

The Effects of Local Enhancement on Mean Food Uptake Rate

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ABSTRACT: A forager searching for food can cue on a distant feeding group to infer the location of a food patch it could share. This behavior, known as local enhancement, reduces variance in time between meals, but its effect on long-term uptake rate is less resolved. An influential simulation study concluded that benefits through reduced variance would be mitigated by reduced long-term uptake rate. This cost comes about through spatial clumping of foragers, leading to overlapping search paths and, thus, reduced aggregate patch finding. Here, we revise the previous model and submit it to more extensive investigation. Our simulations reveal that local enhancement can increase mean uptake rates but only when food patches are scarce in the environment. Contrary to previous speculations, we do not find that high-value patches or strong heterogeneity in patch quality strengthens this potential added benefit to local enhancement. As such, our simulations delineate situations where selection pressures based on maximizing long-term uptake rate act antagonistically or synergistically with starvation-avoidance through reduced temporal variance in feeding.

Keywords: local enhancement, simulation modeling, foraging behavior, groups, joining, food patches.

Introduction

It is well established that vultures often use the position of distant conspicuous scavengers to infer the location of a carcass (Buckley 1996; Kane et al. 2014). This behavioral phenomenon (known as local enhancement) is not restricted to vultures and has been suggested to occur in a wide range of taxa, including other birds (Haney et al. 1992; Rodriguez et al. 2010; Bairos-Novak et al. 2015), reptiles (Whiting and Greeff 1999; Pérez-Cembranos and Pérez-Mellado 2015), mammals (Jourdain and Vongraven 2017; Kane and Kendall 2017), and even invertebrates (Otis et al. 2006). By cuing on a distant foraging group of conspecifics (or heterospecifics) and choosing to join it without having seen the food itself, a searching individual effectively reduces its time spent reaching a patch of food (Pöysä 1992).

Local enhancement is a particularly challenging phenomenon to study empirically because of the spatial scales over which it typically occurs (Thiebault et al. 2014). Most empirical studies focus solely on the foraging group already at the patch but do not observe the joining individual from the moment it makes the decision to join the group (Krebs 1974; Flemming et al. 1992; Kane et al. 2014). In response to this limitation, simulation models have become an important tool to study local enhancement. Such models typically simulate the movements of one (or several) searching individuals that have the ability to detect foraging groups at a food patch from a greater distance than unoccupied food patches. Many studies have used models in combination with empirical observations to better understand the use of local enhancement by a given taxon (e.g., Grünbaum and Veit 2003; Cortés-Avizanda et al. 2014; Kane and Kendall 2017). Models have also been used to predict the effect of population declines on the foraging efficiencies of individuals of species that rely on local enhancement, informing conservation efforts (Jackson et al. 2008; Kane et al. 2014).

Most of these models, however, are tailored to specific species. Only a few studies have provided general models of local enhancement with the aim of studying the potential benefits and costs of the phenomenon (Thompson et al. 1974; Beauchamp et al. 1997; Bhattacharya and Vicsek 2014). One such study gave the surprising prediction that local enhancement leads to decreased uptake rates of food (Ruxton et al. 1995). In other words, the reduction in search time provided by local enhancement does not lead to higher uptake rates, perhaps counterintuitively. Instead, the authors suggested that the benefit of local enhancement may solely lie in a reduction of the variance in time elapsed between meals. This would provide a decreased risk of starvation by preventing a run of bad luck leading to a long interval between stochastic food discoveries. However, this advantage would be traded off with a decreased average rate of food intake. The fact that cuing on the food discoveries of others reduces the variance in time elapsed between feeding bouts is uncontroversial and well established in the literature (Alonso et al.

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1987; Ekman and Rosander 1987; Flemming et al. 1992). The suggestion that local enhancement decreases uptake rates, however, was controversial and novel upon its publication in that it opposed the previously commonly held belief that a decreased search time due to local enhancement leads to more efficient feeding (Pöysä 1992). Following the publication of Ruxton et al. (1995), its results were discussed in major works exploring social behavior (Krause and Ruxton 2002; Beauchamp 2014; Ward and Webster 2016), as well as studies reviewing social foraging behavior (Beauchamp 1998; Giraldeau and Beauchamp 1999; Giraldeau and Dubois 2008; Cortés-Avizanda et al. 2016).

Here, we revisit the Ruxton et al. (1995) model to explore the robustness of its conclusions to biologically motivated changes to parameter values and model assumptions. The original model rests on the assumption that once an individual is in a directed journey toward a food patch, it will not abandon that journey. This has two important implications. The first is that the individual will keep traveling toward a patch even if the latter becomes entirely depleted and disappears during this journey. The second is that the individual will be unable to successfully detect or change its direction toward any patch encountered along the way that could take less time to reach and could offer access to larger amounts of food. Moreover, Ruxton et al. (1995) considered only very small food patches. These could be consumed by a single individual in the time taken to travel four spatial units in their model, yet foragers were drawn to occupied patches from 10 spatial units away. The aim of our study, therefore, is to create a general model of local enhancement derived from that of Ruxton et al. (1995) but different in its biological assumptions and more extensive in its exploration of parameter values. The results of these simulations will contribute to our understanding of the selective pressures on local enhancement. We focus on Ruxton et al.'s (1995) claim that local enhancement reduces mean uptake rate since their argument that it reduces variance in time between feeding bouts is self-evidently correct and well accepted in the literature.

Methods and Results

Model Description

Our model follows that of Ruxton et al. (1995) except where otherwise stated. All simulations were conducted in R (R Core Team 2021). In the model, a number of individuals P forage in a square arena, the opposite ends of which are joined to form a torus. The position of any forager or food patch in this arena can be determined by x - and y -coordinates, which take discrete values from 1 to a number S . The parameter S therefore determines the size of the foraging arena such that $S \times S$ is its total area. A number of food patches N are randomly distributed in the arena in a way that none

occupies the same coordinates. Initially, each patch contains the same amount of food F .

At the beginning of the simulation, all foragers are randomly and independently distributed in the arena. Several foragers can simultaneously occupy the same coordinates. They move by increments of 1 in either of the four directions parallel to the x - and y -axes of the arena. The initial direction of each forager at the beginning of the simulation is randomly and independently determined such that each direction is equally likely.

The simulation runs for a number of time units T . At each time unit, each forager in turn follows a set of conditional rules. The order in which the foragers are considered is randomly determined at each time step. The rules are as follows.

Rule i. If the forager is located at coordinates that also contain a food patch, then it successfully detects the food patch and can start consuming it (i.e., foragers can detect only an unoccupied food patch that shares the same coordinates). It removes a fixed amount of food α from the patch; α is defined as the amount of food removed by a forager from a food patch per time step and is always set to 1. If the patch contains a smaller amount of food than α , it consumes the remainder of the food. The corresponding amount of food is then added to a collective stomach, common to all foragers, and removed from the value of the patch. If the patch becomes depleted, it is removed and a new patch containing an amount of food F is placed at another random location that is not already occupied by a patch. This replenishment means that the total amount of food in the environment does not decline over the course of the simulation.

Rule ii. If the forager is not located on a food patch, then the nearest patch to the forager that is occupied by at least one other forager is considered. If it is located within a distance D of the forager, then it is detected. This reflects local enhancement; that is, for an individual not using local enhancement, this parameter would be set to $D = 0$. The forager then moves one step in the direction that brings it closer to the patch. If two such directions exist, then one is chosen at random, each having equal probability. If two equally distant occupied patches are identified, then one is chosen at random, each having equal probability.

Rule iii. If the forager is not located on a food patch or within a distance D of any occupied patch, it takes one step in its current direction. After this, there is a probability φ (always set to 0.1) that its current direction changes. If it does change, it switches to one of the two directions perpendicular to the one that the forager was following (chosen randomly, each with 50% probability).

Once T time steps have passed, the total amount of food in the collective stomach is divided by the product of the number of foragers P and the number of time steps T to obtain a mean uptake rate per forager, or the mean amount of food ingested per forager per time step.

This model importantly differs from that of Ruxton et al. (1995) in two key ways. First, the searcher will abandon its journey and resume searching randomly if the targeted patch becomes depleted before its arrival. Second, the searcher will conduct a search of its environment at each time step, even if it is traveling toward a detected patch, so that it will be able to detect and forage at any patch it encounters along the way. Other less impactful improvements have also been made in this model and its description.

In order to develop Ruxton et al.'s (1995) work, we conduct seven sets of simulations. We first repeat their original simulation, conserving their parameter values, to solely evaluate the impact of the modified assumptions on the outcome. We then explore, in turn, how varying levels of food patch richness F , varying levels of detectability of occupied patches D , varying sizes of the arena S , and varying numbers of food patches N influence the performance of local enhancement. We then allow foragers using local enhancement, termed "local enhancers," to coexist in the arena with foragers not using local enhancement, termed "nonresponders," while varying the number of food patches N . We next consider whether heterogeneity in the quantities of food on undiscovered patches renders local enhancement more advantageous. Finally, we once more allow local enhancers and nonresponders to coexist in the arena but this time while exploring different values of patch richness F .

Specific Simulations and Model Predictions

Comparison with Ruxton et al. (1995). As an initial simulation, we used the same parameter values as Ruxton et al. (1995) and obtained the predicted mean uptake rate for every number of foragers P between 1 and 30. We chose to repeat this twice, once for local enhancers (with a detection distance $D = 10$), as in Ruxton et al. (1995), and once for nonresponders (with $D = 0$). Using the same parameter values as Ruxton et al. (1995) allowed a direct comparison of models based only on the different assumptions made.

The model used by Ruxton et al. (1995) resulted in a decreasing mean uptake rate of local enhancers as the number of foragers increased (fig. 1; the dashed line is an estimate by eye of the values in Ruxton et al.'s fig. 1). Our model also showed a decrease in the mean uptake rate of local enhancers. However, the decrease was not as steep, resulting in consistently higher mean uptake rates than those obtained by Ruxton et al. (1995). The mean uptake rate obtained for a population of nonresponders, however, remained approximately constant with the number of foragers and higher than the uptake rate of local enhancers as the number of foragers increased.

These results show that the prediction of Ruxton et al. (1995) was not obtained solely because of the assumptions they made about the behavior of individuals responding to the detection of an exploited patch. These assumptions would

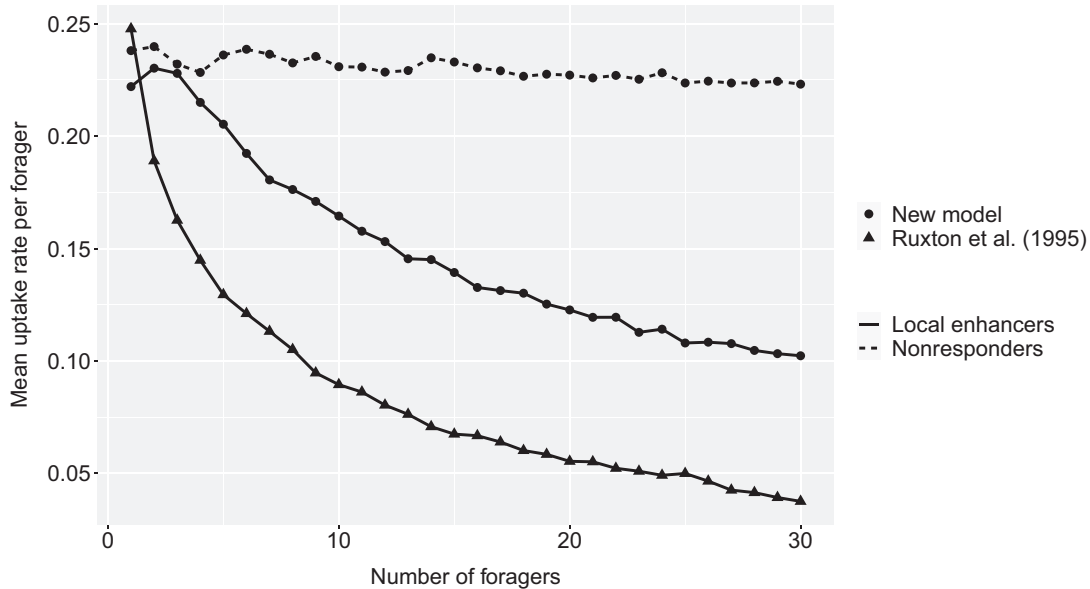


Figure 1: Mean uptake rate per forager depending on the number of foragers in the arena (P), on the model used, and on the strategy employed by the population of foragers. All 90 simulations were conducted for $N = 50$ food patches, an arena size $S = 25$, an amount of food per patch $F = 200/N$, and a detection distance $D = 10$ (circles) or $D = 0$ (triangles). The number of time steps T is not specified by Ruxton et al. (1995) but was set at 10,000 in the new model.

certainly have made local enhancement less efficient, but on their removal we still see that local enhancers suffer reduced mean uptake rates as their number increases, and this effect is not seen in nonresponders. We next turn our attention to Ruxton et al.'s restrictive assumption of very small patch size.

Varying the Number of Foragers and Amount of Food per Patch. The model was implemented again for a varying number of foragers P between 1 and 30, but this was repeated for five scenarios, each time increasing the amount of food available in each patch (F). These simulations were evaluated only for local enhancers (with $D = 10$). When increasing the amount of food per patch, the decreasing uptake rate of local enhancers with the number of foragers seen in figure 1 persisted, even for patches 16 times richer than those considered by Ruxton et al. (1995; fig. 2). Thus, the main driver of the decrease seen in figure 1 and the original Ruxton et al. (1995) article was not the very small patch size assumed.

Varying the Detection Distance and Amount of Food per Patch. We next varied the detection distance D and the amount of food in each patch F . Each integer value of D from 0 to 15 was explored. The same values of F as in figure 2 were used. As D increased, the mean uptake rate per forager followed a generally decreasing trend (fig. 3). Regardless of the amount of food per patch, the uptake rate initially

decreased slowly, then followed a steeper decline before plateauing for values of D from around 13 onward, for which all food patches in a 25×25 arena would be detected. However, we do note for the first time a hint that the trend seen so far of local enhancement leading to decreased mean uptake rates may not be universal. We see for some values of patch richness that those individuals with a short response distance ($D = 1$) have slightly higher uptake rates than nonresponders (i.e., when $D = 0$). We next consider situations where patches are sparsely spread throughout the environment since this is a situation that might be expected to favor local enhancement.

Varying the Number of Foragers and Arena Size. The model was again evaluated for each number of foragers P from 1 to 30. This was then repeated for increasing arena sizes S .

The decrease in mean uptake rate with an increasing number of foragers seen in figure 1 and illustrated by the red $S = 25$ line was attenuated as the size of the arena increased (fig. 4). By $S = 100$, no such decrease could be detected, and, in fact, both local enhancers and nonresponders followed the same constant trend such that their mean uptake rates were indistinguishable. In order to further compare individuals using local enhancement with those not using local enhancement, we now explore how the two strategies fare when both are played by individuals in the same local population, focusing on another situation where patches are sparsely spread throughout the environment.

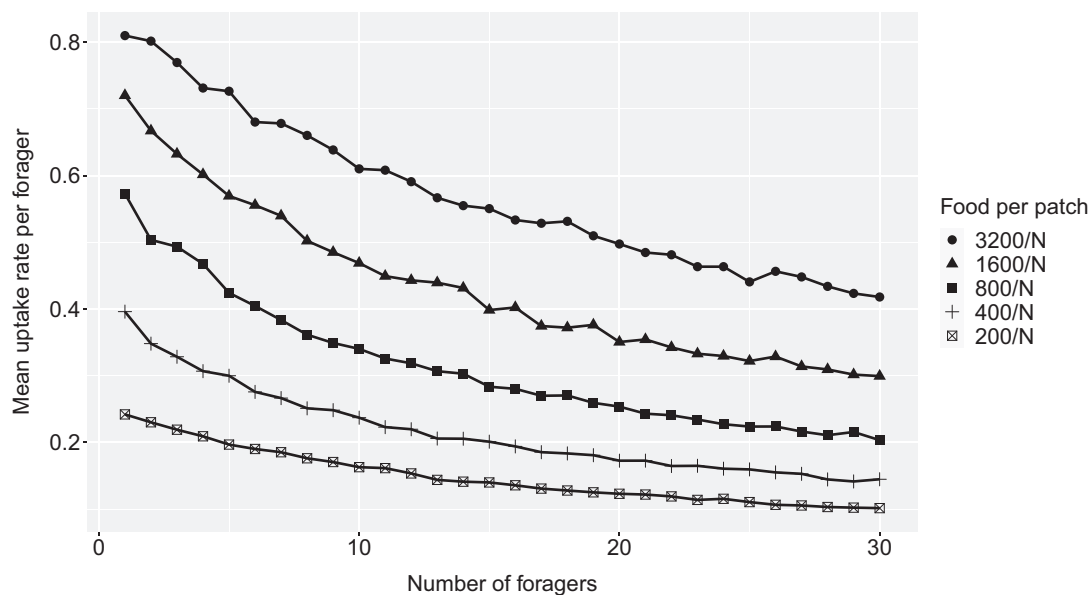


Figure 2: Mean uptake rate per forager of local enhancers, depending on the number of foragers in the arena (P) and on the amount of food per patch (F). All 150 simulations were conducted for $T = 10,000$ time steps, $N = 50$ food patches, an arena size $S = 25$, and a detection distance $D = 10$.

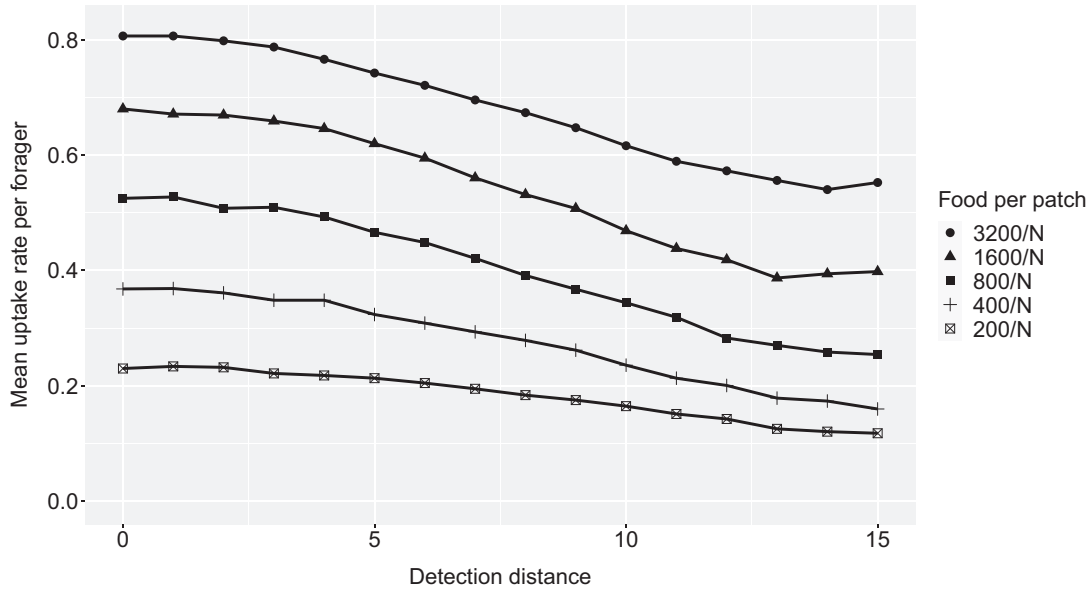


Figure 3: Mean uptake rate per forager depending on the detection distance of each forager (D) and on the amount of food per patch (F). All 75 simulations were conducted for $T = 10,000$ time steps, $N = 50$ food patches, $P = 10$ foragers, and an arena size $S = 25$.

Varying the Proportion of Local Enhancers in the Population and the Number of Patches in the Arena. In these next simulations, both local enhancers and nonresponders foraged in the same arena at the same time. In each simulation, $P = 10$ foragers were used, but the proportion of local enhancers was varied from 0 to 1 in increments of 0.1.

For example, using a proportion of 0.3 meant that three of the 10 foragers were identified as local enhancers (with $D = 10$) and seven as nonresponders (with $D = 0$). Instead of using one collective stomach to record the total amount of food consumed throughout the T time steps, two stomachs were used: one for local enhancers and one for

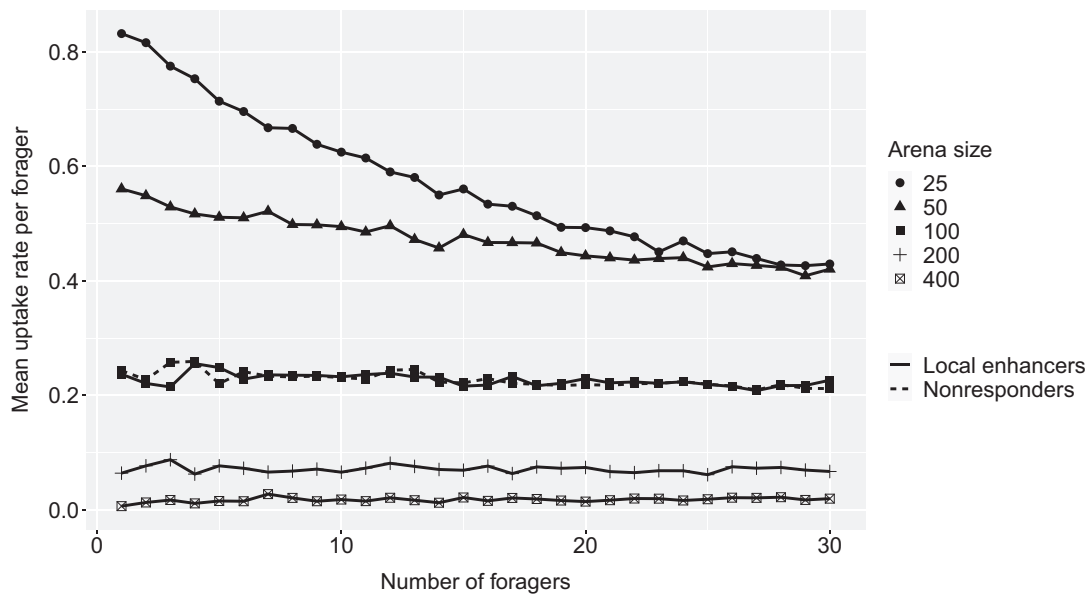


Figure 4: Mean uptake rate per forager depending on the number of foragers (P), on the size of the foraging arena (S), and on the strategy employed by the population of foragers. All 180 simulations were conducted for $T = 10,000$ time steps, $N = 50$ food patches, an amount of food per patch $F = 3,200/N$, and a detection distance $D = 10$ (circles) or $D = 0$ (triangles; shown only for $S = 100$).

nonresponders. The mean uptake rate per forager could therefore be obtained separately for each type of forager. This series of 11 simulations was repeated for decreasing values of N , the number of food patches in the arena. We used $N = 50$, $N = 30$, $N = 20$, and $N = 10$. Because our objective was to test the variation of mean uptake rates when solely varying patch scarceness, we used a constant amount of food per patch of $F = 3,200/50 = 64$.

For $N = 50$ food patches in the environment, the mean uptake rate of local enhancers was largely lower than that of nonresponders (fig. 5A). However, the case of a single local enhancer with nine nonresponders showed a higher uptake rate for the local enhancer than for the nonresponders. This local enhancer had a higher mean uptake rate than not only its nine nonresponding conspecifics but also individuals in a population of the same size made up of only nonresponders. As the patches became more scarce in the arena, this advantage that initially had existed only for a lone local enhancer progressively spread to greater proportions of local enhancers, until for $N = 10$, local enhancers of all proportions had a higher uptake rate than the nonresponders they coexisted with (fig. 5). This is the first example in these simulations of a clear advantage of local enhancement in terms of the mean uptake rate per individual, and it constitutes a counterexample to the claim made by Ruxton et al. (1995)

that local enhancement decreases mean uptake rates. We next turned our attention to the richness of food patches by first relaxing the assumption that all patches are equally valuable, to explore whether local enhancement might lead to enhanced mean uptake rates in this situation by biasing feeding toward the most rewarding patches.

Heterogeneous Food Patches. This set of simulations explored a heterogeneous environment in which the food patches contained a varying amount of food. In order to achieve this, F was determined by taking a sample of size N from a lognormal distribution with a mean of $3,200/N$ and a variance V . Each resulting value of F was assigned to one food patch, which was placed randomly in the environment. Whenever a patch became depleted, the richness (F) of the new patch was drawn randomly from the same distribution. The simulation was run for varying values of the variance V , between 0 and 10,000 in increments of 500. For examples of the distribution of patch richness obtained from this sampling, see figure A1. This was repeated three times, once using a population of nonresponders (with $D = 0$), once using a population of local enhancers with $D = 5$, and once using a population of local enhancers with $D = 10$. The entire process was then repeated twice, for $N = 50$ and $N = 25$.

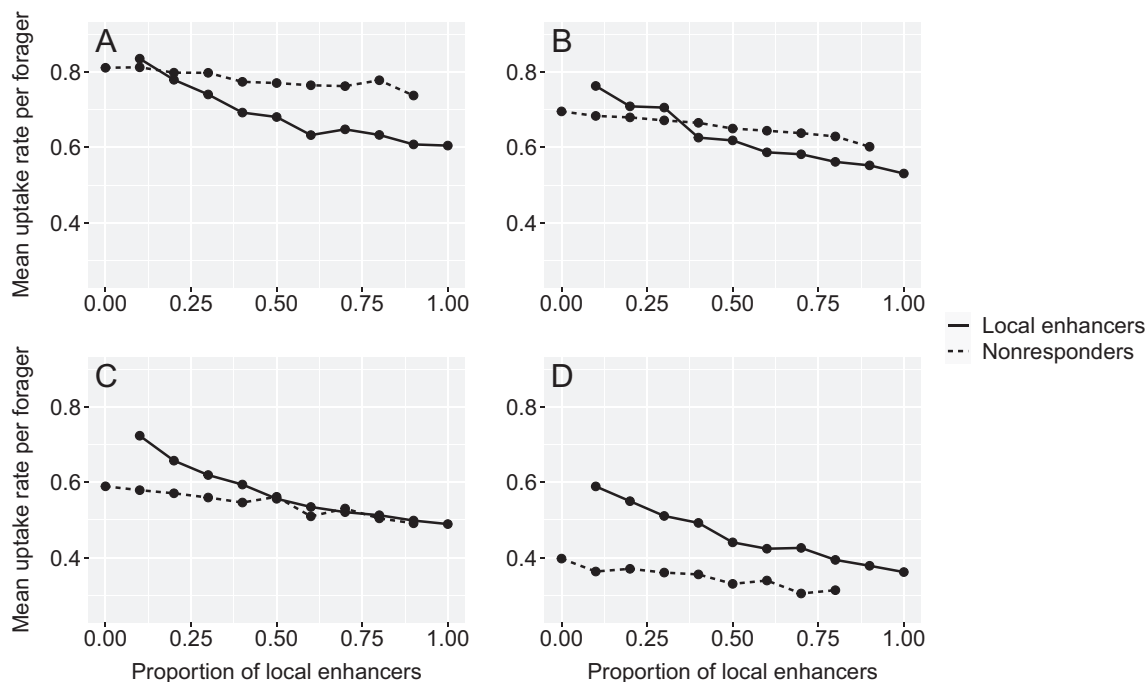


Figure 5: Mean uptake rate per forager depending on the proportion of the foraging population using local enhancement and on the strategy employed within that population for $N = 50$ (A), $N = 30$ (B), $N = 20$ (C), and $N = 10$ (D) food patches in the arena. All 44 simulations were conducted for $T = 10,000$ time steps, $P = 10$ foragers, an arena size $S = 25$, an amount of food per patch $F = 64$, and a detection distance $D = 10$ (circles) or $D = 0$ (triangles).

Simulating a heterogeneous environment was useful in exploring whether local enhancers would preferentially exploit the richest patches in the environment with a better efficiency than the nonresponders. An increased variance V would entail an increase in the amount of food contained by the richest patches in the arena. This would in turn increase the time during which the patch could be exploited. By attracting more local enhancers, this might therefore increase their mean uptake rate.

When the food patches in the arena contained differing amounts of food (F), the mean uptake rate of nonresponders ($D = 0$) was consistently higher than that of local enhancers with $D = 5$, which in turn was higher than that of local enhancers with $D = 10$ (fig. 6). An increase in the variance of the lognormal distribution from which F was drawn did not appear to impact the mean uptake rates. When more food patches were present in the arena ($N = 50$; fig. 6A), the general difference between the mean uptake rates of local enhancers with $D = 10$ and nonresponders was greater than for $N = 25$ (fig. 6B). That is, the mean uptake rates of nonresponders were generally higher, while those of local enhancers with $D = 10$ were generally lower. However, there was no evidence that the performance of

local enhancers (relative to nonresponders) benefits from heterogeneity in patch quality. Thus, high-quality patches may not translate into larger meals for individuals that arrive on the patch by local enhancement. To further test this hypothesis, we once again explore a varying proportion of local enhancers, this time for increasing values of patch richness.

Varying the Proportion of Local Enhancers in the Population and the Richness of Food Patches. In this final set of simulations, we varied the composition of the foraging population, keeping the total number of foragers at $P = 10$ but varying the proportion of local enhancers within the population between 0 and 1 in increments of 0.1. Once again, for each simulation the mean uptake rates of local enhancers and nonresponders were calculated separately. This set of 11 simulations was repeated for increasing values of patch richness (F).

As the amount of food per patch F increased, the mean uptake rate of local enhancers relative to that of nonresponders did not greatly change (fig. 7). Although there was some fluctuation for poor food patches ($F = 500/N$) wherein the advantage of the lone local enhancer was lost, we recognize in all four curves the shape of that obtained in figure 5A, for

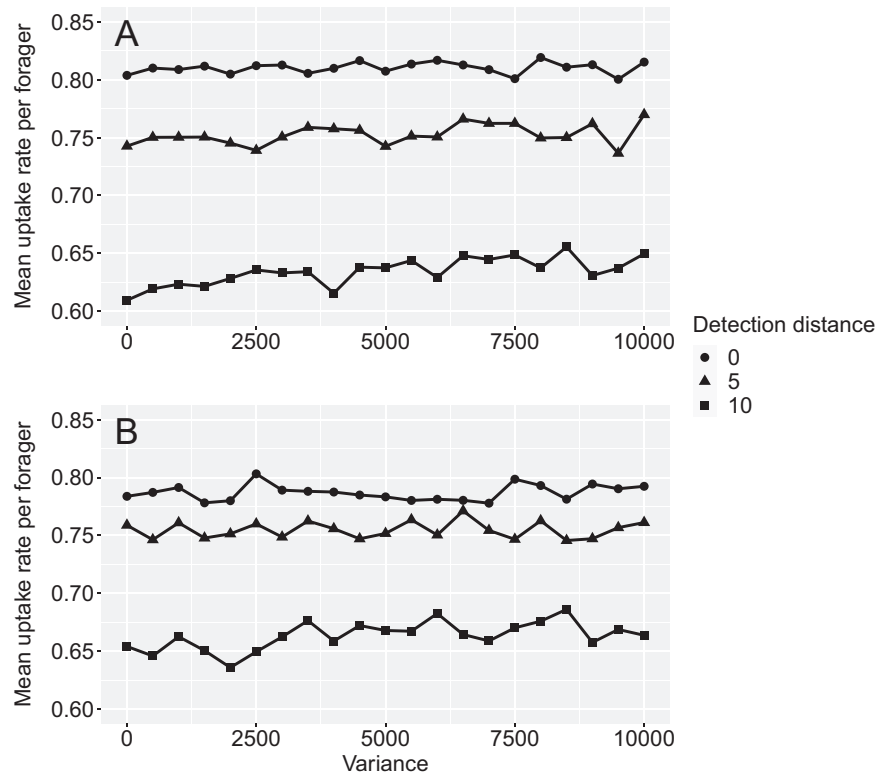


Figure 6: Mean uptake rate per forager depending on the variance of the lognormal distribution with mean $3,200/N$, from which was obtained the amount of food (F) in each patch, and on the detection distance (D). This relationship was obtained for $N = 50$ (A) and $N = 25$ (B) food patches in the arena. All 126 simulations were conducted for $T = 10,000$ time steps, $P = 10$ foragers, and an arena size $S = 25$.

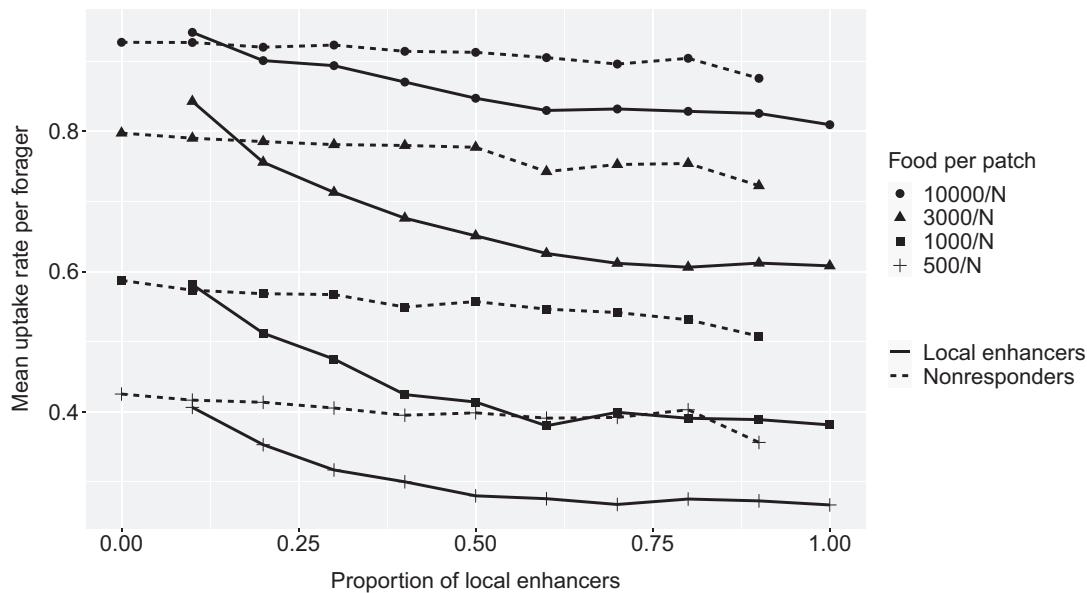


Figure 7: Mean uptake rate per forager depending on the proportion of the foraging population using local enhancement, on the strategy employed within that population, and on the amount of food per patch (F). All 44 simulations were conducted for $T = 10,000$ time steps, $N = 50$ food patches in the arena, $P = 10$ foragers, an arena size $S = 25$, and a detection distance $D = 10$ (circles) or $D = 0$ (triangles).

which we also used $N = 50$ food patches in the arena. Therefore, we confirm the hypothesis made earlier that richer food patches do not increase the uptake rates of local enhancers relative to those of nonresponders.

Discussion

In this study we considered the nature of the selective pressures leading to the foraging strategy of local enhancement. It is already established that one advantage of local enhancement is the reduction in variance of the time elapsed between each meal, thus leading to a reduced risk of starvation. Here, we have developed an understanding of the suggestion made by Ruxton et al. (1995) that local enhancement leads to a reduced mean uptake rate and therefore is disadvantageous in terms of the long-term amount of food consumed. Specifically, we found that even after relaxing a number of assumptions made by Ruxton et al. (1995), the reduced mean uptake rate that they predicted remained in many situations, although to a lesser degree. This disadvantage of local enhancement can appear counterintuitive. Contrarily to Ruxton et al. (1995), we included in our model the assumption that as a searching forager travels toward a detected occupied patch, it is still able to detect any patches along the way. Therefore, it may seem that a directed journey is not much different from a random search of the environment, during which any encountered patch can immediately be exploited. If this were true, then the arrival of the forager at the detected occupied patch, which occurs only if no other patch has been encoun-

tered along the way, would be entirely beneficial. In that sense, the use of local enhancement might initially be seen as simply offering an added bonus in a forager's search of the environment. The shared nature of the patch would not be ideal, but there would be no cost in exploiting this patch since the search for better patches would have been possible along the way. However, our findings suggest that the use of local enhancement can in fact be detrimental. We attribute this cost to the spatial clumping that local enhancement causes. As several individuals are attracted to a single patch via local enhancement, they become physically closer until they are all exploiting the patch. Once this patch becomes depleted, all of these foragers will disperse simultaneously and resume their search for another patch. In doing so, the foragers will be concentrated in one area of the environment. This implies that, first, searching areas will overlap; therefore, each forager will likely be searching an area that has already been unsuccessfully searched by another, so the environment will not be searched collectively in the most efficient way (Ruxton et al. 2005). Second, any patches in the immediate surroundings will be the object of intense competition.

It seems, therefore, that any situation leading to an increased long-term uptake rate resulting from local enhancement will have to reduce this clumping cost. Despite the categorical claim made by Ruxton et al. (1995) that local enhancement reduces uptake rates, we did find, while varying the parameters of our model, a range of simulated conditions in which local enhancement is beneficial. Specifically, we found that as the scarcity of food patches in the environment

increases, so, too, does the advantage of being a local enhancer (fig. 5). We attribute this advantage to two factors. First, the scarcity of food patches dilutes the spatial clumping effect. Indeed, as local enhancers leave a depleted patch, they will have enough time to disperse in random directions before a new patch is found. Second, we suggest that when food patches are scarce, the reduction in search time provided by local enhancement becomes an asset in terms of feeding efficiency. In general, local enhancers have to trade off finding patches more frequently with eating a reduced amount of food per meal. This is the mechanism behind the reduced risk of starvation that local enhancement provides. Nonresponders, however, have to trade off eating an increased amount of food per feeding event with being able to find food patches only rarely. As patches become scarce in the environment, local enhancers' ability to find food patches more frequently outweighs the cost of eating less food per meal. This, in addition to a diluted clumping effect, renders the local enhancement strategy beneficial. The advantage of local enhancement when food patches are scarce can also be seen in figure 6, wherein the gap in uptake rates between local enhancers and nonresponders becomes narrower when the number of food patches is halved. If patch density were to decrease even further to, say, two patches or even one, not only would the gap close but also local enhancers would be expected to have higher uptake rates than nonresponders. This corroborates the empirical findings of many studies that describe the use of local enhancement by specific taxa when resources are particularly sparse (Waite 1981; Whiting and Greeff 1999; Goyert 2015). This advantage to local enhancement was detected in our simulations only when the number of food patches was decreased in a feeding arena. Increasing the size of the arena while keeping the number of food patches fixed resulted in local enhancers becoming indistinguishable from nonresponders only because of the fact that their abilities were rendered negligible by the size of the arena (fig. 4). Beyond the finding that sparse food patches favor local enhancement, we add that when the scarcity of patches is of an intermediate value, the advantage of local enhancers is limited by their proportion in the population. That is, local enhancers will obtain higher uptake rates than nonresponders only if they constitute a fraction of the population. Beyond a critical proportion of local enhancers, which is dependent on the scarcity of the patches, the spatial clumping of local enhancers becomes detrimental and nonresponders obtain higher uptake rates (fig. 5).

There may also be an advantage to local enhancement when it is used on a very small scale, that is, to detect an occupied patch located only one step away in our modeled arena (fig. 3). This can be explained by the fact that moving in directed travel by only one step will not lead to any significant clumping effect. We recognize, however, that this benefit of local enhancement may not reflect biological re-

ality but may be a result of our assumption that a forager can detect an unoccupied food patch only if it is located directly above it. In biological systems, the true detection distance to an unoccupied food patch is likely to be greater, in which case using local enhancement beyond this distance, even to a small degree, might lead to spatial clumping and be detrimental.

Another surprising finding was that the richness of a food patch has no consequence on the performance of local enhancers relative to that of nonresponders (figs. 2, 6, 7). It is commonly stated in the literature that local enhancement becomes advantageous when food patches are both sparse and plentiful (Pöysä 1992; Grünbaum and Veit 2003). Intuitively, richer patches are associated with reduced competition. They also take more time to become depleted so would allow local enhancers to travel to them and successfully exploit them. However, any such patch will have been depleted to some extent by the initial discoverers by the time the next individual arrives, and then both must share the remainder, potentially with further arrivals. Additionally, if rich patches last longer from discovery to depletion, then this may lead to fewer patches being exploited at any one time. Consequently, the strategy of local enhancement, if advantageous in that situation, would become less effective for the remaining searching foragers. Finally, a longer-lasting patch might attract a greater number of local enhancers, which would potentially increase the clumping effect of local enhancement. Therefore, it seems that the advantages typically associated with richer patches may be counterbalanced by the costs of this richness in the context of local enhancement.

Despite the focus of this study on the direct effects of local enhancement, it is important to expand on the fact that it could also be a beneficial strategy, perhaps more indirectly, when the reduction of starvation risk is necessary (Alonso et al. 1987; Krause and Ruxton 2002). In such systems, the reduced variance in time that it provides between meals may be a very important selection pressure biologically. For example, birds have high energetic requirements due to their metabolic activity, and storing too much energy in the form of fat reserves would be detrimental to their ability to fly and escape predators (Lima 1986; Ekman and Hake 1990; Bonter et al. 2013). Therefore, their feeding requirements are higher than those of other endothermic groups (Nagy 2001). By spending too much time searching independently for an exclusive and rich patch of food, birds may run the risk of starving as a result of their minimal stored reserves. As such, local enhancement may provide a vital way to prevent birds from spending long intervals of time without eating. In addition to this, if the time window during which birds can forage during the day is limited, the advantage of using local enhancement may be even greater. For example, vultures are heavy birds that often depend on strong thermal updrafts in order to be able to soar and find food (Mandel and Bildstein

2007). The fact that they can forage only when thermals are strong enough, in combination with the unpredictability of the occurrence of carcasses on which they feed, may mean that cuing on other scavengers is a time-efficient way of reducing the risk of starvation.

Our results suggest that local enhancement is directly beneficial through enhancing long-term uptake rates (rather than through reduced variance in time between meals) in only a limited set of situations. However, empirical studies have reported that local enhancement is commonly used by a broad range of animal taxa (Krebs 1974; Otis et al. 2006; Green and Leberg 2011; Pérez-Cembranos and Pérez-Mellado 2015). This conclusion is supported in these studies by the fact that individuals purposefully join feeding aggregations. While it is possible that these taxa do indeed use local enhancement either because food patches are scarce or to reduce their risk of starvation, these empirical studies cannot exclude the possibility that a group-joining behavior arises for reasons other than local enhancement. Social foraging can be beneficial in providing a reduced need for individual vigilance against predators (Pays et al. 2013), a better availability of food items (Camphuysen and Webb 1999), or even reproductive opportunities (Griffiths and Magurran 1998). Because these empirical studies spatially focus only on the foraging group that is being joined, there is no guarantee that for the studied taxon local enhancement truly constitutes the mechanism driving joining. In systems where food is not particularly scarce and where there is no immediate threat of starvation, our findings suggest that local enhancement is not likely to be a beneficial strategy in that it generally decreases the mean uptake rate of individual foragers. In these situations, any group-joining behavior in a foraging context may be motivated by the benefits of social foraging instead.

Although we offer significant novel insights, there is still further strategic modeling of local enhancement to be done. Specifically, there are limitations to our model with respect to patch discovery that could be addressed in future models of local enhancement. We assumed that the quality of a patch and the number of foragers already on the patch (as long as this is nonzero) do not affect long-range or short-range detectability. This is questionable, as a patch of greater quality, which can reasonably be associated with a larger size, is more conspicuous to a searching forager (Moleón et al. 2015). Similarly, a large aggregation of foragers at a food patch can often be detected from farther away than a lone forager at a patch. An increasing detection distance with group size has been empirically recorded (Thiebault et al. 2014) and included in models of local enhancement (Buckley 1996). More importantly, we might expect that foragers can use information on these aspects to determine whether to join a group (Sumpter 2010; Beauchamp and Ruxton 2014). The search for effective selective-joining strategies may be the next important step in strategic modeling of local enhancement.

Additionally, while our model simulated local enhancement in order to explore its general selective advantages, there is still progress to be made in models depicting local enhancement in specific biological systems. Beyond the usefulness of these models in understanding the foraging behavior of a taxon, they can have conservation applications. Because the use of local enhancement depends on the presence of others, population declines of a given taxon that is habitually reliant on local enhancement can affect its foraging success.

For example, models of the foraging behavior of vultures have been common (e.g., Buckley 1996; Dermody et al. 2011; Cortés-Avizanda et al. 2014). These scavengers have been in decline since the 1990s (Green et al. 2004; Ogada et al. 2016), and some models of their foraging behavior have been created to inform conservation efforts (Jackson et al. 2008; Kane et al. 2014). There have, however, been major discrepancies between models. While at times important assumptions such as carcass depletion have been omitted from models (Jackson et al. 2008; Dermody et al. 2011; Kane and Kendall 2017), of particular concern are the discrepancies in parameter values, which stem from a lack of empirical data. For example, the values often used to represent the distances from which vultures can detect occupied or unoccupied carcasses (4 and 0.3 km, respectively) either are based on a single unreplicated observation (Pennycuik 1972; Jackson et al. 2008; Dermody et al. 2011; Kane et al. 2014) or have no empirical founding whatsoever (Jackson et al. 2008; Dermody et al. 2011; Cortés-Avizanda et al. 2014). While they are commonly considered conservative estimates (Jackson et al. 2008), there is currently no consensus on a reliable empirically based value of these parameters that should be used in all models of vulture foraging behavior.

Parameterizing models of local enhancement to reflect the foraging behavior of a specific taxon, and thus make reliable predictions, will require better data collection in the field. Of particular priority is the collection of data regarding detection distances, particularly the distances from which individuals of a taxon react to a group of foragers at a patch and the distances from which they react to unoccupied patches. While these have been historically difficult to measure because of technical limitations resulting from the scale over which local enhancement occurs, new technologies are emerging that would permit such data collection. Specifically, the use of compact onboard technology such as GPS trackers and microcameras has now become widespread (Votier et al. 2013; Hallworth and Marra 2015; Campion et al. 2020). While seemingly only one study so far has used this technology to estimate reaction distances in the context of local enhancement (Thiebault et al. 2014), this does provide promising evidence that such data can be collected. In light of the results obtained in this study, another important parameter value to measure empirically would be the density

of food patches in the specific system considered, since the performance of local enhancement critically depends on this parameter. Therefore, obtaining accurate and reliable estimates for both detection distances and food patch density in specific systems would be an important next step in furthering our understanding of local enhancement and improving our predictive abilities.

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Statement of Authorship

The study was conceptualized by A.R. and G.D.R.; model development and analysis were performed by A.R. and G.D.R.; the initial draft was written by A.R.; reviewing and editing were conducted by A.R. and G.D.R.

Data and Code Availability

R code is available from <https://doi.org/10.5061/dryad.pzgm sbcmz> or by emailing G.D.R.

APPENDIX

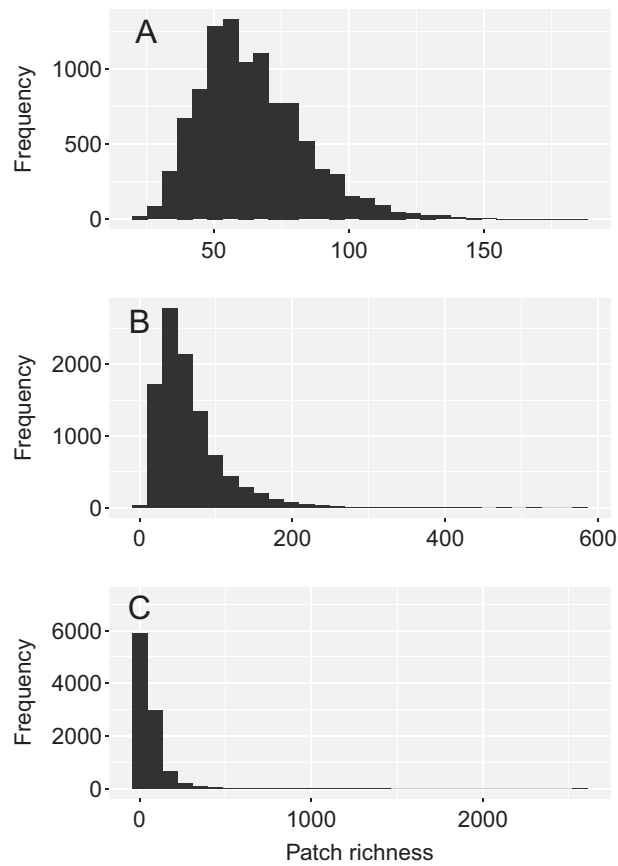


Figure A1: Distribution of 10,000 values of patch richness (F) taken from a lognormal distribution with mean $3,200/N$ and variance 400 (A), 2,000 (B), and 10,000 (C). N is the number of patches in the foraging arena and was set at 50. The maximum value of patch richness obtained in each case was 184 (A), 576 (B), and 2,565 (C).

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“Ten years ago, quite unaware of this controversy, the writer gathered and sketched a selection of mature rose, blackberry, and sumac leaves which presented the problem in very clear terms.” Figured: “Leaves of the dwarf sumac, *Rhus copallina* L.” From “The Development of Pinnate Leaves” by Frederic T. Lewis (*The American Naturalist*, 1907, 41:431–441).