Search rate, attack probability, and the relationship between prey density and prey encounter rate

Christos C. Ioannou,[a] Graeme D. Ruxton,[b] and Jens Krause[a]
[a]Institute of Integrative and Comparative Biology, University of Leeds, LS2 9JT, UK and [b]Division of Environmental and Evolutionary Biology, University of Glasgow, G12 8QQ, UK

Although numerous influential models in ecology assume a directly proportional relationship between prey density and prey encounter rate, a recent test of this assumption found that the actual relationship was nonlinear (rising slower than proportionately). Here, three-spined sticklebacks were used to test 2 recently proposed mechanisms based on predator search behavior that may induce this nonlinearity: the effect of increasing search rate over the course of the search and the effect of spatial correlation in areas searched. The fish explored a novel apparatus of 16 cells (15 × 16 cm) arranged in a ring, with each cell connected to the 2 adjacent cells by small openings. Hence, the arena was effectively one dimensional, simplifying the recording of search paths and removing edge effects. The relationship between prey density and encounter rate was found to be less than directly proportional, confirming the findings of a previous study using great tits searching for caterpillars. In the majority of our trials, the search rate accelerated as more of the arena was searched. Moreover, the greater this acceleration the less prey density and encounter rate were directly proportional. There was no evidence found, however, that spatial autocorrelation had any effect. We also found an interesting effect of prey density on the likelihood that an encounter with a prey would lead to an attack. Once prey were encountered, the probability of attack increased with the number of cells already visited, leading to a higher probability of attacking first-encountered prey at lower prey densities. *Key words:* detection, encounter rate, foraging, search rate, three-spined stickleback. *[Behav Ecol 19:842–846 (2008)]*

An encounter between 2 agents is the first step in any interaction between them, whether they are predator and prey, parasite and host, or randomly moving molecules. In numerous models using encounters between predator and prey, a central assumption is that the encounter rate of a predator with potential prey is directly proportional to prey density (Mols et al. 2004), an assumption forming the basis of many classical models in ecology (e.g., the Lotka-Volterra predator–prey model; Lotka 1925). This assumption seems initially reasonable and follows from analogy with physicists' models of collisions between randomly moving gas particles (e.g., Denny and Gaines 2000). However, a recent experimental study using great tits (*Parus major*) searching for winter moth caterpillars explicitly tested this assumption for the first time and found that the time to first encounter did not decline with increasing density as steeply as would be expected from a directly proportional relationship between prey density and encounter rate (Mols et al. 2004).

Two untested hypotheses have recently been presented to explain this result. First, when prey are aggregated, increasing density should not proportionally reduce the average distance to the nearest prey and thus the time to first encounter prey (Travis and Palmer 2005). Ruxton (2005) proposed an alternative, but not mutually exclusive, mechanism. If predators increase their search rate while exploring an unfamiliar habitat, prey at high densities will be encountered when search rate is relatively low; in contrast, low-density prey will be encountered after a longer period of time, when search rate has

accelerated to higher levels. Thus, prey at low densities will be encountered sooner than would be expected on the basis of the time taken to encounter high-density prey. Following Ruxton (2005), we define search rate as the area searched per unit time, which can be derived from the time spent in each patch searching for food. There is no assumption made about search effort, and other authors have assumed that total search effort remains constant even though search rate varies (Gendron and Staddon 1983).

Another property of predator searching, the degree of spatial correlation, also has an effect on the relationship between prey density and encounter rate (Travis and Palmer 2005). Increasing spatial correlation (i.e., increasing overlap) of the search path increases the time to encounter prey at a low density to a greater extent than at higher densities. Such overlap might occur if prey are stationary and predators do not remember or mark areas that they have previously searched. However, this mechanism predicts the opposite trend to that found by Mols et al. (2004), a trend where encounter rate increases with prey density faster than would be expected from a directly proportional relationship.

In addition to the predicted effect on the relationship between prey density and encounter rate, search behavior is well established as having an important role in other aspects of predator–prey interactions. Gendron and Staddon (1983) proposed a trade-off between search rate and detection of prey, where the probability that prey is detected increases with the time spent searching an area. As animals have a limited attention (Dukas 2002), they must balance the rate at which they search (quantity) with how well the area is searched (quality). Hence, although high-density prey may be encountered more slowly than expected from the time taken to encounter prey at low density, a greater proportion of encounters may lead to detection as more time is spent in each

area. The increase in search rate that Ruxton (2005) proposed to explain the observed relationship between prey density and encounter rate may thus be accompanied by a decrease in the detection rate of encountered prey (Gendron and Staddon 1983).

In this study, we examine exploratory behavior of three-spined sticklebacks (*Gasterosteus aculeatus* L.) in an unfamiliar habitat, testing whether the time taken to encounter prey (*Daphnia magna*) is inversely proportional to prey density. Detailed recording of search paths then allowed us to determine which search behaviors (change in search rate and overlap of the search path) affect this relationship, as proposed by the models of Ruxton (2005) and Travis and Palmer (2005). Further, given that increasing search rate has been predicted to negatively affect the probability that encountered prey are actually detected (Gendron and Staddon 1983), we examined whether prey density and the area already searched affected the probability that prey was attacked once the first encounter had taken place.

MATERIALS AND METHODS

Three-spined sticklebacks (mean length ± standard deviation = 46.0 ± 4.54 mm) were caught from the estuary of the Great Eau river, UK, and were kept in a large glass stock tank (210 × 50 × 50 cm, water depth 35 cm) at 16 °C on a 13:11 day:night light cycle for at least 3 months before testing. Fish were fed frozen bloodworm and live *Daphnia* each day.

Exploratory behavior of sticklebacks was monitored in an arena of discrete compartments they could search for prey. The arena consisted of 16 numbered cells (each ca., 15 × 16 cm, water depth = 11 cm) arranged in a circle (diameter 82 cm), with each cell connected to the 2 cells adjacent by a small opening (3 × 7 cm high). As the fish could move between cells only in one plane (clockwise or anticlockwise), the arena was effectively one dimensional, simplifying the recording and analysis of the movement pattern. In addition, the arena was finite but lacked any boundary, reducing bias between the cells and removing edge effects.

In the first experiment, a test tube (length = 7.5 cm, internal diameter = 1 cm, water depth = 6 cm) was placed on the outer wall of each cell. Two of these tubes contained the same number of *Daphnia* prey (both tubes with either 1 or 10 per tube, with prey group size varied randomly between trials). Tubes containing prey were placed at a randomly selected distance of 1–7 cells in both directions (clockwise and anticlockwise) from the starting cell. Encountering prey at these distances is equivalent to prey densities of 1, 0.33, 0.20, 0.14, 0.11, 0.09, or 0.08 prey per cell (assuming no prey in the starting cell). For example, searching for prey at a density of 0.11 prey per cell would be expected to encounter prey once every 9 cells (Figure 1). A stickleback (fed the previous day) was removed from the stock tank and placed in the starting cell. Starting cells were randomly selected. As the fish moved around the arena, the total number of cells visited (including the cell containing prey), the time taken before entering a cell with prey, and whether an attack was made once prey were encountered were recorded. The trial ended once a cell containing prey was left, regardless of whether an attack was made, as stickleback behavior is known to change after encountering prey (Thomas 1974). Thirty trials were carried out at each group size, with each fish being used only once.

Both prey density and the time taken to encounter prey were log10 transformed. Linear regression was used to estimate the relationship between log10 (prey density) and log10 (time to encounter), as in Mols et al. (2004). The gradient of the regression line in log–log space is equivalent to the exponent
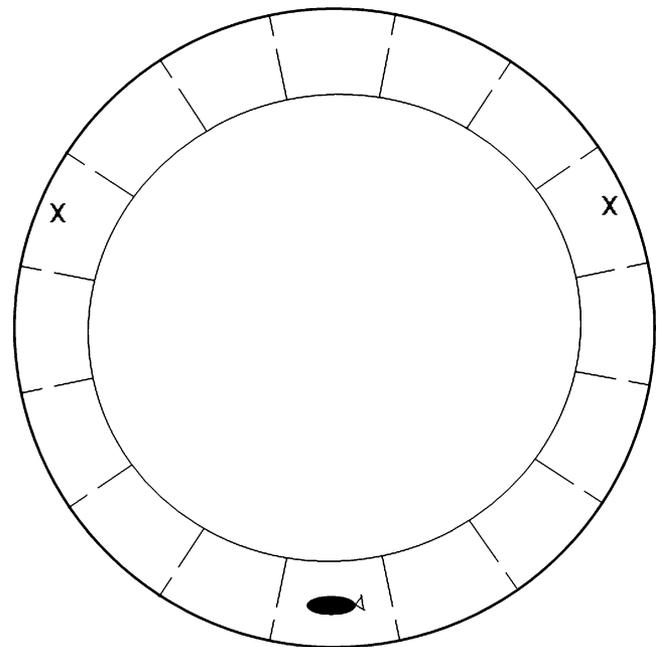
Figure 1
The experimental arena used to assess the relationship between the search behavior and the rate of encountering and attacking prey (not to scale). Each cell is approximately 15 × 16 cm and connected to the 2 cells adjacent by 3 × 7 cm openings. The diameter of the arena is 82 cm. The fish can move in only one dimension (clockwise or anticlockwise); as the arena is continuous, there is no boundary, so edge effects are minimized. Xs mark the position of prey at a density of 0.11 prey per cell, that is, 1 in 9 cells contain prey (not including the starting cell).

of the relationship before log10 transforming. Values equal to −1 indicate an inversely proportional relationship between density and time to encounter, more negative values indicate that time to encounter decreases more rapidly with density than proportionally, and less negative values indicate that time to encounter decreases less rapidly. In addition, the probability that prey was attacked once encountered was analyzed using logistic regression, with prey group size and the number of sites visited as explanatory variables. The effect of density on the proportion of first encounters that resulted in attacks was analyzed using a binomial generalized linear model.

The second experiment repeated the procedure from the first, except that detailed exploratory behavior by the fish was monitored by recording the time spent in each cell and the identity of the cell. In addition, as only the search pattern was of interest and to achieve an extended search path, no prey were present. For any prey distribution postulated, the recorded search path allows straightforward calculation of predicted time to first encounter prey as if such a prey distribution had actually been present. Trials ended when the fish had visited all cells (56% of trials), when they had visited more than 30 cells without visiting all cells (42% of trials), or when they spent more than 20 min exploring the arena without fulfilling either one of these requirements (2% of trials). Fifty trials were carried out in total, with each fish being used only once.

Using the time spent in each cell, the time taken to reach 1, 2, 3, 4, 5, 6, 7, and 8 cells from the starting cell (in either clockwise or anticlockwise directions) was calculated for each of the 50 search paths. This is equivalent to the time taken to encounter prey at these distances from the starting cell as in the first experiment but avoided changes in search behavior
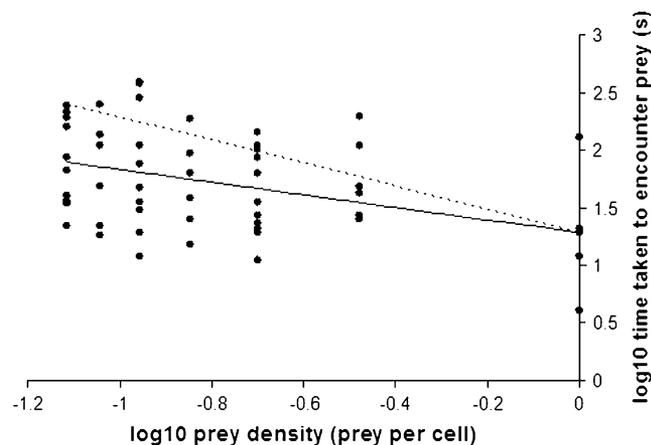
upon encountering prey (Thomas 1974). The exponent of the relationship between hypothetical prey density (derived using the distances from the starting cell) and time to first encounter was determined for each path, using linear regression in log–log space, as in the first experiment. A linear model was then applied with this exponent as the dependent variable and spatial correlation and the change in search rate of each path as covariates. The degree of spatial autocorrelation was calculated as the proportion of cells visited where the fish changed direction (and exits to the same cell that it entered from). The exponent of the relationship between the number of cells visited and the time spent in each cell (again calculated from linear regression in log–log space) was used as a single value to describe the change in search rate over a trial. Negative values indicate an increase in search rate over the course of a trial, zero represents no change, and positive values a decrease in search rate.

All statistical analyses were carried out in R version 2.4.1 or SPSS version 14.

RESULTS

Increased prey density significantly reduced the time taken to encounter prey (Figure 2; linear regression, $t = -3.28$, degrees of freedom [df] = 58, $P = 0.002$). However, the gradient of the relationship was -0.55 ± 0.17 (± 1 standard error), significantly greater (i.e., less negative) than the -1 expected for an inversely proportional relationship between density and time to first encounter ($t = 2.67$, df = 58, $P < 0.01$). Thus, although our experiment predicts an increasing encounter rate with increasing prey density, like Mols et al. (2004) but unlike classical theory, we predict the increase to be slower than linear.

Of first encounters with prey, 23.3% resulted in attacks. The probability of attack was not significantly affected by prey group size (logistic regression, Wald = 0.55, $P = 0.46$), with 6 attacks out of 30 encounters at group size 1 and 8 attacks out of 30 encounters at group size 10. In contrast, the probability of attack increased with the total number of cells visited before encountering prey (Wald = 4.32, $P < 0.05$). The fitted model predicted an attack in less than 10% of encounters
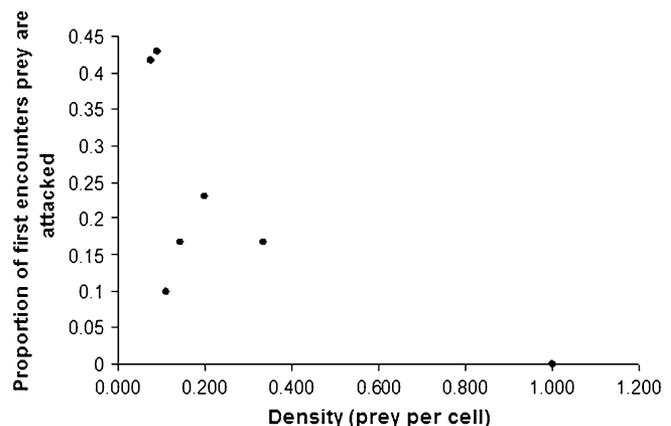
after visiting 2 cells compared with more than 65% after 25 cells were visited. This led to a greater proportion of first encounters at lower prey densities resulting in an attack (Figure 3; generalized linear model, df = 5, $P < 0.05$).

As the trials progressed, the search rate by the sticklebacks increased (Figure 4a). Specifically, the mean exponent of the relationship between the number of cells visited and the time spent in each cell was significantly less than 0 (1-sample t-test, $t = 12.9$, df = 49, $P < 0.0005$). The increase in search rate had a significant effect on the relationship between prey density and the time to first encounter (Figure 4b; general linear model, $F_{1,47} = 29.6$, $P < 0.0001$). The greater the increase in search rate the less steeply encounter rate increased with increasing density. If there was no change in search rate over a trial (i.e., the exponent equaled zero), there was a directly proportional effect of density on encounter rate (i.e., the exponent between density and time to first encounter = -1; Figure 4b). Although there was wide variation in the degree of spatial correlation between trials (the proportion of cells visited where the fish changed direction ranged between trials from 0 to 0.47, with a median of 0.13), there was no significant effect of spatial correlation on the relationship between encounter rate and density ($F_{1,47} = 0.02$, $P = 0.88$) or as an interaction with the increase in search rate ($F_{1,46} = 0.9$, $P = 0.34$).

DISCUSSION

If a predator increases its search rate during a search, the encounter rate with prey increases with prey density slower than expected from a directly proportional relationship, as predicted by Ruxton (2005). The greater this increase in search rate the less effect prey density has on encounter rate. As it takes longer to encounter low-density prey, during which time the rate of search increases, encountering prey at low densities occurs sooner than expected from the time taken to encounter high-density prey (which occurs when search rate is low). This could explain the result of Mols et al. (2004) where this relationship between density and encounter was first observed, but the predator's search pattern was not recorded. Although our setup was highly simplified to minimize edge effects and enable detailed recording of search patterns, it is not dissimilar to the littoral zone where sticklebacks are most often found; the littoral zone consists of small, discrete volumes of space partitioned from one another by macrophytes that may harbor prey or predators.

For search rate to have an effect on the relationship between density and encounter rate, the scale at which the search

Figure 2
The observed relationship between the prey density and the time taken to first encounter prey. The dashed line is the expected relationship if encounter rate is proportional to prey density (i.e., a gradient of -1 between density and first encounter in log–log space), scaled to meet the y axis at the same point as the solid line fitted to the data. The gradient of the fitted line is significantly less than -1.

Figure 3
The proportion of first encounters where prey are attacked as a function of prey density. As prey density increases, the probability that the prey first encountered are attacked decreases.

a)

b)
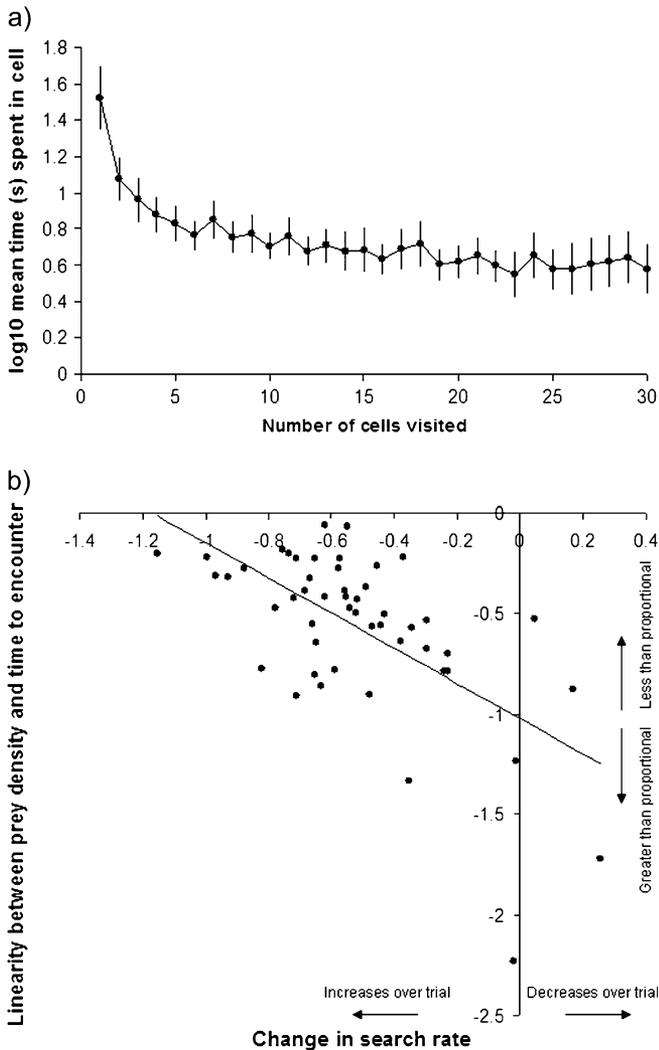
Figure 4

The change in search rate as the arena is explored and its effect on the relationship between prey density and time to encounter. (a) Mean time (with 2 standard error) spent in each cell as a function of the number of cells visited, with no prey being present which may have affected behavior. As the search progresses, search rate increases (i.e., less time is spent in each cell). (b) The effect of change in search rate on the relationship between prey density and encounter rate. Increasing search rate (decreasing values on the x axis) reduces the extent to which prey density and encounter rate are directly proportional (increasing values on the y axis; −1 on the y axis is equivalent to a directly proportional relationship between density and encounter rate).

accelerates must be appropriate to the scale over which prey density varies. The few fish that did not alter search rate during the trial may have accelerated searching over a larger spatial scale but would experience a directly proportional relationship between density and encounter rate at the scale of the experiment. Conversely, if search rate increases and approaches a maximum very quickly, before the first prey is encountered at high densities, there will be little change in search rate when prey are encountered at lower densities. For example, Shipley et al. (1996) demonstrated that smaller mammalian herbivores that accelerate and decelerate rapidly show a more inversely proportional relationship between encounter rate and distance between plants compared with larger herbivores, where the range of distances between plants was the same for all species. This also suggests that the relationship shown

in Figure 4b may change direction and reapproach −1 at accelerations in search rate beyond those observed in our experiment (continuing left along the x axis).

An improvement in searching ability with practice and/or a decrease in perceived predation risk over the trials could also cause an increase in search rate over time (Ruxton 2005). A way to distinguish between these 2 possibilities would be to measure reaction times to a simulated predation event; a more rapid response would indicate a greater degree of vigilance, and if this is negatively related to search rate, it would support the idea of declining perceived risk as the search progresses. Both of these factors depend on predators being initially unfamiliar with their environment (as they were in our experiment). Further, it is expected that temporal and spatial heterogeneity in the predator's environment will have a positive effect on the increase in search rate, providing the scale of heterogeneity is matched to the scale of movement of the predator. Collecting field data on the search patterns of predators from various habitats would be especially illuminating in this regard, helping to determine the generality of the results presented here.

Variation in detection probability once an encounter has taken place was not a component of the models of Ruxton (2005) and Travis and Palmer (2005), although this factor might be expected to also vary with search rate and the distribution of prey. For cryptic prey, it has been shown that increasing search rate can decrease the probability of detecting prey per encounter (Gendron and Staddon 1984). However, our results suggest that, perhaps due to the decrease in antipredatory vigilance by the fish as the search progresses, the increase in search rate is accompanied by an increase in the probability of detection. This would occur if scanning the environment for prey and being vigilant for predators are to some extent mutually exclusive, and declining investment in antipredatory vigilance allows increased investment in prey detection. The model and laboratory study of Gendron and Staddon (1983, 1984) lacked vigilance as a variable component of attention and instead proposed a trade-off between the area searched (i.e., search rate) and detecting prey (positively related to the time spent searching in an area). Essentially, they assumed that the less time a forager spends in a certain area (i.e., the higher the search rate) the less chance any cryptic prey in that area will have of being detected. This is an entirely reasonable mechanism, but here we argue that it may be compensated for or even dominated by the effect of reduced antipredator vigilance allowing both an increase in the rate at which local habitat is encountered and an increase in attention devoted to scanning the currently experienced local habitat for prey.

An alternative explanation for the lack of attacks at high densities is that prey were ignored after being detected. Distinguishing whether prey were not detected or that they were detected but ignored could not be assessed with our experimental design. Both are possible: being unable to detect the prey depends on constraints to limited attention (Dukas 2002), whereas detecting prey but ignoring them can be explained by optimal foraging decisions under the (potential) risk of predation (Lima 1998). Encountering prey early in a search is used as a cue for its abundance in the general habitat, so early encounters may be devalued relative to the potential predation risk involved in foraging activity (Krause and Godin 1996). There is some evidence of dietary conservatism where novel prey are ignored (Marples et al. 1998), although this seems unlikely in this experiment as a familiar, natural prey of the stickleback was used; in addition, prey novelty cannot explain why prey were attacked more often at low densities. Based on absolute and relative encounter rates, most studies have concentrated on the decision of

which prey type to attack (e.g., Kelly 1996; Allen et al. 1998) rather than the decision of whether to attack or not. Ignoring prey at high encounter rates may have a logical basis, although we are unaware of any study that explicitly demonstrates prey encountered early in a search are ignored after being detected.

It has been established that the relationship between prey density and encounter rate can be nonlinear in both the empirical studies that explicitly test this assumption, and evidence is now presented supporting one of the proposed mechanisms for this trend. We can only speculate on what impact this nonlinearity has for ecological models that have so far been built on the assumption of a directly proportional relationship. At spatial and temporal scales greater than those used in this study, predator search rate is also likely to increase with hunger and hence respond to low encounter rates with prey (Wieser 1991). Thus, predator populations should be less adversely affected by low prey densities than originally thought, and, equally, the impact of predation on low-density prey populations will be greater than expected from its impact at high densities. It would be of particular interest to include the relationship between density and encounter rate as a function of environmental heterogeneity (via the increase in search rate), given that heterogeneity has additional effects on ecological processes other than that on predator searching behavior (e.g., see Cronin and Reeve 2005). Additionally, our results apply beyond tropic interactions to any system with actively searching agents, such as pollinators searching for inflorescences and mate searching. In fact, Allee effects (i.e., detrimental effects of low population densities on population size; e.g., Ghazoul 2006) may be partially compensated if search rate is able to accelerate in response to a lack of encounters.

Unlike the explanation proposed by Travis and Palmer (2005), based on prey distribution, our mechanism of increasing search rate is dependent on predator behavior and highlights the importance of considering predators as agents under selection rather than unresponsive sources of risk (Lima 2002). Moreover, our results demonstrate caution should be exercised with untested assumptions, especially when these assumptions form the basis of classical models underpinning our understanding of ecology (e.g., Lotka 1925; Holling 1959). The assumption that encounter rate is directly proportional to density may be met with gas particles showing Brownian motion (Denny and Gaines 2000) but can fail in predator–prey systems when predator search behavior is sufficiently complex that ideal gas particles provide a poor and misleading analogue.

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