



Predator inadvertent social information use favours reduced clumping of its prey

Steven Hamblin, Kimberley J. Mathot, Julie Morand-Ferron, Joseph J. Nocera, Guillaume Rieucou and Luc-Alain Giraldeau

S. Hamblin (hamblin.steven@courrier.uqam.ca), K. J. Mathot, J. Morand-Ferron, J. J. Nocera, G. Rieucou and L.-A. Giraldeau, Groupe de recherche en écologie comportementale et animale, Dépt des Sciences Biologiques, Univ. du Québec à Montréal, C.P. 8888, Succursale Centre-ville, Montréal, QC, H3C 3P8, Canada. Present address for JJN: Ontario Ministry of Natural Resources, Trent Univ., DNA Building, 2140 East Bank Drive, Peterborough, ON, K9J 7B8, Canada.

When animals forage socially, individuals can obtain prey from their own searching (producer tactic) or by using the behaviour of others (scrounger tactic) when it provides inadvertent social information (ISI) that food has been located. This ISI may either indicate the location of food (social information, SI), or it may indicate the quality of the resource (public information, PI). To date, few studies have explored the selective consequences for prey of being exploited by predators that use ISI. Prey exploited by such predators should evolve traits that favour high levels of ISI use (scrounging) because this would result in lower predator search efficiency given that fewer predators would be searching directly for the prey. Our simulations confirm that ISI-using predators should increase their use of ISI when their prey form larger clumps resulting in higher prey survival. Our objective therefore is to explore whether prey will evolve towards higher clumpiness when their predators use ISI, using genetic algorithm simulation. The prey were subjected to one of three types of predators for over 500 prey generations. The predators either used: (1) no social information (NS), (2) SI only, or (3) PI. Surprisingly, the prey evolved the highest clumpiness for NS predators. Prey evolved towards smaller clump sizes with SI predators and the clumps were marginally larger when predators used PI. The result is due to the prey evolving the minimum clumpiness required to cause maximal ISI use by their predators. We discuss how this response by prey may favour the use of PI over SI in their ISI-using predators.

A great deal of research has been invested in exploring how predators influence the distribution of their prey. Most studies have focused on solitary foragers, and the general pattern emerges that prey evolve towards clumped distributions, a response that reduces the efficiency of predator searching (Taylor 1977, Bommarco et al. 2007). Yet, a large number of predators forage socially. Social foraging has been shown to impact predator efficiency at detecting prey (Giraldeau and Beauchamp 1999). This will likely affect the anti-predator strategies evolved by their prey (Barrette and Giraldeau 2006) and, in turn, how predators adapt their search strategies.

When animals forage socially, individuals can obtain prey by searching for food patches themselves (producer tactic), but they may also search for patches discovered by others (scrounger tactic). To use the scrounger tactic, the predator must rely on information provided inadvertently by a successful producer. This inadvertent social information (ISI) can be of two types (Danchin et al. 2004); it may provide social information (SI) simply indicating the location of the resource or it may provide public information (PI; Valone 1989, 2007) that indicates the quality of the resource based on the performance of the individual

already engaged in exploiting it. PI is thought to be better than SI because it is used preferentially when it is equally costly to obtain as other types of ISI (Coolen et al. 2005).

The gains from using ISI are likely to be negatively frequency dependent, as is the case for all producer–scrounger (PS) games (Barnard and Sibley 1991, Giraldeau and Caraco 2000); each tactic does better relative to the other when it is rare (Mottley and Giraldeau 2000). Under most circumstances, we expect the coexistence of both tactics at a stable equilibrium frequency (Mottley and Giraldeau 2000) where payoffs to each tactic are equal. Because scrounging, and hence ISI use, is mutually incompatible with producing (Coolen et al. 2001), any increase in the stable equilibrium frequency of scrounging results in a decreased number of producers that are concurrently searching for prey, and thus, lower predator search efficiency (Coolen 2002). Therefore, prey may be expected to evolve characteristics that can induce high rates of scrounging in their predators to reduce predator search efficiency (e.g. prey crypticity; Barrette and Giraldeau 2006). Another such trait may be prey clumpiness, because larger prey clump sizes are predicted to increase the stable equilibrium frequency of scrounging (Vickery et al. 1991,

Caraco and Giraldeau 1991) and have been demonstrated to reduce predator efficiency at finding patches (Coolen 2002).

The behavioural traits of prey and predators engaged simultaneously in a PS game have only been examined on very short temporal scales, usually by monitoring the immediate response of players to environmental variation. Coolen et al. (2007) made an important step towards rectifying this by showing that scrounging can regulate both predator and prey populations. However, the impacts of scrounging, and thus the rate and type of information use, have never been empirically examined in an evolutionary context. Furthermore, despite the importance of predator–prey interactions in bridging behaviour and population ecology, very few studies have examined simultaneously the evolution of predator and prey, with most studies focusing only on prey response to predation pressure (Abrams 2000, Lima 2002) or vice versa (Murdoch 1973, Readshaw 1973, Cosner et al. 1999).

Here, we simulate a population of predators engaged in exploiting prey and thus explore a system of reciprocal evolution that integrates the behaviour of predator and prey in response to each other. First, we determine whether the optimal response of a predator is to increase its use of ISI and scrounge more when its prey form larger clumps. Then, we use a genetic algorithm approach to investigate whether prey confronted with predators that use: (1) no social information (NS), (2) SI, and (3) PI evolve towards the formation of increasingly larger clump sizes.

Methods

Foraging simulations

Agents played a producer–scrounger foraging game on a 40×40 grid, with predator population size set to 10 and prey population size set to 1000. At each time step, predators played either producer or scrounger. If they played producer, they would search for a prey patch at their immediate location, with discovery being assured if prey were present. If no prey were found, predators would move one square in one of the eight cardinal/sub-cardinal directions and select their strategy again. If predators played scrounger, they would scan the grid for conspecifics exploiting a patch and move towards them to join the discovery if one was found. Predators moving to scrounge at a patch moved at twice the normal rate of movement while searching (i.e. two grid squares per turn; see also Beauchamp 2000). If no conspecifics exploiting a patch were found, agents would move randomly as above and select their strategy again. Predators exploiting a patch, whether as producer or scrounger, would consume one prey item per time step, and continue feeding until the prey were depleted or the simulation ended, whichever occurred first. Predators had neither a minimum required, nor maximum allowed, food intake level. A complete simulation run consisted of 500 iterations of the above cycle.

In the NS scenario, predators can only discover food patches by searching themselves (producer tactic), and the scenario is provided as a reference against which to compare the other two scenarios in which predators do use ISI. In the

SI scenario, predators can locate food themselves (producer tactic), or use foraging conspecifics as a cue to the location of food patches (scrounger tactic), and their allocation to each tactic is determined by the relative payoff sum (RPS) learning rule (Harley 1981). The relative payoff sum is a mathematical decision rule with the following form: $S_i(t) = x \times S_i(t-1) + (1-x) \times r_i + P_i(t)$, where $S_i(t)$ is the value placed on behavioural alternative i at time t , x is the memory factor which determines how highly the past is valued by determining how much the value placed on the alternative in previous rounds is used in calculating the current value placed on the alternative ($x \times (S_i(t-1))$); this might be viewed intuitively as the degree to which past rewards to a strategy affect how the organism currently values the behaviour), r_i is the residual (the cutoff below which the valuation of the alternative cannot go even if the alternative should stop paying off entirely), and $P_i(t)$ is the payoff to the alternative during the current round, calculated as the amount of food ingested during that round by using that alternative (consequently, the payoff to at least one alternative will be zero each round since only one alternative can be used in a single time step). The probability p_s of using the scrounger tactic was then

calculated by matching: $p_s = \frac{S_s(t)}{S_s(t) + S_p(t)}$. The use of a decision rule to model the learning of behaviour follows that found in Beauchamp (2000).

Finally, in the PI scenario, predators can search for food themselves (producer tactic), or use foraging conspecifics as a cue to the location of food patches (scrounger tactic), however, in this case, scroungers were also able to calculate whether they could reach a target patch before the patch was exhausted. This calculation was performed once, when the target search was performed, and was not recalculated as the scrounger moved towards the patch.

At the beginning of the simulation, prey were aggregated according to their clump size, which had initial values ranging randomly from 1–50. The clumping algorithm clumped all prey with an identical clump size together into patches as large as the coefficient itself: as an example, if 45 prey had a clump size of 10, four clumps of 10 would be produced as well as one clump of 5. The initial locations of predators and prey clumps were selected randomly from a uniform distribution over the set of two dimensional grid coordinates.

Genetic algorithms

Genetic algorithms are heuristic algorithms used to solve optimization problems by mimicking the methods of natural selection (selection, mutation, recombination; see Goldberg 1989). In behavioural biology, genetic algorithms are increasingly used to solve complex models of behaviour (Sumida et al. 1990, Hamblin and Hurd 2007, Ruxton and Beauchamp 2008).

Two genetic algorithms running in parallel were used to allow predator and prey characteristics to evolve. The performance of predators was calculated as the sum of the prey eaten over the entire time course of the simulation, while the performance of prey was calculated as the number of iterations in which prey remained alive; thus, for prey a

maximal performance value would be 500, equal to the number of iterations for the simulation. In each genetic algorithm, agents were ranked by their performance and a new population was constructed using roulette-wheel selection (in which the chance of being selected for reproduction or replacement is related to fitness; Goldberg 1989, Lee and Kim 2005) over the top 15% of the population (selected for reproduction) and the bottom 15% of the population (selected for replacement). Mutation and recombination were then applied, with a mutation rate of 0.01 per locus and a recombination probability of 0.5. The simulation component was restarted with the new population when selection and reproduction were completed for both predator and prey populations. This cycle continued for 500 generations of the genetic algorithm.

A three loci chromosome was used for the predators, with one locus for each residual (producer and scrounger) and the memory factor. Values for the residual loci were $\{r_i \in \mathfrak{R} | r_i \geq 0\}$ where \mathfrak{R} is the set of real numbers, while values for the memory factor were $\{x \in \mathfrak{R} | 0 \leq x \leq 1\}$. For prey, the chromosome consisted of a single locus with an integer value ≥ 0 , which was the clumping coefficient. Initial values were randomized; residual values were constrained between 0–5 initially, but allowed to mutate above that, while clumping coefficients were constrained between 0–50 but allowed to mutate above 50. Mutation steps (the allowable range in which mutation can modify the value of a locus) for residuals were $\in[-1.0, 1.0]$, for the memory factor were $\in[-0.1, 0.1]$, and for the clumping coefficient were $\in[-3, 3]$. The results showed no sensitivity to these values.

The code for the genetic algorithm is based on that used and validated previously by Hamblin and Hurd (2007), rewritten in Python (Lee and Kim 2005, Bassi 2007). The source code is available from the authors upon request.

Simulation types

Two simulation types were performed. In the first, the prey used a constant clump size throughout the simulation so that the predators could modify their level of scrounging to maximize their gains. In the first set of simulations, prey clump size was fixed for each run with prey clump sizes stepped from 1 to 50 in steps of five (except the initial step: 1, 5, 10, 15, etc.). In the second set of simulations, prey clump size was free to evolve in the face of predators. For both simulation types, 25 replicates of each parameter combination were run.

To determine whether the simulated evolutionary patterns were directional (i.e. demonstrably different from a random walk), we assessed the patterns for signatures of an auto-regressive (AR) process, a moving average (MA) process, or some mixture of the two (all models were implemented in R ver. 2.6.2). If an AR process (without differentiation) or MA process is apparent in a model, then the pattern cannot have been created from a random walk or drift. We chose this ARIMA (auto-regressive integrated moving average) procedure over estimating a trendline (e.g. with a linear model) to better understand and describe temporal patterns in the data; ARIMA estimates how preceding points influence each point in a temporal data

series to infer underlying evolutionary processes (Box and Jenkins 1976). ARIMA models are specified in the form (p, d, q) , where p is the number of AR parameters, d is the level of differentiation, and q is the number of MA parameters. An example pattern generated from a random process (with or without drift) could thus be represented as $(0, 0, 0)$.

To fit our ARIMA models, the series first had to be stabilized by determining the level of differentiation required (i.e. the variance associated with time must be removed). In our case, all models of clumping behaviour showed a very slow decay, indicating that a first-order differentiation (a model of the form $(p, 1, q)$) was necessary to remove the trend to make the data stationary. No transformations were required for models of scrounging behaviour. As our second step, we then examined temporal autocorrelation in the fitted series to determine whether any AR and MA terms belonged in the model, how many terms were necessary, and the coefficients of each of those terms.

Results

The predators increased their use of the scrounger tactic in response to increased average prey clump size. The increase in scrounger frequency however, was non-linear, and reached an asymptote when ca 60% of individuals scrounged for prey in clump sizes ≥ 15 (Fig. 1A). The number of prey surviving at the end of a foraging bout mirrored those for scrounging: as clumping increased, so

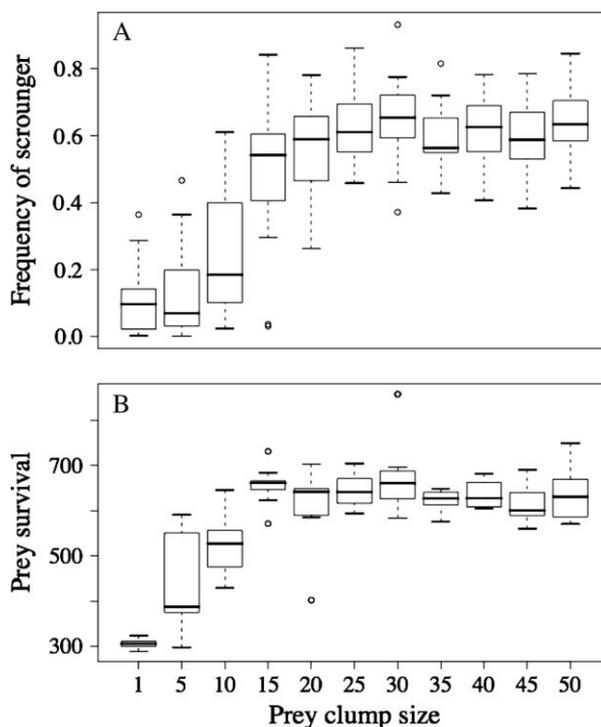


Figure 1. The effect of prey clump size on (A) the frequency of scrounger tactic use by predators, and (B) prey survival (number of prey surviving from a starting population of 1000 prey). Prey clump size was held constant while predator behaviour was allowed to evolve under the social information scenario. Note that prey clump size refers to the clumping coefficients as described in the methods section.

did the number of prey surviving (ANOVA: $F_{10,264} = 96.143$, $p < 0.0001$). For prey survival, as for scrounging, no further increase in prey survival was seen above clumping coefficients of 15, with prey survival reaching an asymptote near 600 (Fig. 1B).

Prey evolved towards increased clumpiness (from 25 starting value to ca 40) with NS predators (Fig. 2A). The increase in prey clump size was non-linear, with an asymptote clump size of 40 reached after approximately 250 generations. The best-fit ARIMA model (0, 1, 2) contained two MA terms with small coefficients ($\theta = -0.16$ and -0.11), which reflect the time series data fluctuating around a slowly increasing mean. These low MA coefficients indicate low resilience in the clumping data, but the fact that there were two MA terms in the model indicates the series is non-random and suggests a tendency to inflect in the direction of the exogenous perturbation (i.e. presence of predators all playing producer and searching for themselves).

When predators used SI and PI, the situation reversed. When predators used SI, prey evolved towards lower clump sizes (from 25 to ca 15). The evolution of prey clump size was gradual, occurring throughout the 500 generations of the simulation. The best-fit ARIMA model (1, 1, 1) indicates the series was not the product of a random walk; the coefficient (θ) of the autocorrelation term was 0.51, and the coefficient (θ) of the MA term was 0.31. At the same time, predators decreased their use of the scrounger tactic from 0.5 to 0.4 (Fig. 2B). The shift in predator behaviour was faster in the PI than in the SI

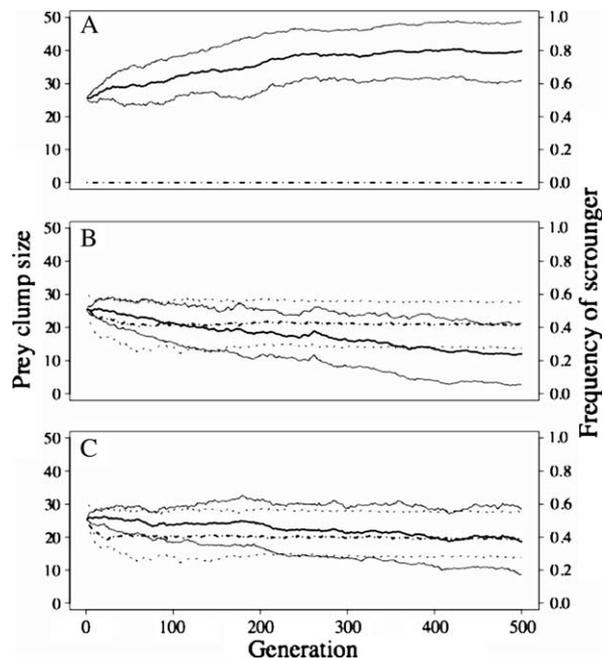


Figure 2. The evolution of prey clump size (solid line) and the frequency of scrounger tactic use by predators (dotted line) when both traits are allowed to co-evolve under three scenarios of information use by the predators: (A) no social information, (B) social information, and (C) public information. Note that prey clump size refers to the clumping coefficients as described in the methods section. Thick lines depict means, and thinner lines show ± 1 SD.

situation, occurring within the first 75 generations, and remaining stable thereafter. Unlike clumping behaviour, temporal autocorrelation explains almost all variability in both scenarios involving scrounging behaviour (Fig. 2B–C). In both cases, the best-fit ARIMA models (1, 1, 0) contained an AR term showing perfect autocorrelation ($\theta = 1.00$) and since the model contained a differentiation term, it is possible the series was generated from randomness.

When predators used PI, prey clump sizes decreased only slightly, from 25 to 20 and also appeared to stabilize more quickly compared with the NS situation, within 100 generations (Fig. 2C). The best-fit ARIMA model (0, 1, 1) indicated the trend in clumping in this scenario was no different than might expected from a random-walk; the single MA term was very low ($\theta = -0.09$) and thus had little statistical power. At the same time, predators decreased their level of scrounging from 0.5 to 0.4, with the adjustment occurring here within the first 25 generations, and remaining relatively stable thereafter.

For all three scenarios, there was no change in prey survival rates over evolutionary time, but the survival rates of prey were better when predators used SI or PI compared with when they used NS (Fig. 3); after controlling for a substantial random effect of ‘run’ (any of the 500 repeated measures of a population), a linear model shows a notably statistically significant difference between the three scenar-

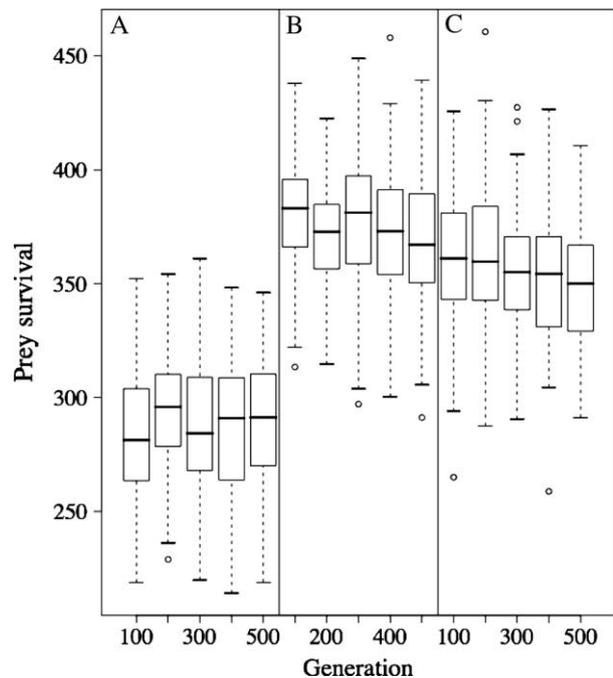


Figure 3. Changes in prey survival rates across generations when predators use (A) no social information, (B) social information, and (C) public information. Generations were pooled together as follows: 100 = generations 1 through 100, 200 = generations 101–200, 300 = generations 201–300, 400 = generations 301–400, 500 = generations 401–500. The bold line of the box plots denote medians, while the higher and lower edge of the box denote the upper and lower quartiles respectively, the whiskers extend to the farther points that are still within 1.5 interquartile ranges from the quartiles.

ios ($F_{2,1497} = 1254.3$, $p < 0.0001$). Tukey HSD post-hoc tests showed highly significant differences between all combinations of group means, showing that mean prey survival rates were higher in both the SI and PI than NS conditions and higher in the SI than in the PI condition.

Discussion

Our results show social information to be an important factor guiding the evolution of predator and prey characteristics; increased prey clump sizes induced increased levels of ISI use by predators (Fig. 1A), which decreased predator search efficiency (as measured by prey survival; Fig. 1B). This result is consistent with experimental tests of PS foraging games (Giraldeau and Caraco 2000, Coolen 2002). However, surprisingly, when prey were free to evolve, they did the opposite: they evolved towards the highest clumping against NS predators (Fig. 2A) and smaller clump sizes against SI and PI predators (Fig. 2B–C). This is the first demonstration of how information use by predators evolves in response to predator–prey dynamics, and here we explore this unanticipated result.

Both the rate-maximizing (Vickery et al. 1991) and risk-sensitive (Caraco and Giraldeau 1991, Barta and Giraldeau 2000) PS models predict an increase in scrounging frequency, and hence ISI use, with increasing prey clump size. However, the predicted effect of clump size on scrounging is non-linear; scrounging increases at a decreasing rate as clump size increases. As a result, any selective advantage of increased prey clumping will decrease as scrounging approaches asymptotic values. Our simulation of predators foraging for prey of different clump sizes supports this yet unrecognized non-linear effect. Our predators increased their use of scrounging when prey were in larger clumps but the level of scrounging reached an asymptote at around 60% scrounging, with no further increase in scrounging at clump sizes > 15 . Moreover, as expected, prey survival increased with increased scrounging (Giraldeau and Caraco 2000, Barrette and Giraldeau 2006).

We suggest that prey failing to evolve towards large clump sizes when faced with predators using ISI can be understood in light of these non-linear effects of clump size on scrounging frequency. When predators use SI, clump sizes decreased to around 15 prey items per patch. This number happens to match the minimum clump size found to induce the maximum level of scrounging in our predators (Fig. 1A). Given that predators are already using ISI at its asymptotic frequency and will not evolve towards greater levels of ISI use, no further increase in clumping will benefit the prey in terms of reducing predator search efficiency. As a consequence, clump size ceases to evolve towards larger values. At this level of clumping, it is noteworthy that predators using only SI are induced to attempt to scrounge at all patches, even those that may well be exhausted by the time they reach them. This blindness to patch quality by the predators is still advantageous to the prey because it allows them to adapt to predator behaviour and clump only so much as to induce maximum levels of scrounging and impose an energetic cost on their predators. Such an advantage, however, may be reduced if the predators are better informed of patch quality and scrounging opportu-

nities by the additional use of PI. When predators use PI, they do not join unless patch richness is such that they will have time to reach the patch before it is depleted.

Generally, information regarding resource location and quality that is more accurate and precise should increase predator efficiency (Valone 1996, King and Cowlshaw 2007). If we assume that NS predators have the least information, those that use SI have more and those using PI the most, then that was not the case in our study; prey survival was lowest against NS predators (Fig. 3). The prey survived better when the predators used either SI or PI, which shows that scrounging, and hence ISI use of any form, actually reduced predator efficiency. Because scroungers inevitably exist in populations of social foragers (Giraldeau and Caraco 2000), such reduced predator efficiency will not be eliminated through selective pressure.

Predator efficiency tended to be higher when predators had access to PI compared with SI, as indicated by the lower prey survival rates (Fig. 3). Given that the ability to use ISI evolves within predators, we would then expect selection to favour predators that shift from using SI to PI, which would allow them to forage more efficiently, mainly by avoiding scrounging attempts directed to less valuable food discoveries. As a result, predators may be less susceptible to manipulation by prey when they have access to PI. Consistent with this suggestion, predators reduced their investment in scrounging much more rapidly when they had access to PI compared with when they had access only to SI. This suggests there would be an advantage to prey to evolve traits that reduce the ability of predators to provide PI while they are being exploited. It would be interesting to explore what such traits would be like.

Our results illustrate some of the long-term consequences of predators opting to search for prey themselves or to collect SI/PI from others, which makes an important step towards understanding the effect of information use on evolution of predator and/or prey. However, we note that the results of our simulations require empirical testing; we have made several simplifying assumptions that might not hold in a realistic biological system. For example, we have assumed that predator survival was entirely determined by foraging success on a single prey species, and have kept population sizes constant throughout the simulated evolutionary process, thereby insulating our populations from density-dependent processes (see Abrams 2000 for a discussion on the impact of density-dependent process in predator–prey coevolution). Moreover, we have assumed that prey could not flee or adjust their behaviour to reduce their immediate risk of detection or mortality. Our conclusions may have been different if we assumed other benefits from clumping such as prey dilution and evasion, or improved predator detection. Nonetheless, we suggest that our genetic algorithm approach provides the possibility of addressing these intriguing possibilities.

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