Social information-mediated population dynamics in non-grouping prey

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Abstract

Inadvertent social information (ISI) use, i.e., the exploitation of social cues including the presence and behaviour of others, has been predicted to mediate population-level processes even in the absence of cohesive grouping. However, we know little about how such effects may arise when the prey population lacks social structure beyond the spatiotemporal autocorrelation originating from the random movement of individuals. In this study, we built an individual-based model where predator avoidance behaviour could spread among randomly moving prey through the network of nearby observers. We qualitatively assessed how ISI use may affect prey population size when cue detection was associated with different probabilities and fitness costs, and characterised the structural properties of the emerging detection networks that would provide pathways for information spread in prey. We found that ISI use was among the most influential model parameters affecting prey abundance and increased equilibrium population sizes in most examined scenarios. Moreover, it could substantially contribute to population survival under high predation pressure, but this effect strongly depended on the level of predator detection ability. When prey exploited social cues in the presence of high predation risk, the observed detection networks consisted of a larger number of connected components with smaller sizes and smaller ego networks than corresponding randomized networks; this resulted in efficient information spread among connected individuals in the detection networks. Our study provides hypothetical mechanisms about how temporary local densities may allow information diffusion about predation threats among conspecifics and facilitate population stability and persistence in non-grouping animals.

Keywords: social information use, detection networks, predator-prey relationship, non-grouping animals, equilibrium population size, individual-based model

Significance Statement

The exploitation of inadvertently produced social cues may not only modify individual behaviour but also fundamentally influence population dynamics and species interactions. Using an individual-based model, we investigated how the detection and spread of adaptive antipredator behaviour may cascade to changes in the demographic performance of randomly moving (i.e., non-grouping) prey. We found that social information use contributed to population stability and persistence by reducing predation-related per capita mortality and raising equilibrium population sizes when predator detection ability reached a sufficient level. We also showed that temporary detection networks had structural properties that allowed efficient information spread among prey under high predation pressure. Our work represents a general modelling approach that could be adapted to specific predator-prey systems and scrutinize how temporary local densities allow dynamic information diffusion about predation threats and facilitate population stability in non-grouping animals.

Introduction

Organisms have to gather information about their surroundings to overcome challenges such as finding resources and avoiding danger (Dall and Johnstone 2002). For that, individuals directly interact with the environment to gain up-to-date information about its state (‘personal information’; Dall et al. 2005), but they can also complement that knowledge by utilizing social information for optimal decision-making (Galef and Giraldeau 2001; Bonnie and Earley 2007; Hoppitt and Laland 2013). One type of social information is associated with inadvertently produced social cues that include 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 information about current environmental conditions. Inadvertent social information (ISI) use is known to occur in many ecological contexts, including predator avoidance, foraging and habitat choice (Danchin et al. 2004; Gil et al. 2018), and is usually associated with species where social interactions promote information transmission among group-mates (King and Cowlishaw 2007; Duboscq et al. 2016; Gil et al. 2017).

Under predation risk, dynamic information about threats is transmitted from alarmed group members to naïve ones, a phenomenon that is commonly called collective detection (Lima 1990; Pays et al. 2013). This process often takes place through evolved signals such as alarm calls, but social cues including sudden movements (Coleman 2008; Hingee and Magrath 2009; Boujja-Miljour et al. 2017), fright responses (Chivers and Ferrari 2014; Cruz et al. 2020), or changes in posture (Brown et al. 1999; Pays et al. 2013) have also been found to convey information about the presence of predators in animal collectives. Adjustments to the behaviour of others (also referred to as ‘behavioural contagion’; Firth 2020) do not only affect individual fitness by increasing survival probabilities, but can also lead to the emergence of correlated behaviours and space use in many individuals and thus influence system-level functions (Goodale et al. 2010; Gil et al. 2018; Tóth 2021). Previous theoretical models have predicted that ISI use can prevent population collapses under high predation pressure (Gil et al. 2017, 2018) and facilitate the coexistence of competing species that share common predators (Parejo and Avilés 2016; Gil et al. 2019). Empirical evidence also indicates that the utilization of social information can influence the material flux on the ecosystem level (Gil and Hein 2017). By promoting adaptive behavioural responses to environmental uncertainties (e.g., due to anthropogenic effects [Greggor et al. 2017], in the distribution of resources [O'Mara et al. 2014] or predation risk [Crane et al. 2021]), ISI use has the potential to render morphological, physiological or genetic adaptations redundant or only partially necessary (Laland 1992).

Lacking motivation for social cohesion, non-grouping animals do not maintain spatial proximity with others, and thus direct interactions between conspecifics can be infrequent. Nevertheless, such individuals may also exploit social cues (e.g., visual, acoustic, chemical or vibrational cues) when these are within the range of relevant sensory perception. Moreover, social information may also diffuse among nearby observers via 'detection networks' (reviewed in Tóth et al. 2020). If so, spatial changes in social cues over time (e.g., relative differences in activity and associated conspicuousness; Chivers and Ferrari 2014) can provide dynamic information about predation threats in many terrestrial and aquatic systems (Gil et al. 2017). In accordance with this idea, wood crickets (*Nemobius sylvestris*) adaptively change their behaviour after having observed the predator avoidance behaviour of knowledgeable conspecifics, and this information is transmitted to and utilized by other naïve individuals as well (Coolen et al. 2005). In temporary aggregations, escape responses of Iberian green frogs (*Rana perezi*) are also influenced by the behaviour of adjacent conspecifics (Martín et al. 2006). In mixed-species aggregations of non-schooling fish, the density and behaviour (when to feed in and when to flee from the foraging area) of nearby individuals are being used as inadvertent social information (Gil and Hein 2017). The resulting behavioural coupling among individuals, in turn, affects both species abundance and the amount of algae consumed and as a result, determines the total material flow in the coral reef ecosystem. While such observations prove that threat-related social cues can be exploited by non-grouping animals in some instances, the general conditions under which ISI use exerts a positive effect on population stability and persistence in such species have remained largely unexplored. For example, thresholds associated with the cost of antipredator behaviour and probabilities of cue detection (i.e., the detection of predators or conspecifics' behaviour) may set boundaries for social information-modulated population-level effects under different predation pressure regimes. Similarly, detection networks may have only a limited capacity to provide efficient information pathways for the emergence of such effects.

In this study, we investigated how the detection and spread of predator avoidance behaviour among conspecifics affected demographic performance in non-grouping prey. We constructed an individual-based model of prey and generalist predator populations where individuals (both prey and predators) moved randomly on the landscape, and social information could diffuse through the observation of antipredator behaviour in prey. This model, an extension of our earlier model presented by Tóth (2021), allowed us to assess qualitatively how ISI use may cascade to changes in population size and examine the structural properties of detection networks in prey populations that lack social structure.

Materials and Methods

Model construction

We simulated a continuous 2D landscape (80 × 80 spatial units) where both prey and predators moved randomly by exhibiting correlated random walks (CRW). CRW considers short-term correlations between successive step orientations and has been used to model animals' random search paths for a long time (Benhamou 2006; Codling et al. 2008). At the start of a simulation cycle, 500 prey and 150 predators were randomly placed on the landscape, and then individuals performed a given set of behaviours (Fig. 1, Table 1). During movement, each individual's movement distance was randomly selected between zero and a maximum value given by the parameters d_{prey} and d_{P} for prey and predators, respectively. Turning angles were determined by random deviates drawn from wrapped Cauchy circular distribution with μ=0 and ρ=0.8. At the landscape edge, individuals moved to the opposite side of the landscape when crossing a boundary and continued moving (i.e., torus landscape with no edge). Both prey and predator could also detect other individuals through the landscape boundary. We assumed that only one individual could survive within the range of one spatial unit due to competition in both prey and predators (after movement and dispersion of offspring; see Fig. 1), introducing density-dependent mortality in their populations. In this system, we assumed non-dynamic predators that can exert high pressure on the prey population, thus predator population size was determined only by their reproductive rate and density-dependent mortality, but was unaffected by the success of hunting (as if switching to alternative prey when necessary). Consequently, predator and prey populations were noncyclic and demographically decoupled (for a similar approach, see Gil et al. 2019), and prey populations experienced predation pressures that were directly proportional to the given value of predators' reproduction-related parameter (Table 1).

In the absence of predators, prey moved, competed, fed and reproduced in the simulated landscape. Prey population size resulted in this scenario was regarded as being in equilibrium at the carrying capacity of the environment. When present, each predator could consume a maximum of two prey individuals in a cycle within its hunting range, which was defined as an r_{P} distance from the predator's position in any direction. Prey could detect predators that were r_{prey} distance with a probability given by P_{detect} (determined by individual Bernoulli trials). Upon successfully detecting a predator, prey became alarmed and hid, and thus was undetectable to predators. However, these individuals did not feed either and consequently could have a reduced reproduction rate. Thus, prey animals were capable of behaviourally adjusting their exposure to predators (with the probability ranging between 0.1 and 0.9; see Table 1), but this antipredator behaviour potentially incurred a fitness cost. Lima and Dill (1990) summarized supporting evidence for such scenarios in multiple taxa. Predators hunted on visible, feeding prey with a 50% success (determined by individual Bernoulli trials). Prey could also detect predators indirectly by observing alarmed conspecifics within r_{prey} distance with a probability given by P_{isi} (determined by individual Bernoulli trials). Being alarmed had the same consequences (i.e., immune to predation, reduced reproduction rate) irrespective of the detection mode. We did not manipulate cue reliability in the model, we simply considered that ISI use had a higher cost when social cues could also be false and individuals responded to those indiscriminately. Prey feeding occurred once in a cycle in prey that was not hiding. The number of offspring for each individual was sampled from a Poisson distribution with the shape parameter given by λ_{reduced} for alarmed prey, λ_{max} for fed prey, and λ_{P} for predators in each cycle. Offspring dispersed in the same cycle 8, 9 or 10 spatial units away (randomly chosen) from the parent in both prey and predators. These higher step values (10 spatial units is the double of maximum d_{prey} and d_{P}) were chosen to reflect that juvenile dispersion distances can far exceed adult movement ranges.

Detection networks

From the spatial distribution of prey, we defined detection networks based on the range within which individuals could observe the behaviour of others (i.e., exploit social cues if present) in each simulation cycle (Fig. 2). In such networks, nodes represent individuals, and edges denote the possibility of mutual observation. If a prey individual became alarmed because it successfully detected a predator, information could spread from this individual to other conspecifics in the network 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 (corresponding to the probability of information spread from one node to another through the edge between them and 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 shortest paths were used to minimize the “travel time” of information between nodes in the network. During simulations, the maximum number of steps between the focal and the observed nodes was set to two and the total number of observed neighbours to ten (i.e., k_{max}=2 and $\sum(n)_{\mathrm{max}}$=5 in each k step). Thus, an individual could receive information from a maximum of ten of its neighbours that were a maximum of two steps away in the detection network. With such restrictions, ISI use did not facilitate the emergence of large aggregations in prey and did not occur far outside the hunting range of predators. If there were more than five nodes at k step to a focal node, we randomly selected five. For any individual, the total probability of receiving information from its neighbours was calculated using the inclusion-exclusion principle (Allenby and Slomson 2010).

Analysis of simulation outputs

All simulations and calculations were performed in R 4.0.4 (R Core Team 2021). Instead of frequentist hypothesis testing, we focused on evaluating the magnitude of differences between simulation runs with different parameter settings (White et al. 2014). We ran the population simulations for 200 cycles (this interval was sufficient to reach equilibrium prey population size in the studied scenarios; see in Fig. 3a) and used the data from the last cycle in all calculations. R script for model construction and simulated data are available at Figshare (https://figshare.com/s/34fc714342dab9123193).

We characterised prey population sizes by calculating the mean, standard deviation, maximum and minimum values in four settings: in the absence of predators, with minimal P_{detect}, with nominal P_{detect}, and with nominal P_{detect} and P_{isi} parameter values, respectively. All other parameters were set to their initial values; for each model type, simulations were iterated 50 times. When the predator detection probability was set to its minimal value, the prey population died out in a single iteration; prey extinction was not observed in other settings.

We used Morris's „OAT" elementary effects screening method (Morris 1991) with the extension introduced by Campolongo et al. (2007) as a global sensitivity analysis (SA) to rank the model parameters according to their impact on prey population size. We chose this SA because it produces results comparable to the more complex methods (Confalonieri et al. 2010) and is applicable to uncover the mechanisms and patterns produced by individual-based models (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, whereas the standard deviation of the elementary effect (σ_i) indicates possible non-linear effects or interactions among variables (Campolongo et al. 2007; Iooss & Lemaître 2015). We also ranked the model parameters using a global index (GI) (Ciric et al. 2012) calculated as:

$$GI = \sqrt{\left(\mu^{*}_{i}\right)^{2} + (\sigma_i)^{2}}$$

For the space-filling sampling strategy proposed by Campolongo et al. (2007), we generated $r_2 = 1000$ Morris trajectories and then retained $r_1 = 50$ with the highest 'spread' in the input space to calculate the elementary effect for each model parameter.

We examined how predator density affected mortality rate due to predation in prey in the presence of minimal P_{detect}, nominal P_{detect}, and nominal P_{detect} and P_{isi} parameter values, respectively. All other parameters were set to their initial values. In each setting, simulation runs were iterated 50 times. If the prey population died out before the 200th simulation cycle, the given run was omitted from the dataset (*n*=209; only in the 'minimal predator detection' setting).

We also explored a specific part of the parameter space that included the parameters P_{detect}, P_{isi}, λ_{P} and λ_{reduced}. Specifically, we investigated the effect of ISI use at low, intermediate and high levels of predator detection probabilities. In each scenario, predator avoidance behaviour had either no cost or incurred moderate fitness cost (i.e., decreased by one third compared to the maximum) and predation pressure was either low (0.025), intermediate (0.05) or high (0.075). In each setting, we used the complete range of parameter values for P_{isi} (Table 1). Simulations were iterated 30 times. In the low predator detection probability scenario coupled with high predation pressure, the prey population died out in the majority of simulation runs (*n*=581); these simulation outputs were omitted from the assembled dataset.

We generated network data by running the model with $\lambda_{\text{P}}=0.075$ (i.e., under a high level of predation pressure) and $P_{\text{isi}}=0$ or 0.5 (all other parameters were set to their nominal values). Then, we calculated the number of components, component size, average ego network and average global efficiency as structural network properties to characterize the emerging detection networks. Simulations were repeated 50 times in each parameter setting. To test whether the global structure of these networks is different from random, we calculated the same characteristics for randomised detection networks. These were constructed from the observed detection networks by randomly reshuffling the edges between nodes while also retaining the original degree distributions. Thus, randomisation was constrained based on the most fundamental structure of the original networks (Croft et al. 2011). The number of components represents the number of connected parts in the detection networks (isolated nodes excluded). We computed component size as the number of components divided by the number of connected nodes; this measure denotes the average number of nodes embedded within components. We calculated the average size of ego networks as the mean number of reachable nodes within two steps in the components. To estimate transmissibility within components, we used the measure ‘global efficiency’ (Pasquaretta et al. 2014; Romano et al. 2018; Latora and Marchiori 2001). Global efficiency for a graph with N vertices is:

$$E_{\mathrm{global}}(\mathrm{G}) = \frac{1}{N(N-1)} \sum_{i \neq j} \frac{1}{d_{ij}}$$

where d_{ij} is the shortest path length between nodes i and j. The value of this measure ranges from 0 to 1, and represents how fast information may spread from the source to the most peripheral network positions with the least number of connections (Romano et al. 2018). We computed global efficiency for the largest components in the networks. For the calculation of the above network properties, we used the ‘igraph’ and ‘brainGraph’ R packages (Csardi and Nepusz 2016; Watson 2020).

Results

We found that nominal predation pressure coupled with minimal predator detection probability (P_{detect}=0.1) led to small prey population size with high variation among runs compared to the null model when predators were absent and prey population existed at the carrying capacity of the environment (Fig. 3a, Table 2). Nominal predator detection probability (P_{detect}=0.5) increased mean prey population size and stabilised the prey population at higher abundance values, while in the presence of nominal probability of ISI use in prey (P_{detect}=0.5 & P_{isi}=0.5), prey population size increased further by approx. 53%. The sensitivity analysis also confirmed that P_{isi} was an influential model input in the constructed model (Fig. 3b). As expected, the parameters driving antipredator behaviour, i.e. the level of predation pressure, the probability of predator detection directly or via conspecifics, and the cost associated with performing antipredator behaviour, were all important and characterised by non-linear effects on prey abundance and/or strong interactions with other parameters. The parameters d_{prey} and d_{P} had considerably less influence on the dispersion of the model output, and were fixed to their nominal values in the subsequent analyses. The mechanism behind the effect of P_{isi} was that the presence of ISI use could decrease the per capita mortality due to predation across the whole range of the examined predation pressure regime and substantially mitigate the positive relationship between predation-related mortality rate and predator population size (Fig. 4).

Consistent with expectations, P_{isi} affected prey number in all examined P_{detect} scenarios in interaction with the effect of cost and predator pressure (Fig. 5). This relationship was positive and nonlinear in most cases. When the predation pressure was low, P_{isi} positively influenced prey abundance to a limited extent, while the effect of the associated cost, especially at lower P_{isi} values, depended on the value of P_{detect}. When the predation pressure was intermediate or high, P_{isi} exerted a more substantial influence on prey abundance and had the capacity to double the number of prey individuals irrespective of the presence or absence of associated cost. Importantly, ISI use could counteract high predation pressure only when P_{detect} had a sufficient value (directly dependent on the degree of predation pressure), and did not compensate for low predator detection ability as indicated by the high prevalence of population extinctions in prey when high predation pressure was coupled with low predator detection ability. The presence of associated fitness cost in the high predation pressure settings greatly reduced the magnitude of the effect of ISI use on prey population size, but P_{isi} could still increase prey population size even at intermediate values if $P_{\mathrm{detect}}>0.25$.

All structural properties of the detection networks differed qualitatively from corresponding randomised networks under high predation pressure, but mostly when social information spread through the detection networks (Fig. 6). In this scenario, the observed detection networks were characterized by higher numbers of components that consisted of fewer connected individuals and smaller ego networks than their randomized counterparts. Global efficiency within the largest components, therefore, was also high in the observed detection networks, indicating efficient information transmission among individuals whenever connected prey was able to detect nearby predators. These attributes of functioning detection networks were not the direct consequence of higher prey population size in the presence of ISI use, because the corresponding randomized networks did not show the same degree of structural changes compared to the P_{isi}=0 setting.

Discussion

Social information use has been assumed both to increase individual fitness and to affect population- and community-level processes (Dall et al. 2005; Gil et al. 2018). We expected that such effects could emerge in randomly moving non-grouping prey if behavioural contagion can occur through detection networks, i.e., a dynamic system of temporary observation-based connections between conspecifics. We found that irrespective of the apparent stochasticity in our model, the sharing of adaptive antipredator behaviour could contribute to population stability and persistence in prey by mitigating predation-related per capita mortality and raising equilibrium population sizes. We also showed that temporary detection networks had structural properties that allowed the efficient spread of adaptive antipredator behaviour among prey under high predation pressure. In animal groups, information spreads via social connections among individuals and social network positions strongly interact with individual spatial behaviour (Firth and Sheldon 2016; Spiegel et al.

2016; Webber & Vander Wal 2018; Albery et al. 2021), thus movement characteristics and space use are shaping information transmission by affecting social connections. Our findings indicate that non-grouping animals, by being embedded in detection networks based on their perception attributes and spatial locations, can benefit from similar information transmission processes as well.

Our results corroborate with previous studies indicating that social information may act as a stabilizing mechanism in systems where predators can exert high pressure on prey populations (Gil et al. 2017, 2018, 2019). While in those models social information directly reduced (following a specific function) the per capita mortality (e.g., Gil et al. 2018), the presented work offers a more mechanistic understanding of how inadvertent social information could propagate through a population of randomly moving individuals. Our findings indicate that predator detection ability had to reach a sufficient level, strongly dependent on the actual level of predation pressure, for ISI use to facilitate prey population persistence. Notably, when this condition was met, ISI use exerted a detectable positive influence on prey population size by relaxing predation pressure even at low probabilities and even if the adaptive antipredator behaviour incurred a fitness cost. Although the depth of our understanding of the detected non-linear relationships and potential thresholds is limited by their coarse-grained variation in these parameters examined here, simulations nonetheless prove that in a substantial part of the parameter space social information use can be expected to raise non-grouping prey population size and facilitate its persistence. These findings may have crucial implications in many theoretical and applied ecological contexts, ranging from the invasive dynamics of predator-prey systems to the efficiency of biological control practices. For instance, the recognition of novel predators by naïve prey has been associated with social information use via different perception modalities in fish (Ferrari et al. 2005; Manassa et al. 2013), and similar utilization of social cues in birds has been shown to facilitate the spread of novel aposematic prey (Thorogood et al. 2017; Hämäläinen et al. 2021). Such social information-mediated interactions between prey and predators might be more prevalent in natural ecosystems that include non-grouping species as well, contributing to deviations from the predictions of theoretical models in the dynamics of trophic interactions (Polis et al. 2000). When natural enemies are used as biological control agents for pest management, social diffusion of antipredator responses may substantially reduce predation rates rendering these practices less effective and profitable. Besides, it may also mitigate the expected positive impact of the non-consumptive effects of predators (NCEs; Preisser et al. 2007; Sih et al. 2010) such as decreased crop damage due to reduced feeding rate in pests (Beleznai et al. 2017; Tholt et al. 2018). This inflation of NCEs due to information spread can generate discrepancies in the findings of large-scale field studies and laboratory experiments (see in Weissburg et al. 2014), and should be taken into consideration in investigations that aim to evaluate how NCEs may trigger trophic cascades in different ecosystems (Herman and Landis 2017; Haggerty et al. 2018; Pessarrodona et al. 2019).

Detection networks had distinct structural characteristics compared to the randomised networks when prey experienced high predation pressure and exploited social cues to avoid predators. These networks typically consisted of many components with few connected individuals and small average ego networks, and within these small components, social information could spread with relatively high efficiency. The key to understanding the differences in structural properties of detection networks in the presence and absence of ISI use lies in identifying the process that generates more and smaller components. One plausible explanation is that prey distribution in the simulated landscape could remain more homogeneous due to a decreased susceptibility to predation in the vicinity of predators as the diffusion of social information greatly enhances the probability of predator detection even among a few nearby individuals. While high network efficiency has previously been identified in small groups, cognitive abilities and strong social affiliations have usually been involved in explaining this emergent property (Waters and Fewell 2012; Pasquaretta et al. 2014). Our findings indicate that incidental connections may generate networks that have similar favourable attributes. In addition to differences in the sizes of connected components, there may be other key differences in how information spreads through detection or sensory networks among group-living (Strandburg-Peshkin et al. 2013; Rosenthal et al. 2015; Davidson et al. 2021) and non-grouping individuals, however. First, behavioural contagion can be complex, and the number of non-alarmed individuals within the detection range influences the likelihood of adopting a specific behaviour (Firth 2020). Previous works on social species have provided mounting evidence for such complex contagion (Hoppitt and Laland 2013; Grüter and Leadbeater 2014; Kendal et al. 2018). Second, imperfect copying might decrease the intensity of behavioural responses with each transmission step, and under a given threshold intensity, social cues exert no response from nearby observers. In this case, individuals' ability to convey information about predation hazards is related to the extent of behavioural change compared to a baseline level (Chivers and Ferrari 2014). Third, phenotypic heterogeneity among individuals may influence information diffusion if individual traits (e.g., related to hunger, age or developmental stage) or functional traits that transcend species (e.g., similarity in body size that may lead to shared predators) affects the individual capacity to produce social information (Farine et al. 2015).

To describe how ISI use may affect population dynamics in non-grouping prey, we constructed a tentative model with naturalistic predator-to-prey ratios (1:1.03 [when predator detection probabilities was set to minimal]–1:4.23 [with nominal predator detection and ISI use probabilities]; see in Donald and Anderson 2003). Previous observations indicate that predator detection probability, which has been found to play a crucial role in the emergence of social information-mediated effects in our study, can have a value within the upper half of the range examined here (i.e., >0.5) under relevant conditions (e.g., Tisdale and Fernández-Juricic 2009; Manzur et al. 2018). However, being strongly dependent on the neuronal pathways underlying detection mode and the processing capacity of the brain (Clark and Dukas 2003, Pereira and Moita 2016), it can differ significantly between species and even within the same species as it may also depend on the forager's state of energy reserves (Clark and Mangel 2000). Therefore, to construct a more realistic model, both species-specific and context-specific information for existing predator-prey relationships need to be incorporated, which can be done only at the expense of generality. Model precision may be further enhanced by incorporating additional variables including the functional response of specific predator species (Dunn and Hovel 2020), different non-consumptive effects (other than reduced feeding rate) (Peckarsky et al. 2008), a measure of social cue reliability (Dunlap et al. 2016), social information use in predators (Falk et al. 2015), or landscape heterogeneity that could alter the space use of individuals (Albery et al. 2021). The effects of different transmission modes can also be tested, for instance, by weighting the probability of information diffusion among conspecifics by the proportion of alarmed and non-alarmed individuals within the detection zone or incorporating heterogeneity among individuals in attributes that affect their propensity to act as social cue producers. Our work, thus, represents a general modelling approach that could be applied to predator-prey systems in which populations are demographically decoupled, and prey may mitigate predation hazards through the exploitation of incidentally produced social information.

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Conflict of interest

The authors have no conflict of interest to declare.

Ethics approval

Not applicable.

Consent to participate

Not applicable.

Consent for publication

Not applicable.

Data availability

Data files supporting the results are archived and available at Figshare (https://figshare.com/s/34fc714342dab9123193). Upon reasonable requests, R codes for the model functions are also available from the corresponding author.

Authors' contributions

ZT and CG 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. CG contributed substantially to the text and revisions.

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Table 1. Model parameters and their range for sensitivity analysis (SA). Maximum movement distances indicate the maximum number of spatial units that an individual could travel on the landscape in a simulation cycle; the actual integer value was randomly selected between zero and this maximum value.

Symbol	Description	Nominal value	Unit/Scale	Range for SA
d_{prey}	Prey maximum movement distance	5	1	3-8
d_{P}	Predator maximum movement distance	5	1	3-8
r_{prey}	Prey detection range	2.5 (constant)	-	-
r_{P}	Predator hunting range	3.5 (constant)	-	-
r_{c}	Competition range within which only one individual could survive	1 (constant)	-	-
P_{detect}	Probability of prey detecting a nearby predator; determined by individual Bernoulli trials	0.5	0.1	0.1-0.9
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
λ_{max}	Prey reproduction-related shape parameter when prey feed; used to draw a random number of offspring for each individual from a Poisson distribution	0.75 (constant)	-	-
λ_{reduced}	Prey reproduction-related shape parameter	0.75	5×10^{-2}	0.5-0.75

	when prey is alarmed (i.e., does not feed); used to draw a random number of offspring for each individual from a Poisson distribution			
λ_P	Predator reproduction-related shape parameter; used to draw a random number of offspring for each individual from a Poisson distribution	5×10^{-2}	5×10^{-3}	2.5×10^{-2}-7.5×10^{-2}

Table 2. Descriptive statistics of the simulated prey populations computed from the 200th simulation cycle calculated from 50 replicates (49 in the case of the second model type as prey population died out in a single iteration).

Models	Parameters		Prey population size	
	P_{detect}	P_{isi}	Mean ± SD	Range
No predators (n=50)	-	-	1198.16 ± 24.37	1115-1251
Minimal predator detection (n=49)	0.1	0	154.45 ± 56.49	24-257
Nominal predator detection (n=50)	0.5	0	516.18 ± 50.36	408-637
Nominal predator detection & ISI use (n=50)	0.5	0.5	789.52 ± 48.05	632-891

Figure legends

Figure 1. Model flowchart for a single simulation cycle. Sequential prey and predator behaviours are listed together with the model parameter(s) associated with the given steps. Behavioural steps resulting in a decrease in population size, i.e., mortality due to intraspecific competition (in rounded rectangles) or predation (in diamond) are shown in light and dark grey, respectively.

Figure 2. Schematic figure of a detection network (a) and segment of an individual ego network embedded within that network (b). Nodes represent individuals and edges denote the possibility of mutual observation. The probability of information acquisition from one node to another 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 neighbours is calculated using the inclusion-exclusion principle. In our model, we used the settings k_{max}=2 and $\sum n_{max}$=5 in each k step, so the focal individual (black circle) could receive social information from a maximum of ten neighbours that were a maximum of two steps away in the detection network (orange circles).

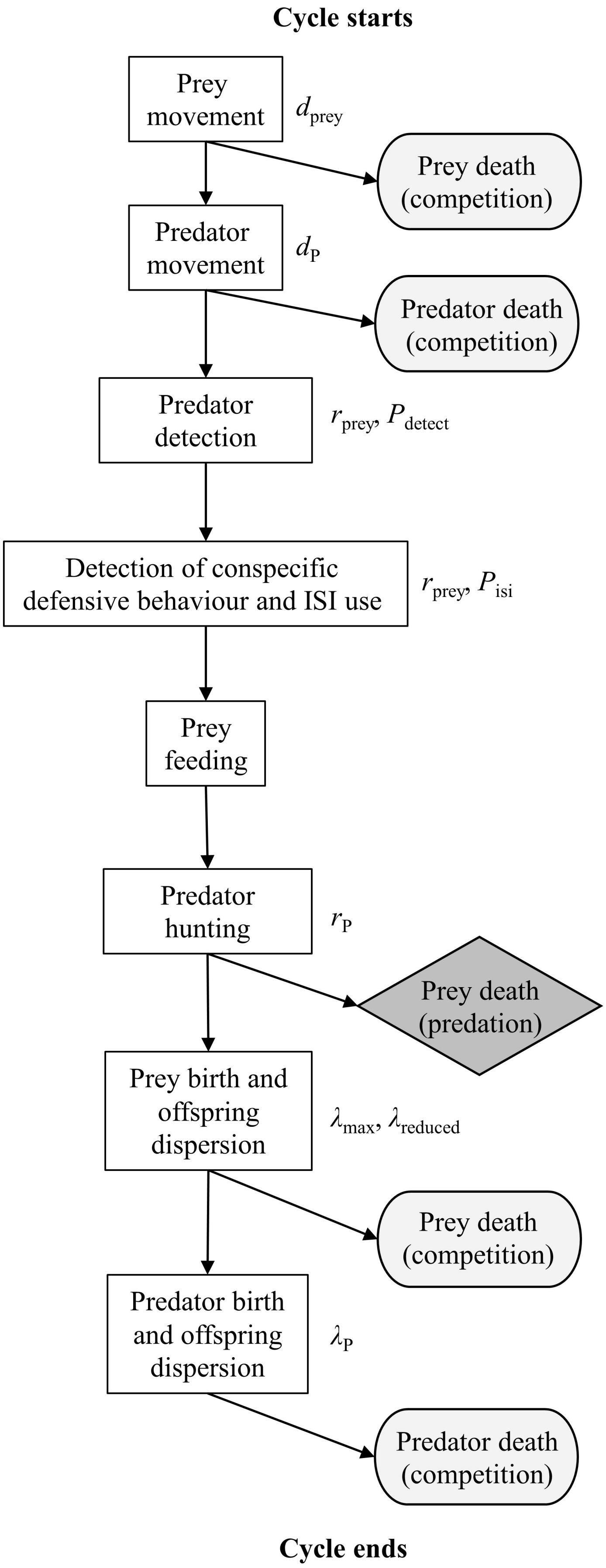
Figure 3. Effects of the P_{detect} and P_{isi} model parameters on the prey population. (a) Temporal fluctuations in prey abundance (means with range) without predators (grey) and under nominal parameter settings (with nominal P_{detect} & P_{isi} – orange, with nominal P_{detect} – dark blue, with minimal P_{detect} – light blue). When the predator detection probability was set to its minimal value, the prey population died out in a single iteration; in all other cases, the number of iterations was set to 50. (b) 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 prey

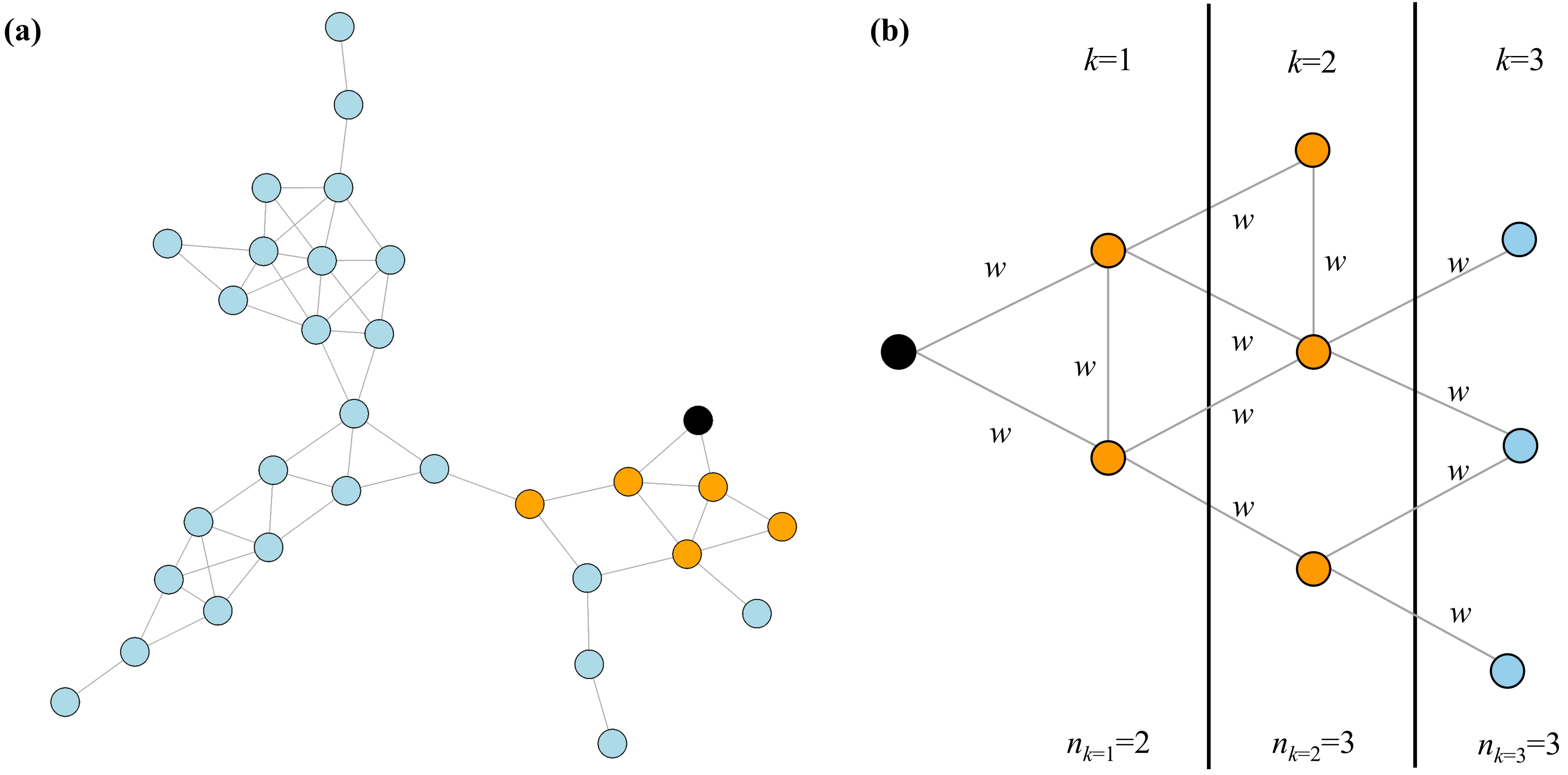
abundance; mean ± SD values for each parameter were calculated from five independent SA runs. Inset shows the model parameters ordered according to their overall influence on the model output.

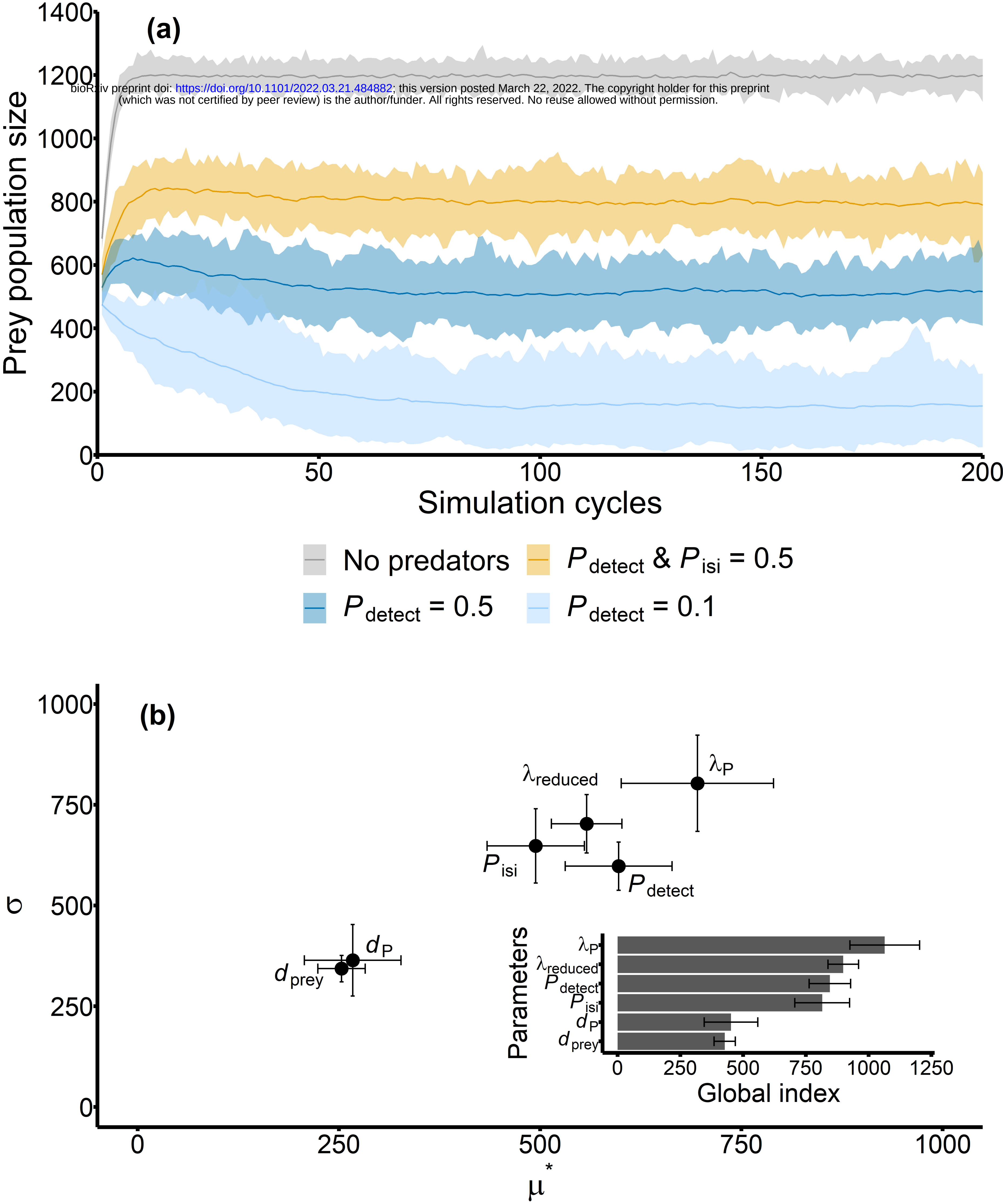
Figure 4. The relationship between per capita mortality due to predation and the number of predators using the same parameter settings as in Fig. 3a (but without the 'No predators' group). Trend lines were fitted using second-order polynomial approximation. Simulation results from incomplete runs (i.e., simulation cycles were less than 200) were omitted from the dataset (n=204; only in the 'minimal predator detection' model type).

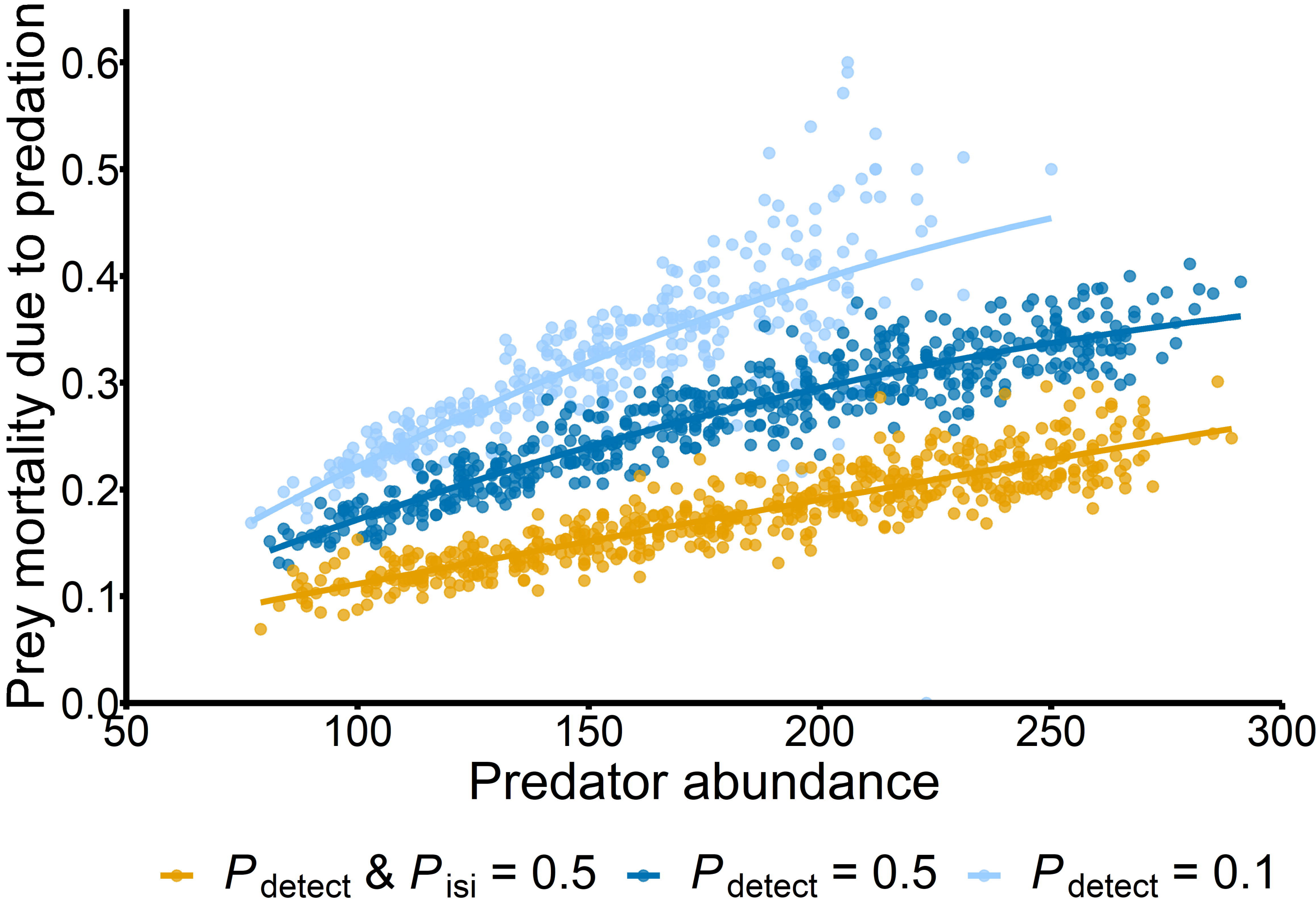
Figure 5. Interactive effects of the probability of ISI use (P_{isi}), predation pressure (λ_{P}) and the presence of fitness cost (associated with the defensive behaviour; $\lambda_{\mathrm{reduced}}$) on prey population size in three P_{detect} scenarios. The colour of the boxplots indicates the level of predation pressure (purple: high, blue: intermediate, green: low), while the colour tone is associated with the presence of cost (dark: costly defensive behaviour, light: no cost). Trend lines were fitted using the 'LOESS' regression method for smoothing with the default value of span (0.75); presented only for illustration purposes. Simulation results from incomplete runs were omitted from the dataset (n=581; only in the 'P_{detect}=0.25' setting).

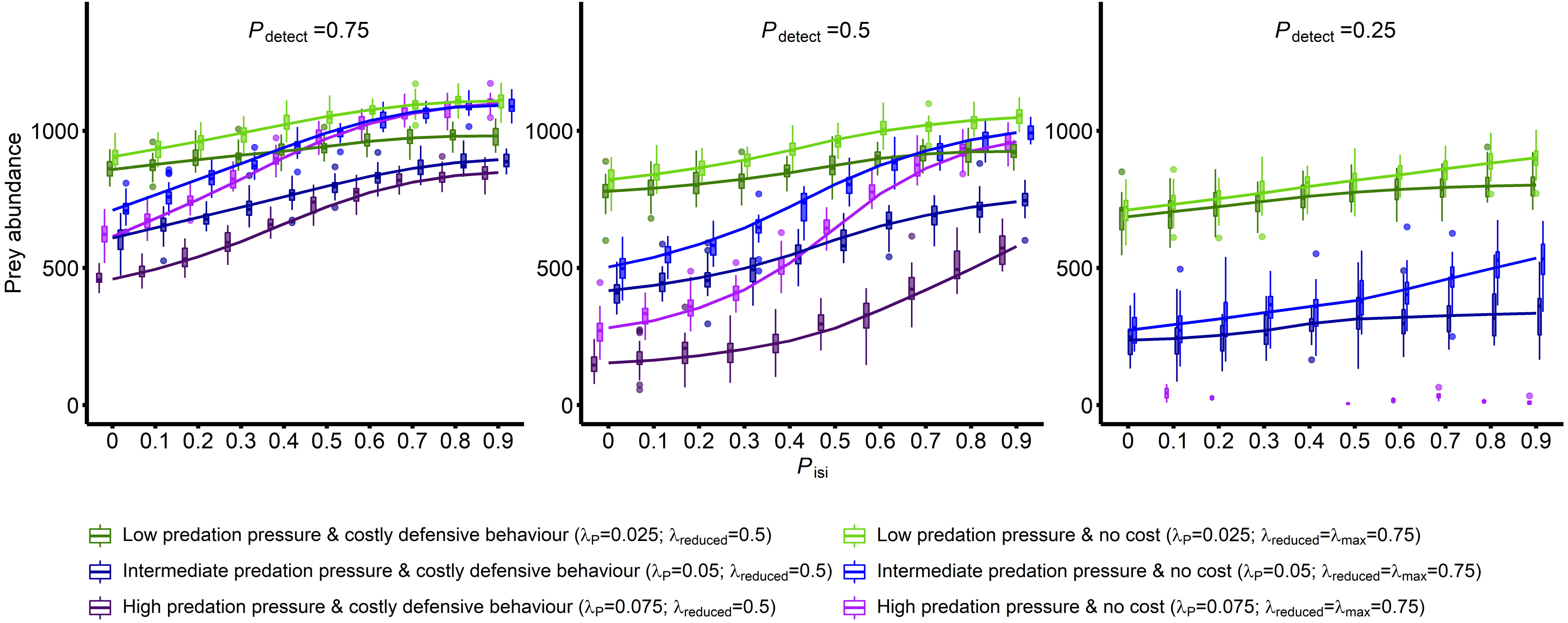
Figure 6. Four structural network properties (a: number of components, b: component size, c: average size of ego networks, d: global network efficiency in the largest components) calculated for the observed detection networks (circles) and corresponding randomized networks (diamonds). Predation pressure was set to 'high' (i.e., λ_{P}=0.075). The colour of the boxplots indicates the absence (gray; P_{isi}=0) or presence of ISI use (orange; P_{isi}=0.5).

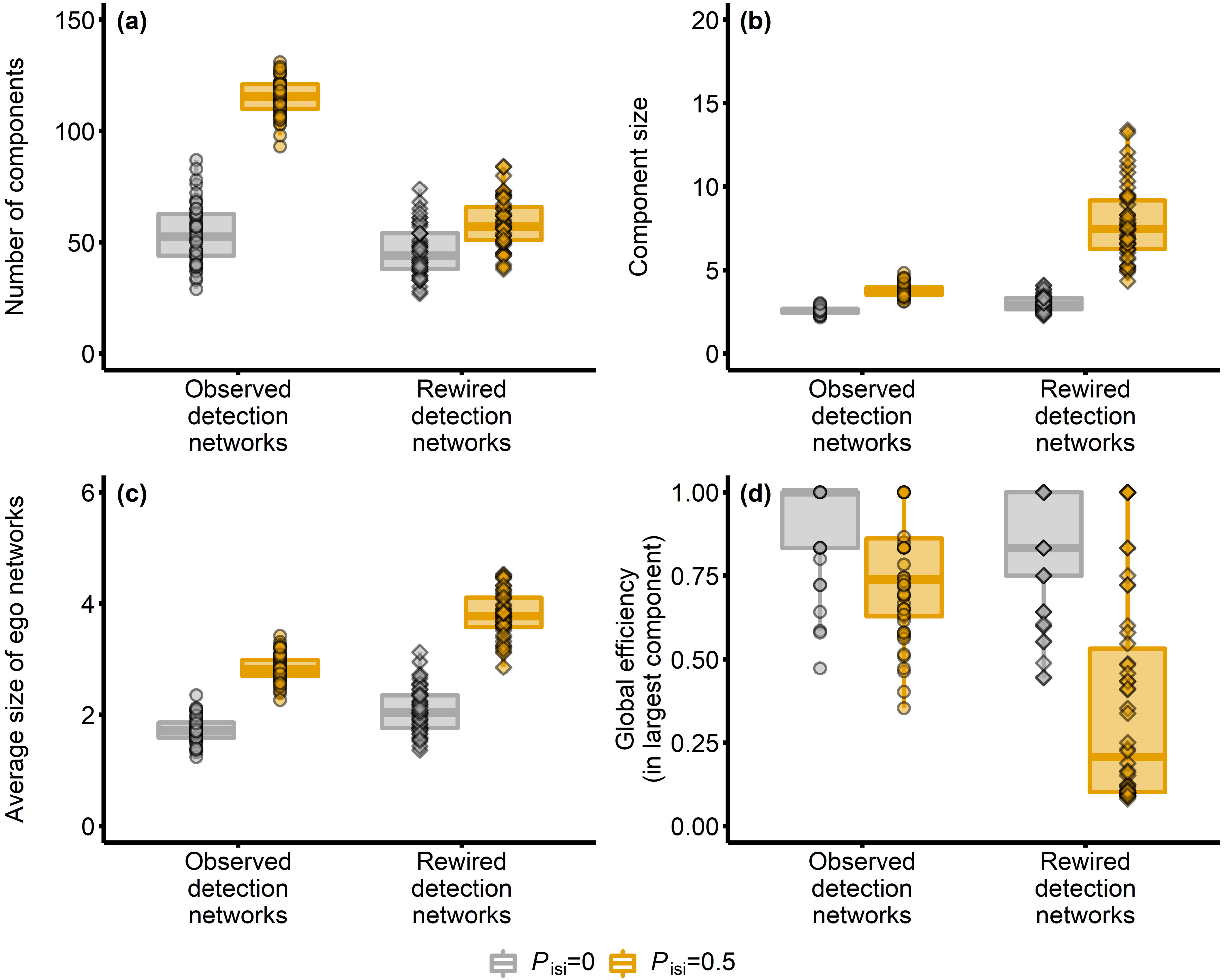

Cycle starts
Prey movement
d_{prey}
Prey death (competition)
Predator movement
d_{P}
Predator death (competition)
Predator detection
r_{prey}, P_{detect}
Detection of conspecific defensive behaviour and ISI use
r_{prey}, P_{isi}
Prey feeding
Predator hunting
r_{P}
Prey death (predation)
Prey birth and offspring dispersion
λ_{max}, $\lambda_{\mathrm{reduced}}$
Prey death (competition)
Predator birth and offspring dispersion
λ_{P}
Predator death (competition)
Cycle ends


(a)
(b)
k=1
k=2
k=3
w
w
w
w
w
w
w
w
w
w
w
w
n_{k=1}=2
n_{k=2}=3
n_{k=3}=3


(a)
Prey population size
0
200
400
600
800
1000
1200
1400
Simulation cycles
0
50
100
150
200
No predators
P_{detect} & P_{isi} = 0.5
P_{detect} = 0.5
P_{detect} = 0.1
(b)
σ
0
250
500
750
1000
μ^*
0
250
500
750
1000
λ_P
$\lambda_{reduced}$
P_{isi}
P_{detect}
d_P
d_{prey}
Parameters
λ_P
$\lambda_{reduced}$
P_{detect}
P_{isi}
d_P
d_{prey}
Global index
0
250
500
750
1000
1250


Prey mortality due to predation
0.0
0.1
0.2
0.3
0.4
0.5
0.6
50
100
150
200
250
300
Predator abundance
P_{detect} & P_{isi} = 0.5
P_{detect} = 0.5
P_{detect} = 0.1


P_{detect} =0.75
P_{detect} =0.5
P_{detect} =0.25
Prey abundance
0
500
1000
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9
P_{isi}
Low predation pressure & costly defensive behaviour (λ_P=0.025; $\lambda_{reduced}$=0.5)
Intermediate predation pressure & costly defensive behaviour (λ_P=0.05; $\lambda_{reduced}$=0.5)
High predation pressure & costly defensive behaviour (λ_P=0.075; $\lambda_{reduced}$=0.5)
Low predation pressure & no cost (λ_P=0.025; $\lambda_{reduced}$=λ_{max}=0.75)
Intermediate predation pressure & no cost (λ_P=0.05; $\lambda_{reduced}$=λ_{max}=0.75)
High predation pressure & no cost (λ_P=0.075; $\lambda_{reduced}$=λ_{max}=0.75)


(a)
Number of components
150
100
50
0
Observed detection networks
Rewired detection networks
(b)
Component size
20
15
10
5
0
Observed detection networks
Rewired detection networks
(c)
Average size of ego networks
6
4
2
0
Observed detection networks
Rewired detection networks
(d)
Global efficiency (in largest component)
1.00
0.75
0.50
0.25
0.00
Observed detection networks
Rewired detection networks
P_{isi}=0
P_{isi}=0.5