GL and NG prey and negatively affected the rate of change in both per capita consumption and prey energetic state in the two prey types. When prey detection range exceeded that of predators, ISI use fundamentally altered the dynamics of per capita prey consumption, especially in NG prey: the per capita consumption of individuals was very low along with a low energetic state throughout the simulation runs, risking that they could detect nearby predators by themselves only with a substantially reduced probability.

Observations in the first quartile of the total consumption distribution (equivalent to a 50.47–70.34% decrease compared to the

corresponding 'no predator' setting) occurred in both prey types, but only in the presence of ISI use and if prey detection range exceeded that of the predators (Fig. 3b). This pattern confirms that ISI use fundamentally enhances the consequences of predators' PE if risk-related cues can be detected by prey from a greater distance compared to that from which predators can detect prey.

4. Discussion

Understanding the contribution of predation-risk effects to the net effect of predators is pivotal for predicting the conditions under which predators exert strong impacts on prey (Thaler and Griffin 2008; Hermann and Landis 2017). In this study, I showed that inadvertent social information use in prey is an organismal trait that can fundamentally mediate the magnitude of PE on both herbivore abundance and plant damage. Specifically, ISI use decreased prey total consumption through PE irrespective of the relation between prey and predator detection ranges and the type of prey social organisation, while also contributing to higher prey abundance by lowering predation-related mortality. According to the expectation, ISI use compensated for strong CEs, especially in group-living prey, but its overall impact on total consumption was negligible due to the exerted increase on the predation-risk effect
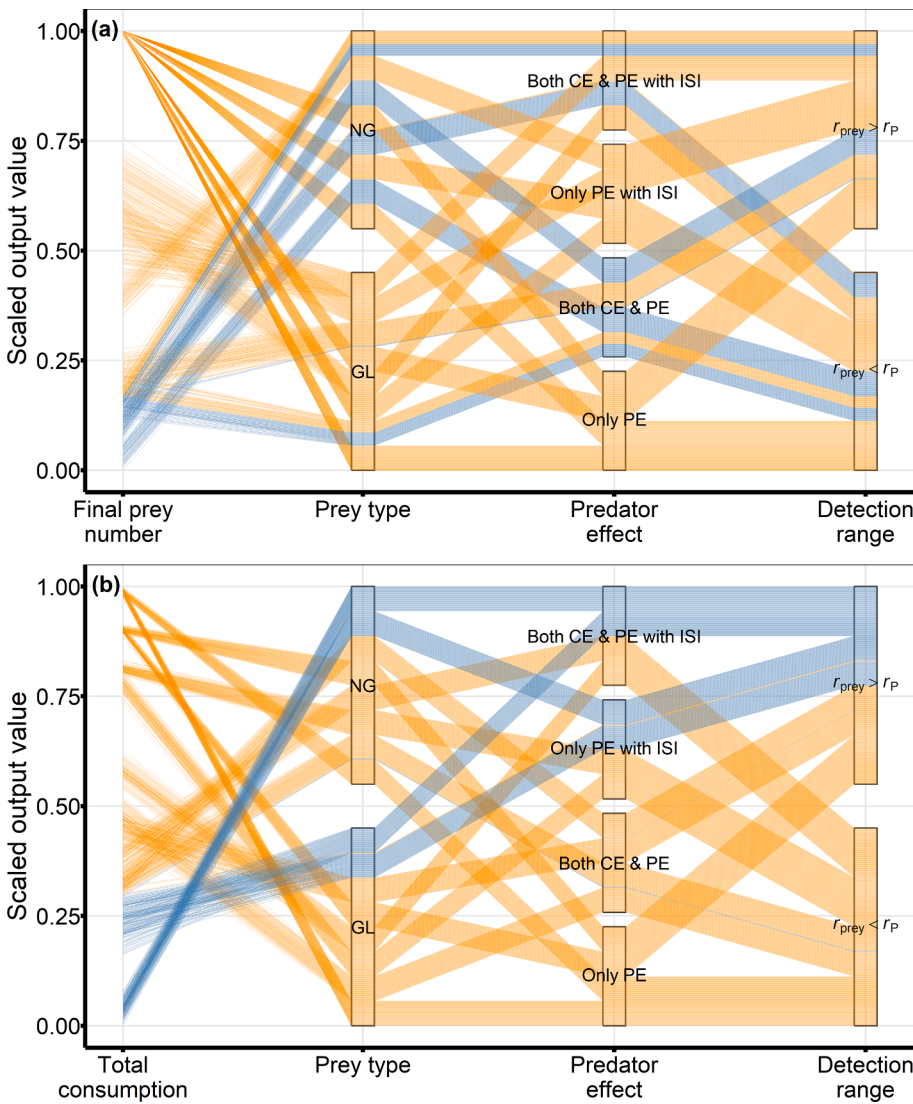
Fig. 3. Occurrences of final prey number (a) and total consumption (b) observations in the explored parameter combinations. Prey type denotes the social organisation of prey (GL: group-living, NG: non-grouping), predator effects indicate the effects that predators exert on the prey population (only PE or both CE & PE) with or without ISI use, and detection range indicates the relation between prey detection range (r_{prey}) and the detection range of predators (r_P). Observations in the first quartile of the output distributions are indicated by blue lines, the rest is shown in orange.

(<7% induced changes). Compared to GL prey, I found only small effects of ISI use on prey abundance in NG prey in some settings, most probably due to the implemented physiological constraints that led to low predator detection probabilities in individuals with low energy levels. Previous works proved that at least moderate detection probabilities are needed for NG prey to utilize social information in a predation avoidance context, while this condition is not crucial for GL prey (Tóth and Csöppü 2022; Tóth et al. under review). When prey detection range exceeded that of the predators, prey abundance decreased in the presence of PE without a consumptive effect as well. This finding was attributable to the rapid depletion of initial energy reserves during the simulation runs that resulted in a forced increase in the per capita consumption of prey. Under natural circumstances, risk-induced habitat shifting may emerge instead of starvation to death or risking a high probability of predation, leading to a similar reduction of prey density in risky habitats (Orrock et al. 2013). This idea corresponds to the 'landscape of fear' (LOF; Laundré et al. 2001) concept, according to which prey adjust its feeding spatially and temporally to the predatory stimuli present within its sensory landscape (Bleicher 2017; Ducsai et al. 2023). Social information use is known to act as a stabilising mechanism in systems where predators can exert high pressure on prey populations (Gil et al. 2017, Gil et al. 2018) and accordingly, ISI use affected prey numbers positively by reducing per-capita mortality due to predation in these simulations as well. However, here I also showed that access to and

use of risk-related social information will not only result in more prey individuals exhibiting an antipredator response but also leads to strong behavioural PEs with substantial consequences on prey consumption.

The estimated strengths of the investigated predator effect components are comparable to the findings of previous *meta*-analyses. Preisser et al. (2005) analysed the results of 166 studies on various predator–prey interactions and found that on average 60% of the total effect of predators on prey and 85% of the effect of predators on prey's resources was attributable to PE. The performed simulations showed that PE has a negligible effect on prey abundance unless prey detection range exceeds that of the predators. If so, PE's contribution could reach 73% of the total effect but only in the presence of ISI use. In the case of total consumption, the corresponding value is 10.2–98.5% depending on additional parameter settings, but the highest contribution of PE was observed under the same conditions as for prey abundance, i.e., in the presence of long-range detection of predators and ISI use in prey. In a recent study on arthropods, predators' PE was found to reduce prey feeding by 40% compared to predator-free scenarios (Buchanan et al. 2017). In corresponding comparisons, I found that such large PE on prey consumption was also associated with the presence of ISI use, and its value ranged from 16.5 to 67.2% depending on prey social organisation and the relationship between prey and predator detection ranges. Obviously, the relative difference between CE and PE depends on the strength of predation pressure, which can be influenced by several

predator traits such as age, size or hunting mode (Preisser et al. 2007; Davenport et al. 2014; Buchanan et al. 2017). Moreover, ISI use in predators may also alter selection pressures for prey defences at multiple predation stages (Hämäläinen et al. 2022; Thorogood et al. 2018). Nevertheless, these results imply that PEs with magnitudes similar to the ones observed in previous experiments can arise in different combinations of the incorporated model parameters.

Prey detection range, within which prey can observe conspecifics and detect predators before getting attacked, was one of the most influential parameters in this study. When prey individuals were able to detect predators from a greater distance than predators could detect prey, PE and the impact of ISI use on PE was substantially larger and contributed to a greatly reduced prey abundance and total consumption. This pattern corroborates that sensory modalities that can perceive relevant risk-related cues over long distances have a substantial role in the emergence of strong PEs. Detection ranges can vary both among and within species depending on the morphological and physiological attributes of prey individuals and the structural properties of the landscape they inhabit (Hannon et al. 2006; Griesser and Nystrand 2009). Within these ranges, prey uses multimodal cues to sense predators, among which acoustic, chemical and visual cues can all convey detailed information about predators' presence, type and threat level over long distances (Weissburg et al. 2014; Hettyey et al. 2015; Hermann and Thaler 2014; Fischer and Frommen 2019). When predator cues last for an extended period and remain detectable, risk-induced behavioural alterations can also persist in the absence of further cues (e.g., Ng and Gaylord 2020) and be copied by nearby observers (e.g., Coolen et al. 2005). Although long-range predator detection may be ubiquitous in the animal kingdom, studies on the relative influence of PEs are biased toward the investigation of chemosensory predator detection in aquatic habitats (Preisser et al. 2007; Weissburg et al. 2014). PEs were also found to contribute 1.6–1.9 times more to the total predator effect in aquatic compared to terrestrial ecosystems (Preisser et al. 2005). Because of that, this simulation result offers an important insight that prey need to detect risk-related cues from a safe distance from predators for a maximal PE to appear irrespective of prey habitat type and sensory modality.

The magnitude of PEs is inherently context-dependent. While previous works examined how some fundamental organismal traits affect its strength (Buchanan et al. 2017; Weissburg et al. 2014), this study is the first to address the impact of ISI use on the non-consumptive effect of predators in herbivore prey. According to my findings, the strongest PEs on resource depletion are predicted in those predator–prey systems, where social information use is present in prey and long-range cue detection is possible. Simulation results regarding how ISI use enhances abundance-related consequences of PE may also have important implications as non-consumptive effects have been shown to stabilize herbivore control over multiple generations (Ingerslew and Finke 2020; but see Kimbro et al. 2017). Comparability with previous findings demonstrates the ability of the applied modelling framework to qualitatively assess the relative influence of predation-risk effects in herbivore organisms using social information and to provide relevant predictions for future investigations of relevant natural predator–prey systems.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocontrol.2023.105339.

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