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The relative importance of social information use for population abundance in group-living and non-grouping prey

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ABSTRACT

Predator–prey relationships are fundamental components of ecosystem functioning, within which the spatial consequences of prey social organization can alter predation rates. Group-living (GL) species are known to exploit inadvertent social information (ISI) that facilitates population persistence under predation risk. Still, the extent to which non-grouping (NG) prey can benefit from similar processes is unknown. Here we built an individual-based model to explore and compare the population-level consequences of ISI use in GL and NG prey. We differentiated between GL and NG prey only by the presence or absence of social attraction toward conspecifics that drives individual movement patterns. We found that the extent of the benefits of socially acquired predator information in NG highly depends on the prey's ability to detect nearby predators, prey density and the occurrence of false alarms. Conversely, even moderate probabilities of ISI use and predator detection can lead to maximal population-level benefits in GL prey. This theoretical work provides additional insights into the conditions under which ISI use can facilitate population persistence irrespective of prey social organisation.

1. Introduction

Predator-prey interactions and their population-level consequences have been at the centre of ecological investigations for almost a century (e.g., Holling, 1959; Rosenzweig and MacArthur, 1963; Begon et al., 1996; Peckarsky et al., 2008; Ceron et al., 2022). At the conceptual core of this body of work is how predators' consumption is related to the gradient of prey density. This relationship quantifies the importance of predation in prey population dynamics and forms a functional link between different hierarchical levels of ecosystems (Kreuzinger-Janik et al., 2019; Dunn and Hovel, 2020; Beardsell et al., 2021). However, it can be fundamentally affected by prey organismal traits, altering predator feeding efficiency and thus the stability of predator and prey populations (Fryxell et al., 2007; Fryxell et al., 2022). Grouping behaviour is one such trait, occurring in a wide variety of animal taxa and leading to characteristic spatial clustering via movement rules that facilitate aggregation and maintain cohesion among individuals (Krause and Ruxton, 2002; Reluga and Viscido, 2005).

Among other effects, group formation is known to reduce the rate of encounter with predators (Wrona and Dixon, 1991; Cosner et al., 1999), dilute the per capita risk of mortality due to predation (Hamilton, 1971; Lehtonen and Jaatinen, 2016; Gil et al., 2017), and facilitate the access to and use of social information on predation risk (Duboscq et al., 2016; Ward and Webster, 2016; Goodale et al., 2017). Despite these benefits to prey in avoiding predation, predation may not be the only selection force that drives the evolution of grouping behaviour. Crook (1964) and Jarman (1974) hypothesized that variability in social organization is directly associated with resource distribution in weaverbirds (family *Ploceidae*) and African ungulates, respectively. These ideas were recently confirmed by modern phylogenetic comparative works (Szemán et al. 2021; Song et al., 2022), indicating that prey populations can indeed be primarily organised and regulated by food abundance rather than predation (for additional empirical evidence, see Lindström, 1989; Mduma et al., 1999; Fryxell et al., 2007; Månsson et al., 2017). However, even in such cases, the resulting social organisation exhibits movement patterns that exert a substantial influence on predation, for instance, by altering search efficiency in predators (Cosner et al., 1999; Fryxell et al., 2007; Fryxell et al., 2022).

While many ecological variables can facilitate group formation in prey, not all benefits above are confined to group-living species. Predator-related social information is often transmitted from alarmed group members to naïve ones through either evolved signals such as

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alarm calls or via inadvertently produced social cues including fright responses (Chivers and Ferrari, 2014; Cruz et al., 2020), changes in posture (Brown et al., 1999; Pays et al. 2013) or sudden movements (Coleman, 2008; Hingee and Magrath, 2009; Boujja-Miljour et al., 2017). Mounting evidence suggests that such inadvertent social information (ISI) is utilised in animals regardless of their social organisation (reviewed in Tóth et al., 2020; McCune et al. 2022), and ISI use may alter predators' capacity to regulate prey populations in non-grouping prey species as well (Tóth, 2021, Tóth and Csöppü, 2022). The use of such inadvertent social information can manifest in adjustments to the behaviour of others (resulting in the phenomenon of 'behavioural contagion'), both increasing the probability of individual survival and leading to correlated behaviours and space use among nearby animals (Firth, 2020). Previous theoretical works indicate that the process of ISI use in non-grouping organisms can be adequately modelled via the use of detection networks (Tóth et al., 2020; Tóth and Csöppü, 2022), within which temporary local densities allow information diffusion about predation threats among conspecifics. However, the difference in the extent by which social information can contribute to abundance in group-living and non-grouping prey populations is still unknown. Furthermore, thresholds associated with prey density, cost of the antipredator response, or predator detection and information transmission probabilities may also set different boundaries under which ISI use is most likely to occur in these two prey types in the presence of predation threats.

In group-living species, group members exhibit social attraction toward each other and maintain short inter-individual distances. Consequently, perception ranges markedly overlap and individuals have immediate access to social cues produced by group mates (Strandburg-Peshkin et al., 2013). In non-grouping animals, social cohesion among individuals and the resulting spatial proximity is lacking, but animals can still detect inadvertently produced cues of conspecifics (visual, acoustic, chemical, and vibration-related, etc.) within their perception range or come across remnants/scent marks that others left at a different time (Tóth et al., 2020). The emerging temporary detection networks between prey animals typically consist of many separate components with few connected individuals and small average ego networks. However, through such networks, the sharing of adaptive antipredator behaviour can still mitigate predation-related per capita mortality and raise equilibrium population sizes (Tóth and Csöppü, 2022).

Here we build a tentative individual-based model to compare the population-level consequences of ISI use in group-living and non-grouping prey under relatively constant predation pressures exerted by a generalist predator. We differentiate between group-living and non-grouping animals only by the presence or absence of social attraction toward conspecifics that drives individual spatial decisions. Thus, prey species do not differ from each other except for the motivation to form or not to form cohesive groups during movement (and related to this, also in offspring dispersion; see below), and group-living emerges and is maintained in the model irrespective of the level of predation or distribution of resources. Previous works have shown that grouping in prey and predators substantially alters predator–prey interactions (e.g., Lett et al., 2004; Mchich et al., 2006; Fryxell and Berdahl, 2018; Fryxell et al. 2022) and social information use promotes group formation in prey (Gil et al., 2017). Nevertheless, the interplay between the population-level effects of risk-related social information and the intrinsic properties of grouping is still poorly understood. Using a modelling approach, we first ask how predator functional response, i.e. the rate at which an individual predator consumes prey, changes due to ISI use at different population sizes in group-living (GL) and non-grouping (NG) prey. Second, we explore the multiplicative effect of the level of predation pressure, detection probabilities and costs associated with the antipredator response on prey abundance. Third, we examine if social information-mediated population-level effects are density-dependent, limiting the advantage of ISI use at low prey densities. Fourth, we investigate how the random emergence of costly antipredator responses influences the benefits of social information use in the two prey types.

2. Methods

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models (Grimm et al., 2006), as updated by Grimm et al., (2020). Below, we describe the following model features: the purpose of the model, entities, simulation landscape, and model implementation. The rest of the ODD protocol (including all elements of the design concept and submodels) is provided in the Supporting Information. We also included an '*Analysis of model outputs*' section to the Methods to introduce the analytical methods we used for describing and comparing the outputs of different simulation runs.

2.1. Purpose and patterns

The presented model is primarily designed for theoretical exploration. Its ultimate purpose is to generate predictions about the population-level consequences of the proposed information transmission mechanism under specific movement rules in prey, which follow-up observational and experimental studies could test.

The model builds on the previous work of Tóth and Csöppü (2022), where we have shown that ISI use and its diffusion through temporary detection networks may act as a stabilising mechanism under high predation pressure in non-grouping prey. The present model also utilises detection networks constructed based on simulated entities' spatial locations and perception ranges. However, the two models differ in several ways. First, group-living prey is introduced and characterised by movement and dispersion rules that result in characteristic group sizes. Second, both types of prey have intrinsic mortality independent of their spatial distribution in the new model. Third, we calculated movement distances for each entity by drawing a random value from a parameterised distribution, and detection ranges and reproductive outputs also take on different values. Nevertheless, the present model generates similar naturalistic predator-to-prey ratios as the previous one (1:2.55 in GL and 1:1:23 in NG prey [when the predator detection probability was set to minimal]–1:3.81 in GL and 1:3.48 in NG prey [with nominal predator detection and ISI use probabilities] at $K = 2500$; Donald and Anderson, 2003).

We evaluated our model by its ability to reproduce three characteristic patterns. The first pattern is the difference in social organisation (per cent of singletons and mean group size) between the group-living and non-grouping species as depicted in Fig. S1. We used only a single value for parameter m, but this does not mean that group size is uniform; larger groups appear when offspring join their parent group or when randomly moving groups cross each other's path. Singletons also emerge when groups split into small fragments and move in different directions. Similarly, temporary aggregations may emerge in non-grouping prey and therefore average group size is higher than one in this prey type as well (for real-life examples of both prey types in ungulates, see Wirtz and Lörscher, 1983). The second pattern is simply that the carrying capacity of the environment sets a boundary for prey population growth in the absence of predators in both types of prey (Fig. S2), whereas predator abundance is directly related to the reproduction-related parameter λ_P (the relationship is not linear due to density-dependent intrinsic mortality; Fig. S3). The third pattern is that inadvertent social information (i.e., the antipredator response of conspecifics) can diffuse through the constructed detection networks in both group-living and non-grouping prey and may result in ISI use (i.e., expression of the same response) in individuals that could not detect the predators themselves (Fig. 1).

2.2. Entities, model variables, and scales

The model includes two kinds of agents: prey (group-living or non-grouping) and predators. Conspecific entities do not differ in age or

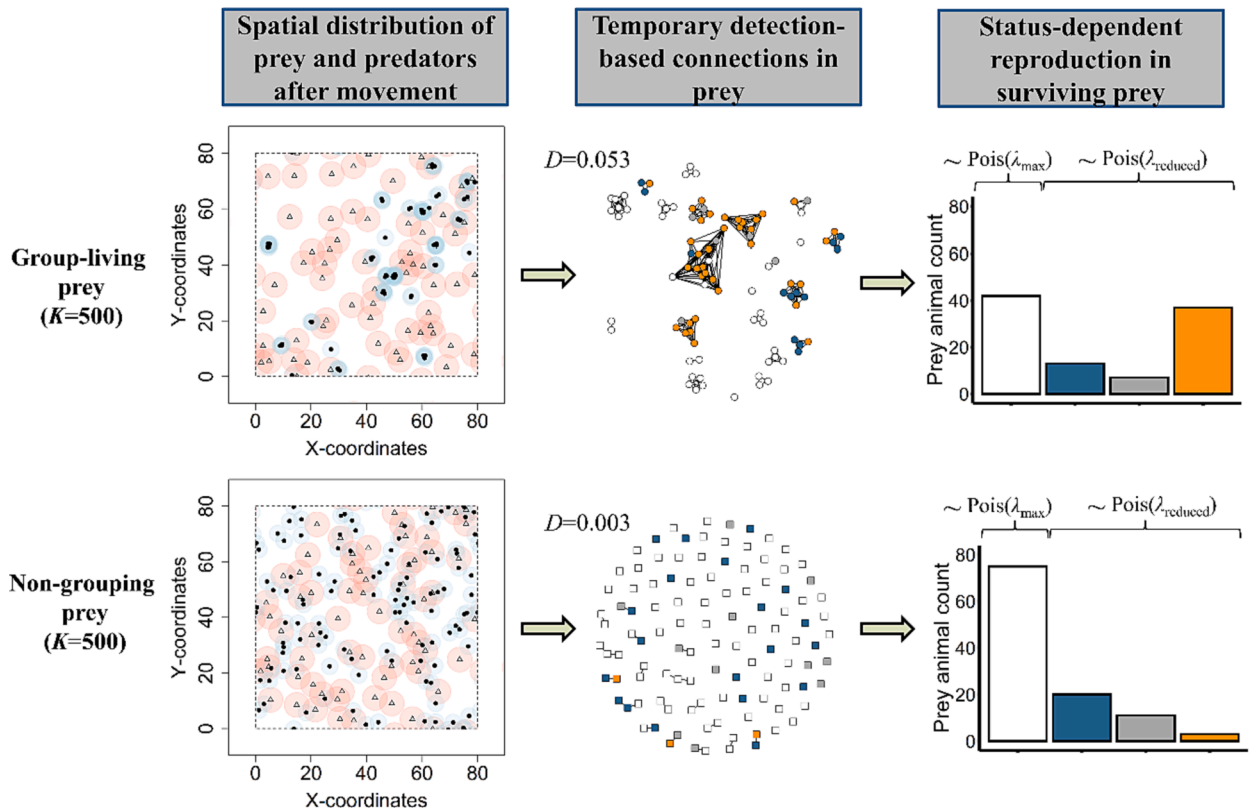

Fig. 1. Schematic figure of how spatial distributions and detection rules translate into changes in prey abundance in the model. Prey and predators (circles: group-living prey, squares: non-grouping prey, triangles: predators) move on the simulated landscape following specific movement rules, resulting in a characteristic spatial distribution of these entities (A). Within individual perception ranges, entities can detect the presence of both heterospecifics and conspecifics with given probabilities. Social information can be transmitted among prey through temporary detection networks, where nodes represent prey individuals and edges denote the possibility of mutual observation (B). Density (D) of the connections in these networks is characteristic to prey type. Prey may perceive predation threats and become alarmed if they detect a nearby predator (steel-blue symbols). Alternatively, some prey individuals may exhibit non-induced, random antipredator responses in the absence of genuine risk (grey symbols). Finally, prey may use inadvertent social information (ISI) by copying the defensive behaviour of others (dark orange symbols). The probability of information acquisition from one node to another in the network is given by w^k, where w is the edge weight and k is the number of steps on the shortest path between the two nodes. For any individual, the total probability of receiving information from the neighbours is calculated using the inclusion–exclusion principle. We used the conservative settings of $k_{max} = 2$ and $\sum n \leq 5$ in each k step, so a focal individual could receive social information about predation threats from a maximum of ten neighbours that were a maximum of two steps away in the detection network. The reproductive output of prey is state-dependent (C): unalarmed prey face predation risk but have the highest possible reproductive success (λ_{max} denotes the reproduction-related shape parameter that is used to draw a random number of offspring from a Poisson distribution for each unalarmed prey), whereas being alarmed can incur a fitness cost in the form of reduced numbers of offspring ($\lambda_{reduced}$ indicates the reproduction-related shape parameter for alarmed prey; see also in Table 1). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

sex. Non-grouping prey and predators exhibit correlated random walks (CRW). In group-living prey, individuals form groups by moving toward the closest conspecific if any are within their detection range. Once the given individual gets near to others (i.e., within attraction range), it becomes part of the group; groups move under the same rule as non-grouping individuals. If the group size exceeds the parameter m, the group splits into several smaller groups, assigning the membership 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 CRW. During movement, each individual's movement distance is randomly selected from a Weibull distribution (shape $= d_{prey}/2$ and scale $= d_{prey}$, respectively). Turning angles are determined by random deviates drawn from wrapped Cauchy circular distribution with $\mu = 0$ and $\rho = 0.8$. CRW considers short-term correlations between successive step orientations and has often been regarded as a null model for non-orientated animal movement (Benhamou, 2006; Fagan and Calabrese, 2014; Reynolds, 2014). Prey can detect predators that are r_{prey} distance with a probability given by P_{detect} (determined by individual Bernoulli trials). If a prey successfully spots a nearby predator, it becomes alarmed and hides, thus undetectable to predators. Prey can also detect conspecifics and copy their antipredator behaviour within r_{prey} distance with a probability given by P_{isi} (determined by individual Bernoulli trials). Alarmed individuals have reduced feeding rates and consequently may have fewer offspring than unalarmed conspecifics (for examples of costly behavioural responses to predation risk, see Lima and Dill, 1990). Prey can also exhibit antipredator behaviour (as a non-induced startle response) with a probability of P_{random} (determined by individual Bernoulli trials). Predators attack a maximum of five unalarmed prey within their hunting range, defined as a distance r_P from the predator's position in any direction. Hunting success is set to 50 per cent (being consumed is determined by individual Bernoulli trials for the attacked prey). Predation is modelled as a random process (Lehtonen and Jaatinen, 2016). We assumed generalist predators that exert a relatively constant predation pressure on prey, its level being directly proportional to the value of the predators' reproduction-related parameter. The size of predator populations was unaffected by prey consumption (as if switching to alternative prey when necessary); consequently, predator and prey populations were noncyclic and demographically decoupled (as in Gil et al., 2019; Tóth and Csöppü, 2022). State variables and parameters are listed in Table 1.

Table 1
Model parameters, state variables and their ranges used in the simulations.

Symbol	Description	Nominal value	Range (unit)	Prey type
n	Spatial extent of the simulated 2D landscape (in both x and y directions)	80	–	both
K	Parameter determining the carrying capacity of the environment and thus maximal prey population size in the absence of predators	2500	500–2500 (1000)	both
m	Group size threshold above which a group splits into smaller groups during movement	15	–	only group-living
d_{prey}	Parameter related to prey movement distance (determines the shape and scale parameters of the Weibull distribution from which movement distances are randomly drawn)	10	–	both
d_P	Parameter related to predator movement distance (determines the shape and scale parameters of the Weibull distribution from which movement distances are randomly drawn)	15	–	both
r_{social}	Range of social cohesion, i.e. within which group-members maintain spatial proximity	1.5	–	only group-living
r_{prey}	Prey detection range	3	–	both
r_P	Predator hunting range	4.5	–	both
r_c	Competition range within which only one predator could survive	2.5	–	both
P_{detect}	Probability of prey detecting a nearby predator; determined by individual Bernoulli trials	0.5	0.1–0.9 (0.2)	both
P_{random}	Probability of exhibiting non-induced, random antipredator response by prey	0.1	0–0.9 (0.1)	both
P_{isi}	Probability of prey ISI use (i.e., copying the antipredator response of others); determined by individual Bernoulli trials	0.5	0–0.9 (0.1)	both
'Alarmed' variable	Prey state denoting whether an individual exhibits the antipredator response (alarmed) or not (unalarmed)	–	–	both
'Feeding' variable	Amount of food consumed by prey depending on its state of being alarmed (reduced) or unalarmed (maximal)	–	–	both
λ_{max}	Prey reproduction-related shape parameter when unalarmed; used to draw a random number of offspring for each individual from a Poisson distribution	1.25	–	both
$\lambda_{reduced}$	Prey reproduction-related shape parameter when prey is alarmed; used to draw a random number of offspring for each individual from a Poisson distribution	1.25	0.875–1.25 (0.125)	both
λ_P	Predator reproduction-related shape parameter; used to draw a random number of offspring for each individual from a Poisson distribution	0.75	0.15–0.75 (0.2)	both

Note. For parameters related to probabilities, we used uniform distributions with large ranges as relevant biological information can be highly species-specific and context-specific. In the supplementary analyses (Figs. S1–S3), greater ranges for parameters K, m and λ_P were explored (K: 500–3250 (250), m: 4–24 (2), and λ_P: 0.15–1.15 (0.2)).

Individuals can detect and copy the adaptive antipredator behaviour of others (i.e., thus exploit social cues when present) in each simulation cycle. We build temporary detection networks based on individual locations and detection ranges to track the emerging pattern of ISI use among prey (i.e., the diffusion of social information in their population). A detailed description of these networks can be found in Tóth et al., (2020) and Tóth and Csöppü (2022). Briefly, nodes in these networks represent individuals, and edges between a pair of nodes denote being within each other's detection range. If a prey individual becomes alarmed because it successfully detected a predator, information about the predation risk can spread from this individual to other conspecifics in the network through the edges under the following rules. 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. Only the shortest paths are used to minimise information's "travel time" between 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., $k_{max} = 2$ and $n \leq 5$ at each k step). When there are more than five individuals at k step to a focal individual, we randomly select five. For each node in the network, we used the inclusion–exclusion principle to calculate the probability of receiving information from its identified neighbours (Allenby and Slomson, 2010).

We simulated a homogeneous, continuous 2D landscape with an extent of 80 × 80 spatial units. Natural habitats of this type include grasslands, agricultural plantations, beaches, deserts or those where resource patch distribution is uniform or random at a large scale (Byers, 2001). When crossing the landscape edge, entities moved to the opposite side and continued moving (i.e., torus landscape with no edge). Entities can also detect hetero- and conspecifics through the edges within their detection range. At initialisation, 500 prey and 150 predators are placed randomly on the simulated landscape with random orientation. The model runs at an integrated time step (or simulation cycle), during which entities move, feed/hunt, reproduce and die. Unlike any other processes, mortality occurs twice: after movement and after the dispersion of offspring. In prey, parameter K sets an upper limit for prey population size by adjusting the probability of mortality in individual Bernoulli trials to the total number of individuals (N) irrespective of spatial location:

$$P_{mortality} = 1 - e^{-N/K}$$

In predators, only one individual survives within the range of competition given by parameter r_{comp}, with the surviving individual being selected at random from the competing individuals.

2.3. Process overview and scheduling

The model is developed to cover a simplified annual cycle of the simulated entities and is structured in 14 different processes (Table S1). First, prey moves on the landscape, and their abundance is adjusted to the environment's carrying capacity through mortality. Then, predators also move and experience competition-related mortality. In their new spatial location, prey can detect predators within their detection range with P_{detect} probability. When ISI use is allowed in the model, prey individuals may also detect the defensive behaviour of conspecifics within their detection range with P_{isi} probability. Successful detection of a predator or copying the antipredator response of others directly affects the subsequent feeding process and results in a reduced feeding rate in alarmed prey. Following that, predators detect and hunt non-alarmed prey. Then, surviving prey reproduces, with the potential cost of the antipredator response influencing the reproductive output irrespective of the detection mode. During this process, offspring disperse 8, 9 or 10 spatial units away (randomly chosen) from the parent in non-grouping prey, reflecting a short-distance dispersal that is not uncommon in nature (Sutherland et al., 2000). In group-living prey, offspring remain in the parental group. Then, the prey experiences mortality for the second time. Next, predators reproduce with offspring dispersing 8, 9 or 10 spatial units away from the parent. Subsequently, competition-related mortality occurs in the predator population for the second time. Some of the above processes occur in pairs, with the prey taking action (e.g. movement, feeding, and reproduction) first and the predators performing a corresponding action immediately afterwards; reversing the order of prey and predators in these pairs of processes has no substantial effect on the simulation outcomes (Fig. S4). Data on abundance (both prey and predators), demonstration networks, occurrences of antipredator responses prior to and after ISI use, and attacking and hunting success of predators are obtained at relevant parts of each simulation cycle. We run the simulations for 150 cycles, sufficient to reach stable population sizes in all scenarios (Fig. S5). We use the data from the last cycle in the subsequent analyses. We ran the simulations 100 times in each particular setting (with one exception where the number of iterations was 30; see below).

2.4. Analysis of model outputs

All simulations and calculations were performed in R 4.0.4 (R Core Team, 2021). We did not apply frequentist hypothesis testing during the analysis; instead, we followed the recommendations of White et al., (2014) and evaluated the magnitude of differences between simulation runs with different parameter settings. R scripts for model construction and data supporting the results are archived and available at Figshare (doi: https://doi.org/10.6084/m9.figshare.22109954).

We started by considering four scenarios in which we characterised prey population sizes: in the absence of predators (M1), with minimal P_{detect} (M2), with nominal P_{detect} (M3), and with nominal P_{detect} and P_{isi} parameter values (M4), respectively. Parameter K was 500, 1500 or 2500. All other parameters were set to their nominal values. We used per cent changes in GL and NG prey population sizes for comparisons with the 'no predators' scenario. Furthermore, we visually explored the differences between GL and NG prey abundance in these four modelling scenarios with GL prey being characterised by different m values (2, 5, 10, 15 [the default value], 20, 30) at $K = 2500$. We also examined the relationship between prey abundance and the number of consumed prey in those scenarios when predators were present using the 'frair' R package (Pritchard, 2017). Data was generated by running the simulations at the complete range of parameter K to obtain sufficient variation in prey. We fitted a model with Holling's type I linear or type II decreasing prey function to estimate the relevant coefficients for the two prey types in each scenario (a represents the capture rate of a predator and h is usually referred to as the handling time of each prey). Then, we bootstrapped the fitted predator–prey functional responses ($n = 999$) to calculate 95 % confidence intervals for the optimised coefficients. Polynomial logistic functions to proportional consumption data were used to check which response type is suitable to approximate the observed relationships (Pritchard et al., 2017).

We conducted a local sensitivity analysis and explored a specific part of the parameter space by visualising the combined effect of the parameters P_{detect}, P_{isi}, λ_P and $\lambda_{reduced}$ on prey population sizes. Specifically, we investigated the effect of ISI use at five levels of predator detection probabilities (0.1, 0.3, 0.5, 0.7 or 0.9), four levels of predation pressure (0.15, 0.35, 0.55 or 0.75), and four levels of costs associated with the antipredator response (1.25 [no cost], 1.125, 1 or 0.875 [two third of λ_{max}]). We used the complete range of P_{isi} (Table 1) while holding other parameters constant and assessed how variation in P_{isi} affected prey abundance. Parameter K was 2500, whereas all other parameters were set to their nominal values. The number of iterations was 30 in this analysis. In four settings (representing the different combinations of the highest and lowest values of λ_P and $\lambda_{reduced}$) with P_{detect} equalling 0.1, 0.5 or 0.9, we fitted threshold regression models to determine if any thresholds exist under/above which P_{isi} can contribute to prey population size (i.e., the 95 % CI of the relevant slope does not overlap with zero) using the 'segmented' R package (Muggeo, 2003; 2008). We tested for one or two break-points in the linear relationship between prey abundance and P_{isi} with the 'pscore.test' function. Then, we fitted the appropriate regression model with segmented relationship (s) to obtain break-point estimates with 95 % CI. Finally, we used the 'slope' function to compute the slopes of each 'segment' in the fitted model to identify thresholds.

We investigated the effect of P_{isi} on the relationship between prey abundance and parameter K to determine if the emergence of population-level consequences of social information use is density-dependent. We conducted this investigation at two levels of predation pressure ($\lambda_P = 0.15$ or 0.75) and fitness cost ($\lambda_{reduced} = 1.25$ or 0.875). P_{isi} was set to 0 or 0.5, and all other parameters were at their nominal values. In each predation pressure-fitness cost setting, we randomly paired simulation runs from the two P_{isi} settings at each K value and calculated the differences in prey population sizes for all possible pairs. Then, we randomly selected 100 values from this vector of differences for each K. We fitted linear polynomial models on the assembled dataset with K as a predictor at each level of λ_P and $\lambda_{reduced}$ for each prey type. The optimal number of degrees was determined for each model using the k-fold cross-validation method ($k = 10$, $h = 1$, 2 or 3; Hastie et al., 2009). From the fitted models, we estimated coefficients with 95 % CI to characterize the relationship between the contribution of ISI use to population size and parameter K. Requirements were checked by plot diagnosis.

We also examined the effect of P_{isi} on the relationship between prey population size and the probability of random alarms to determine if randomly occurring, non-induced alarms can also contribute to social information-mediated population growth. We conducted this examination at two levels of predation pressure ($\lambda_P = 0.15$ or 0.75) and fitness cost ($\lambda_{reduced} = 1.25$ or 0.875). P_{isi} was set to either 0 or 0.5. P_{detect} equalled 0.1, whereas all other parameters were at their nominal values. In each predation pressure-fitness cost setting, we randomly paired simulation runs from the two P_{isi} settings at each value of P_{random} and calculated the differences in prey population sizes for all possible pairs. Then, we randomly selected 100 values from this vector of differences for each P_{random}. We fitted linear polynomial models on the assembled dataset with P_{random} as a predictor at each level of λ_P and $\lambda_{reduced}$ for each prey type. The optimal number of degrees was determined for each model using the k-fold cross-validation method ($k = 10$, $h = 1$, 2 or 3). From the fitted models, we estimated coefficients with 95 % CI to characterize the relationship between the contribution of ISI use to population size and parameter P_{random}. Requirements were checked by plot diagnosis.

3. Results

With the applied parameter setting, GL and NG prey population sizes were nearly identical in the M1 scenario at all three K values (Fig. 2; Table S2). In the M2 scenario, population size was more affected by predation in NG (reduced to ~25 % of M1) than in GL prey; in the latter prey type, it also increased with K (43–64 % of M1). This pattern indicates that forming and moving in groups itself effectively lowers the hunting efficiency of randomly moving predators. At $K = 500$ in the M2 scenario, prey population died out in nine out of 100 iterations in the NG prey, whereas GL prey went extinct only on a single occasion, implying that group-living improved the persistence of GL prey population by contributing to an overall higher population size. As prey extinctions did not happen in the $P_{detect} = 0.5$ (either with or without ISI use) or $K > 500$ settings, the potential influence of ISI use on population persistence could not be assessed within the examined parameter space. At $K = 500$, higher P_{detect} in M3 resulted in similar abundance in GL and NG prey, whereas at $K > 500$, abundance in GL was slightly higher than in NG prey (approx. by 10 %). Overall, the increase in the value of P_{detect} between M2 and M3 had a more substantial effect on population size in NG compared to GL prey at all K. At $K = 500$, M3 and M4 did not differ in NG prey, indicating the negligible positive effect of a nonzero P_{isi} value when prey density is low due to the limited carrying capacity of the inhabited landscape. At the highest K value, however, ISI use could contribute to prey abundance to a similar extent in NG and GL prey (~25 % compared to M3). Nevertheless, predation exerted a greater influence on prey population size even in the presence of ISI use in NG than in GL prey at all K values (64–87 % vs. 89–95 % of M1). Prey abundance was also higher in GL than in NG prey irrespective of the value of m, but increasing group size within GL prey was associated with increasing benefits of grouping (Fig. S6).

Predator functional response curves showed the characteristics of Holling's (1959) type II relationship in all scenarios in GL prey, whereas it took the form of a type I relationship in the M2 scenario and type II relationships in the M3 and M4 scenarios in NG prey (Fig. 3; Table S3). Functional responses were substantially affected by the value of P_{detect} and the presence of P_{isi}. Including these parameters in the model caused a qualitative deviation from the initial relationship in NG prey and substantially altered the estimated value of at least one functional response parameter in both prey types. In both prey types, social

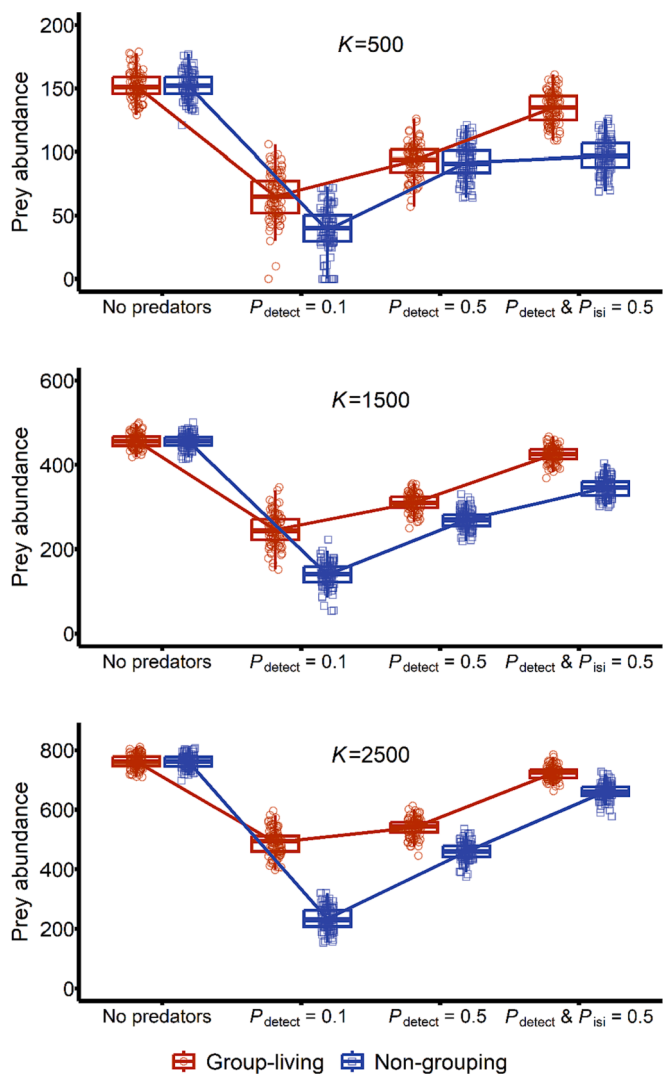

Fig. 2. Effects of the K, P_{detect} and P_{isi} model parameters on the group-living (red) and non-grouping (blue) prey abundances in four modelling scenarios. Boxplots show the median and interquartile range, whiskers show values within 1.5-fold of the interquartile range, and dots indicate individual values (circles: group-living prey, squares: non-grouping prey). When the predator detection probability was set to its minimal value (i.e., $P_{detect} = 0.1$) and K was 500, the group-living prey died out in a single iteration, whereas the non-grouping prey population went extinct in nine iterations. Lines are presented only to illustrate trends. Note that axes differ between the panels. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

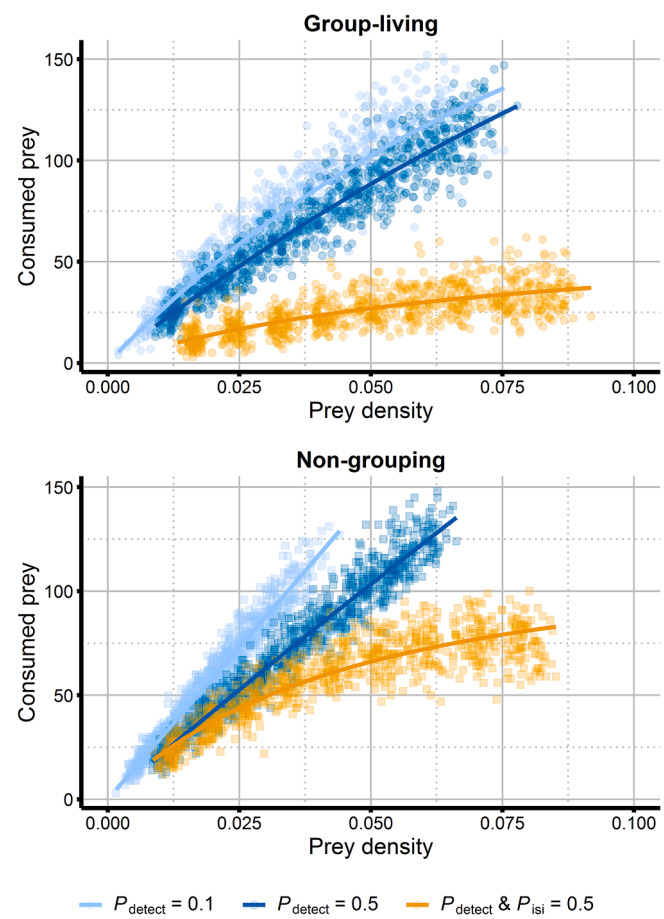

Fig. 3. Relationships between the number of prey consumed by the predators and prey density in the group-living (circles) and non-grouping (squares) species in the three modelling scenarios with predators (i.e., without the 'No predators' scenario). Trend lines denote model predictions. Simulation results from incomplete runs (i.e., when prey populations went extinct before the 150th simulation cycle) were omitted from the dataset ($n = 6$ in GL and $n = 11$ in NG prey; only in the '$P_{detect} = 0.1$' scenario).

information use in prey (M4 scenario) increased parameter h many times over compared to its value in M2 and M3, resulting in a much reduced asymptotic consumption. This reduction of the asymptote in GL was approximately double that in NG. In NG, higher P_{detect} resulted in a non-zero h and a shift from type I to type II relationship, whereas in GL, it slightly reduced the value of h. Only in GL, parameter a also decreased in the presence of ISI use, leading to lower consumption of the predators at lower prey densities.

We found substantial differences between GL and NG prey in the conditions under which ISI use can be expected to evolve and contribute to prey population size (Fig. 4). In general, increasing cost decreased the positive effect of P_{detect} on prey population size and the contribution of ISI use at a given P_{detect}, while increasing predation pressure increased the relative influence of both P_{detect} and P_{isi} on prey abundance. However, P_{detect} had a more fundamental effect in NG than in GL prey on the abundance both in itself and in interaction with P_{isi}, corroborating that the importance of this parameter is on par with that of P_{isi} in this prey type. High P_{isi} could counteract low P_{detect} values only in GL prey. The relationship between prey abundance and P_{isi} was curvilinear in most settings (except at lower predation pressures and high fitness costs), predominantly asymptotic in GL and logistic in NG prey. Threshold regression analysis revealed that ISI use in GL prey increased prey population size typically if its value was lower than 0.5 (except for two 'no cost' scenarios; Table S4) and an upper threshold existed for the positive relationship between P_{isi} and prey population size in seven out of nine settings where at least one break-point was identified. In the 'costly-low predation pressure' setting, no threshold was found. Still, the examined relationship had small slopes at all P_{detect} values reflecting a negligible contribution of ISI use to abundance (estimates with SE denoting the increase in abundance per one unit increase in P_{isi}: 1.13 ± 0.52 at $P_{detect} = 0.1$, 2.54 ± 0.43 at $P_{detect} = 0.5$ and -0.10 ± 0.48 at $P_{detect} = 0.9$). In NG prey, however, P_{isi} was positively related to prey abundance within its whole range in most settings (nine out of 11 settings with break-points), especially under high predation pressure. In the 'costly-low predation pressure' setting where P_{detect} was set to 0.1, there was only a weak positive connection between this model parameter and the simulation outcome (3.84 ± 0.64 at $P_{detect} = 0.1$).

In the examined range of parameter K, the contribution of ISI use to

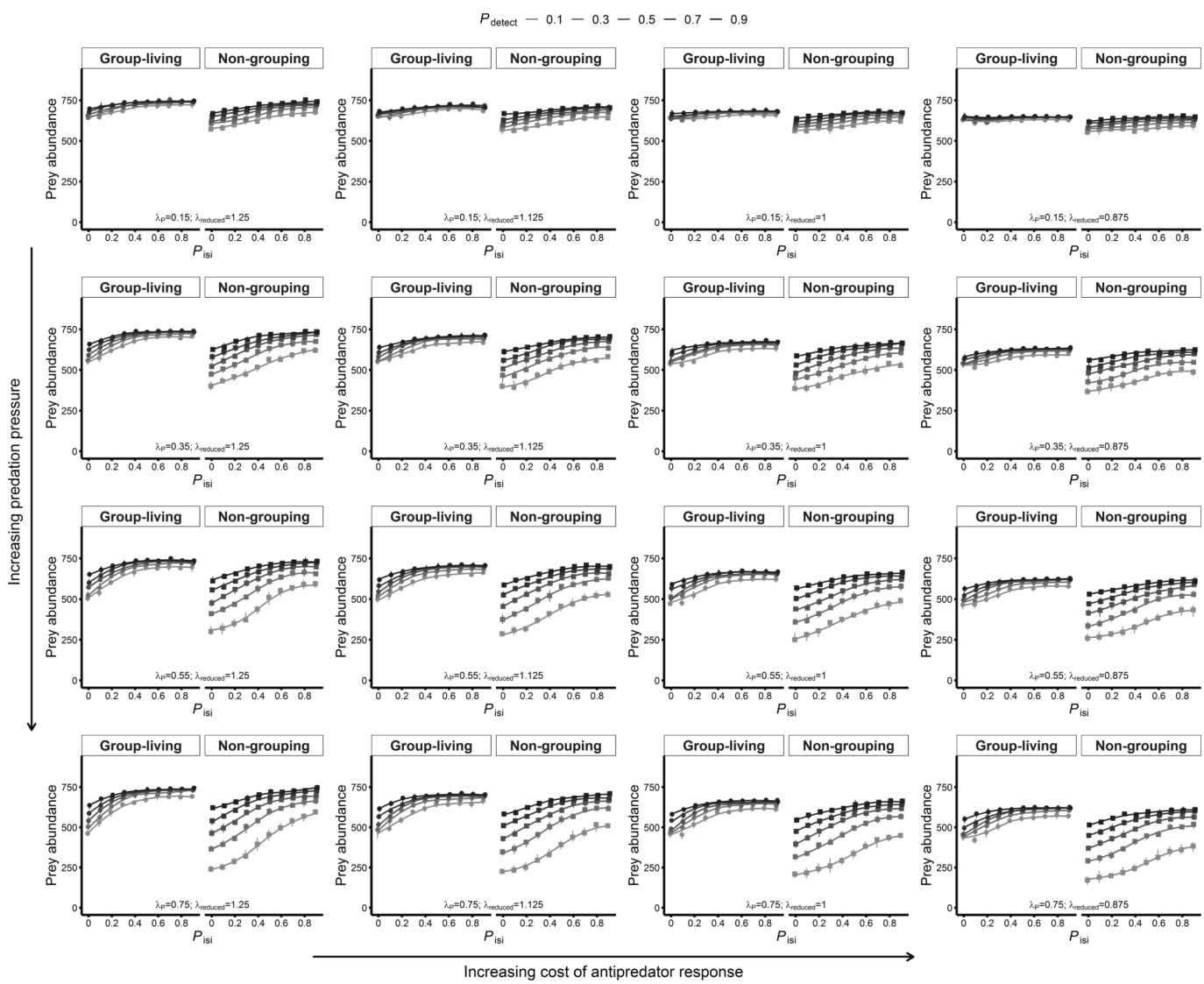

Fig. 4. Interactive effects of the probability of ISI use (P_{isi}), probability of predator detection (P_{detect}), predation pressure (λ_P) and the cost of antipredator response ($\lambda_{reduced}$) on the population sizes of group-living (circles) and non-grouping (squares) prey. Symbols represent median values and vertical lines indicate corresponding interquartile ranges; these values were calculated from 30 iterations for each parameter combination. Different colours indicate different P_{detect} values (shown in the legend). Trend lines were fitted using the 'LOESS' regression method for smoothing with the default value of span (0.75); presented only for illustration purposes. Parameter K was set to 2500.

population size increased with K in both prey types (Fig. 5; Table S5). Low adjusted R^2 values (all < 0.11) indicated poor model fit when the predation pressure was low and the antipredator response was costly. When the antipredator response was not associated with a fitness cost, the positive relationship was linear in GL prey, whereas convex nonlinear in NG prey, indicating an increasing contribution of ISI use to abundance as K increased in the latter prey type. In high predation pressure, polynomial approximations could characterise all relationships. Parameter K explained a greater proportion of the variance in the measured simulation outcome compared to the low predation pressure scenarios (adjusted R^2 ranging between 0.57 and 0.81). The cost associated with the antipredator response did not alter the characteristics of these relationships but decreased the extent of the contribution to population size in both preys. In GL prey, the curvilinear relationships were asymptotic but did not show any turning points within the range of K investigated here; these relationships revealed a positive effect of ISI use on prey abundance even when prey density was low. In NG prey, ISI use did not increase prey population size at the lowest K value, confirming that a sparse spatial distribution of prey individuals hinders the detection of and adjustment to conspecifics' antipredator response. The convex nonlinear relationships denoted an increasing contribution of ISI use to abundance as the value of parameter K increased within its examined range. ISI use increased prey abundance more substantially in NG than in GL prey at high prey densities (at $K = 2500$, the predicted contribution of ISI use was 173.79 individuals [24.02 % of the equilibrium population size] in GL and 197.70 individuals [29.92 %] in NG prey in the absence of a fitness cost).

The investigation of the relationship between the contribution of ISI use to prey population size and the probability of random alarm revealed similar patterns in the two prey types (Fig. 6; Table S6). Most importantly, all relationships could be approximated with higher-order polynomial fits that indicated the existence of non-zero random alarm probabilities that maximise the contribution of P_{isi} to abundance. Under low predation pressure, the turning points were estimated to be 0.61 and 0.43 in the 'costly' setting, while 0.36 and 0.30 in the 'no cost' setting in GL and NG prey, respectively. However, the contribution of ISI use to prey abundance was moderate even at these critical points. The examined model parameter explained only small proportions of the variance in the simulation outcome (all adjusted $R^2 < 0.29$). When the predation pressure was high, turning points ranged between 0.27 and 0.35 in both prey types and the probability of random alarm better explained the variance in the contribution of ISI use to population size than in the 'low predation pressure' scenario (adjusted R^2 ranging between 0.55 and 0.72). The increase in population size was similarly high at the critical P_{random} values in the two prey types when the antipredator response was costly (~164 individuals), and exceeded 200 individuals in both GL and NG prey without costs. A minor difference between the GL and NG prey was that ISI use increased abundance in the latter prey type only moderately in the 'no cost' setting when the probability of random alarm was zero. Consequently, the change in the value of P_{random} from zero to 0.1 increased the contribution of ISI use to population size more substantially in NG than in GL prey.

4. Discussion

Our results show that social information can mediate prey population dynamics under high predation pressure regardless of the type of prey social organisation. As expected, we also found some characteristic differences between GL and NG prey species in the conditions under which ISI use is likely to occur and increase abundance. In GL prey, group formation itself reduced the encounter rate with predators (Fryxell et al., 2007) and enhanced population persistence at low population sizes, while the transmission of risk-related social information among group-mates increased prey abundance even under less favourable conditions. In NG prey, the probability of predator detection, prey density, and the occurrence of false alarms were identified as critical parameters that, at low values, diminish the contribution of ISI use to population size. Simulation results indicated that the lack of social

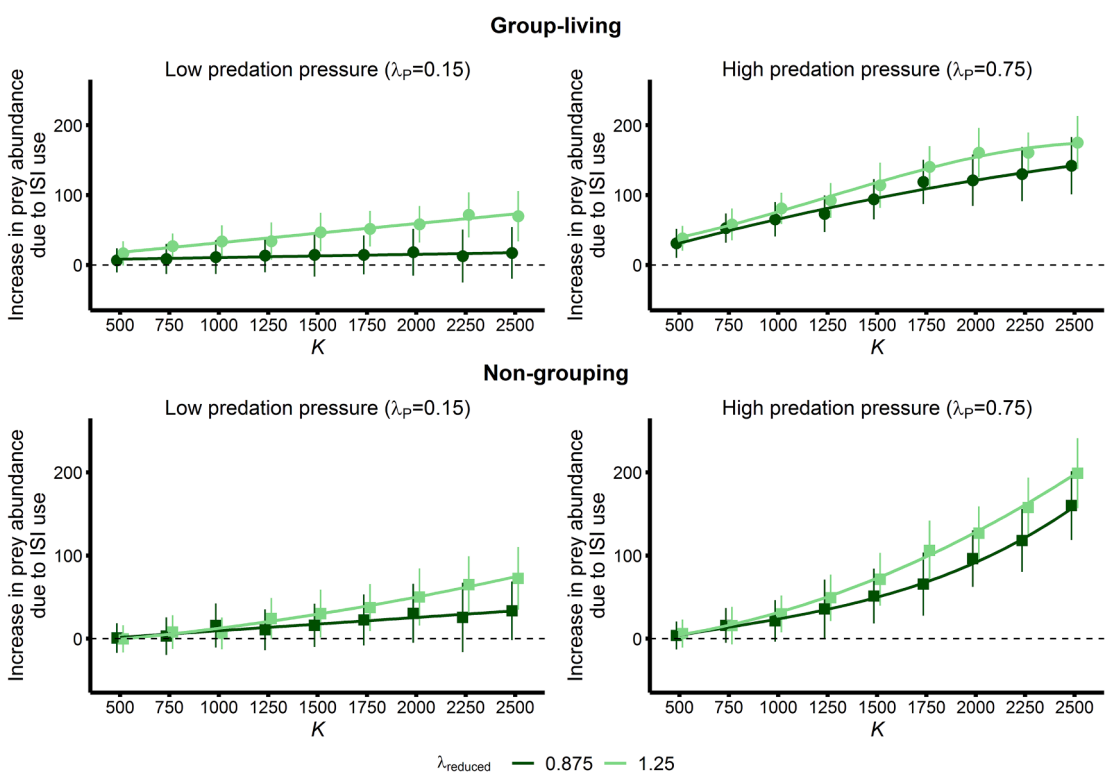

Fig. 5. Increase in population size due to ISI use in group-living (circles) and non-grouping (squares) prey at different K values. Symbols represent mean differences (i.e., the mean difference in population sizes between the $P_{isi} = 0$ and $P_{isi} = 0.5$ settings at each K) and vertical lines show the corresponding SDs. Trend lines were fitted using polynomial approximations with the degree of the best-fitting models. P_{detect} was set to 2500.

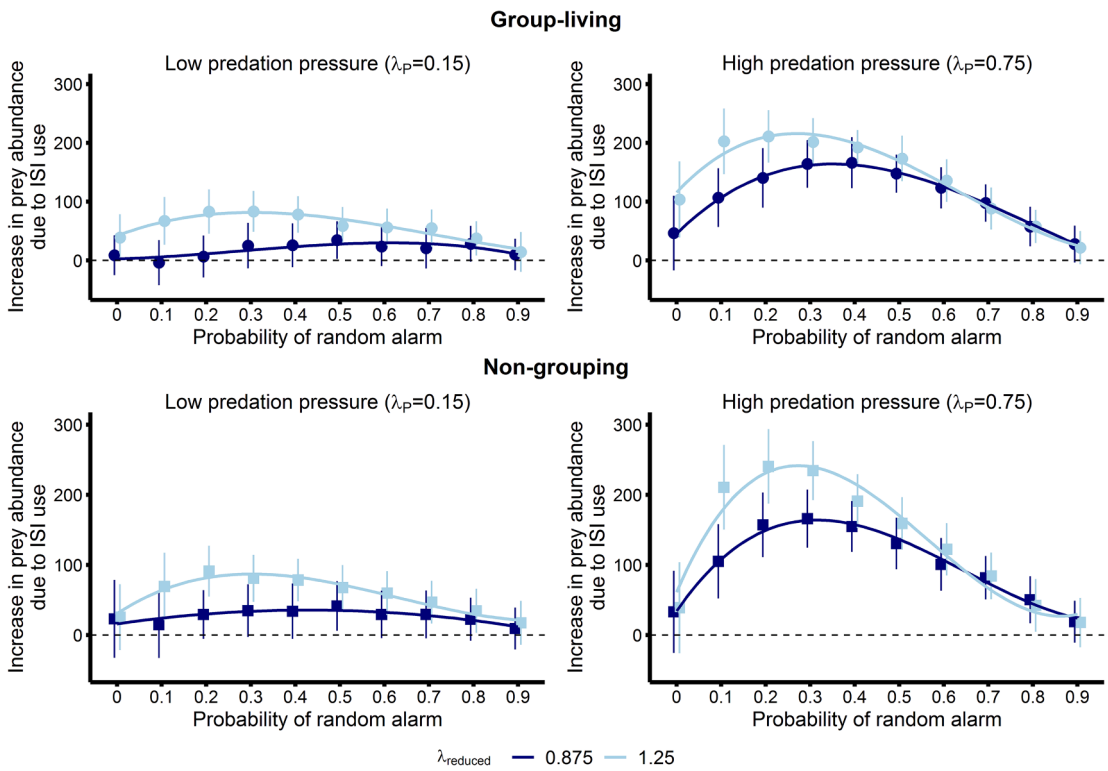

Fig. 6. Increase in population size due to ISI use in group-living (circles) and non-grouping (squares) prey at different P_{alarm} values. Symbols represent mean differences (i.e., the mean difference in population sizes between the $P_{isi} = 0$ and $P_{isi} = 0.5$ settings at each P_{alarm}) and vertical lines show corresponding SDs. Trend lines were fitted using polynomial approximations with the degree of the best-fitting models. Parameter K was set to 2500 and P_{detect} to 0.1.

cohesion in NG prey results in spatial distributions that limit the use of social information and differences in the efficacy of ISI use between GL and NG prey exist even when GL prey forms smaller groups (although to a lesser extent compared to large groups; Fig. S6). Predators' performance depends on how the prey is distributed in their habitat, so ignoring the spatial consequences of social organisation may seriously under- or overestimate predation rates at the population level (Cosner et al., 1999; Vandermeer and Goldberg, 2013; Nachman, 2006; Fryxell et al., 2022). Such biases have important ecosystem-level implications regarding how predators can regulate populations of their prey (Dunn and Hovel, 2020) or how vulnerable prey populations are to predator-mediated Allee-effects (Gascoigne and Lipcius, 2004). We found that ISI use induced quantitative changes in the relationship between prey density and the functional response of the predators: the spread of risk-related social information markedly reduced the per capita feeding rate of predators (Fig. 3). However, the asymptotic limit of predation-related mortality was higher in NG prey in all scenarios compared to GL prey. The presented simulations provide a mechanistic explanation for the emergence of population-level consequences of ISI use in prey populations and supplement previous findings on these effects in NG organisms (Tóth, 2021; Tóth and Csöppü, 2022).

The ability of prey to detect predators before getting attacked primarily determines its chances of escaping predation (and similarly, the ability of predators to detect prey before getting noticed substantially affects their hunting success) and so it has been the target of evolutionary arms races in countless predator–prey relationships (Fischer and Frommen, 2022; Paterson et al., 2020; Zimmer et al., 2021). Under natural conditions, predator detection probability can vary among and within species depending on both the morphological and physiological attributes of prey individuals and the structural properties of the landscape their populations inhabit (Hannon et al., 2006; Griesser and Nystrand, 2009). Using a range of detection probabilities in which the majority of observable values are likely to fall (between 0.1 and 0.9), we showed that the probability of ISI use in GL prey had an upper threshold in most parameter settings above which it did not increase prey abundance at any predator detection probabilities (Fig. 4). This intriguing result indicates that over-reliance on social information (i.e., high probabilities of response copying) is unnecessary for acquiring the maximal population-level benefits of ISI use. If we assume that the probability of predator detection is directly related to vigilance behaviour, our findings also support previous theoretical and empirical works that per capita predator detection can be low in GL prey (decreasing with group size; e.g., Beauchamp, 2008; Gil et al., 2017; Wang et al., 2021), while it has a substantial effect in NG prey (Tóth and Csöppü, 2022). We also showed that social information use in NG prey increased population size at the complete range of ISI use probabilities. However, crucial prerequisites existed for the emergence of positive effects: a sufficiently high prey density and non-zero probability of random alarms if predation detection probabilities were low. The first provided the necessary number of conspecifics within detection range; the latter supplemented the predator detection ability of prey by enhancing the number of cue producers (see below). Notably, GL and NG prey did not differ in how predation pressure and costs associated with the adaptive antipredator response influenced the magnitude of population growth due to ISI use and copying costly responses (representing a ~30 % decrease in offspring number) was beneficial under high predation pressure regardless of the type of prey social organisation. To test these predictions of our model, systematic observations on the ranges and probabilities of detection for predators or prey are required. Available literature data include the measurement of flight initiation distances to simulated predation risk imposed by approaching humans or (artificial) natural predators (e.g., Caro, 2005; Weston et al., 2012; Møller and Erritzøe, 2014), alarm calls with measured or estimated distances at which alarm calls or flight responses occur (e.g., Janson et al., 2014; McLachlan and Magrath, 2020; Dutour et al., 2021), or distances based on the initiation of attack or stalking behaviour in open-habitat predators (e.g., Eaton, 1970; Elliott et al., 1977). Besides, long-term/detailed investigations of specific predator–prey relationships might also yield

sufficient data for model parametrisation (e.g., Quinn and Cresswell, 2004; 2005; Cresswell et al., 2000; Cresswell et al., 2010; Cresswell and Quinn, 2011).

Density-dependence of the effects of social information use has been advocated by previous works (e.g., Schmidt et al., 2015; Gil et al., 2018) and confirmed by our model within the examined parameter range, particularly under high predation pressure (Fig. 5). A crucial component of this effect is the relation between the density and detection range of prey within which social cues can be perceived and utilized. Due to the maintained group cohesion in GL species, some conspecifics are usually within detection range, whereas, in NG species, independent movement paths can lead to rare conspecific detections. Consequently, as our results indicated, social information cannot spread among NG prey individuals and contribute to abundance at low population sizes even under favourable conditions. This limitation is essential as current models predict that the benefits of increased access to social information due to increasing density exceed the competition costs primarily at low population size (Gil et al., 2018). A possible solution to this problem is the utilization of heterospecific social cues, which has also been shown to occur in predation avoidance context in various non-grouping species (see in Tóth et al., 2020). As population density grows, the competition for resources among conspecifics also increases, so we can expect that a critical density exists in both GL and NG prey above which the costs of resource competition eventually outweigh the benefits of social information. Density-dependence in encounter rates and social information use have been documented in various GL species (e.g., Vander Wal et al., 2014; Schmidt et al., 2015; Berdahl et al., 2016; Schmidt, 2017), but similar patterns remained largely unexplored in NG prey (but see Gil and Hein, 2017).

Our simulation results showed that the probability of random alarms had an optimal range at which ISI use increased prey population size to the greatest extent (Fig. 6). These ranges largely overlapped in GL and NG prey and emerged under high predation pressure even if the antipredator response was costly. In our model, the antipredator response was perfect and guaranteed complete safety from predators, whereas its cost was associated with the reproductive performance of prey. In natural conditions, this relationship is likely to be more strongly affected by the interplay between the energetic and 'lost opportunity' costs (*sensu* Gray and Webster, 2023) and the efficiency of the antipredator response. Nevertheless, this finding highlights two important issues regarding inaccurate or false alarms. First, false alarms are often viewed as an unappreciated cost of group foraging (e.g., Beauchamp and Ruxton, 2007). Still, predators are rarely noticed from a safe distance with constantly high probability and therefore prey with imperfect predator detection may benefit from random alarms due to the higher number of social cue producers. Second, the level of predation pressure represents a more crucial ecological parameter than the associated costs, fundamentally determining the role of and responsiveness to false alarms when risk-related ISI use occurs in prey.

Empirical evidence shows that false alarms are ubiquitous in many GL species (Blumstein et al., 2004; reviewed in Beauchamp and Ruxton, 2007; Hollén et al., 2008) and can occur at a surprisingly large rate within all produced alarms. For instance, the ratio of false to real alarms was observed to be 4.5–6.8 to 1 in flocks of semipalmated sandpipers, *Calidris pusilla* (Beauchamp, 2010), 2.6 to 1 in wintering redshank, *Tringa totanus*, flocks (Quinn and Cresswell, 2004) and 3.4 to 1 in willow tits, *Poecile montanus* (Haftorn, 2000); these values are comparable to the estimated optimal frequency of false alarms (3–4 to 1) in our simulations when the predator detection probability was set to minimal under high predation pressure. While the frequency of false alarms is predicted to increase with group size (Beauchamp and Ruxton, 2007), this connection was not observed in all studied systems (e.g., Lindström, 1989; Cresswell et al., 2000). Overall, our result supports the idea that maintaining responsiveness to all cues reflecting potential threats can incur population-level benefits and represents a low-cost strategy against predation following the "better-safe-than-sorry" principle (Beauchamp, 2010). Interestingly, the population-level consequences in NG prey were similarly substantial than in GL prey. Social cues transmitted among NG prey, even inaccurate ones such as randomly occurring alarms, can mitigate predation risk even though such individuals generally have poor predator detection ability. Moreover, such alarms can be the only source of social cues if the detection range of predators greatly exceeds the detection range of prey, which, for instance, can be a common feature of many predator–prey relationships involving raptors. Thus, while the occurrence of false alarms can lead to costly misinformation cascades and may represent a risk to using social information (Rieucau and Giraldeau, 2011; Gray and Webster, 2023), we argue that regarding false alarms unequivocally disadvantageous in all circumstances may distract our attention from the role these responses can play in social information-mediated population dynamics.

Our results support that ISI use can be adaptive and increase population abundance in environments characterised by high predation pressure, even if using risk-related social cues incurs fitness costs. The presented model makes several predictions about the conditions under which social information-mediated population dynamics are expected to emerge in NG and GL prey. We proved that NG could acquire population-level benefits from social information use, but the extent of these benefits highly depends on the prey's ability to detect predators and the existence of adequately high prey density at which information can spread among conspecifics at risk. Conversely, with the intrinsic consequence of grouping on the encounter rate with generalist predators, even moderate probabilities of ISI use and predator detection lead to maximal population-level benefits in GL prey. Furthermore, our study is the first theoretical work that provides initial insights into the causal relationship between the occurrence of false alarms and the benefits of socially acquired predator information. These findings should encourage further studies to consider the role of ISI use in population persistence irrespective of prey social organisation.

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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Author contributions

ZT, RB, ZN and VRS conceived and designed the study. ZT constructed the model, performed the simulations, analysed the model output, wrote the initial manuscript, and revised and edited the subsequent versions. RB, ZN and VRS contributed substantially to the text and revisions.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtbi.2023.111626.

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