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An experimental design and a statistical analysis separating interference from exploitation competition

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Abstract Previous experimental studies of competition among foragers rarely distinguished between exploitation and interference competition. In many systems this separation is experimentally impossible without interfering with the natural behavior of the animals. Consequently, these studies can only demonstrate the combined effect of interference and exploitation on the forager's feeding rate, namely, it usually decreases in a decelerating rate as a function of density. We suggest here a simple experimental and statistical procedure that facilitates the separation of the effects of interference from those of exploitation. This procedure includes manipulation of both predator density and the foraging experiment duration. The statistical analysis is based on multiple linear regression. The working assumption is that exploitation can be neglected at the beginning of the foraging experiment because, initially, predators do not experience diminishing returns in prev capture rates. Using both the results of an individual-based simulation and a field experiment dataset of gerbils foraging for seeds in an artificial food patch located in the field, we demonstrate that our procedure can successfully detect and separate the effect of interference from the

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Keywords Functional response · Individual based model · Searching behavior

Introduction

Competition can be simply described as the negative effects organisms have on each other's fitness (i.e., per capita rate of change) by depleting or preventing access to shared resources that are limited (Connell 1983; Schoener 1983; Gurevitch et al. 1992; Keddy 2001). Ever present in nature, competition has considerable implications for populations and communities (Gurevitch et al. 1992; Morin 1999). Historically, ecologists usually distinguished between intra- and interspecific competitive interactions and between direct and indirect types of competition (Morin 1999). Direct or interference competition occurs when one individual prevents others from accessing shared and limited resources and thus directly and negatively affects the fitness of others. Indirect or exploitation competition occurs when a shared resource of limited availability is depleted, and consequently fitness is indirectly reduced (Morin 1999; Keddy 2001).

Based on earlier reviews (e.g., Connell 1983; Schoener 1983), Tilman (1987) concluded that most experiments examining competitive effects documented only how a change in the density of one species led to a change in another species' density without providing a mechanistic explanation for these patterns. He suggested that identification of the mechanism driving competition will improve our understanding of community dynamics, thus enabling stronger, better formulated predictions on issues such as

how an increase in a given resource level influences the interaction among competitors. Moreover, Hart (1987) claimed that the various mechanisms driving competition are highly relevant, since the effect of different types of competition on higher levels of organization may not be similar.

Previous competition experiments, for the most part, investigated interspecific competitive interactions at the community level (e.g., Schoener 1983; Gurevitch et al. 2000). Separating direct and indirect effects in such a multi-species system is sometimes possible when the approach of structural equation modeling or path analysis is adopted (e.g., Wootton 1994). Hart (1987) used a postexperiment path analysis to estimate the relative magnitude of interference and exploitation in a single-species system, but because his path coefficients did not significantly differ from 0, he could not interpret the relative magnitudes of the different components of competition. Similar attempts to identify the mechanism driving competitive effects are uncommon and are done mainly at the community level (e.g., Wootton 1994), while very little attention has been devoted to making such a distinction in a single-species system. Furthermore, there is a solid set of theoretical studies evaluating functional responses concerning both exploitation and interference competition (e.g., DeAngelis et al. 1975; Huisman and De Boer 1997). Yet, very few studies incorporated simple experimental manipulations (with the exception of preserving a constant resource level) or basic statistical analyses to differentiate between exploitation and interference (but see Hart 1987; Anholt 1990; Peckarsky 1991; Smallegange et al. 2006).

Smallegange et al. (2006), for example, evaluated the strength of interference competition by manipulating predator density and maintaining a constant resource level. Each time a predator caught a prey item, a new one was introduced into the system. Thus, the easiest way to separate interference from exploitation is to keep the resource level fixed. However, sustaining the resources at a constant level is not always possible without severely disturbing foraging animals (e.g., Vahl et al. 2005), and it also demands the use of sophisticated devices (e.g., Nicholls and Doxtator 1960; Smallegange et al. 2006). This method was shown to be possible especially in aquatic systems in which adding prey did not affect the predator behavior and when prey items were large enough that an observer could monitor prey density and react by adding prey. Indeed, Sutherland and Koene (1982) and Vahl et al. (2005) both admitted that their experimental systems did not distinguish between the effects of interference and exploitation and warned that unaccounted exploitation may lead to an overestimation of the level of interference (Sutherland and Koene 1982).

In this paper we suggest that by manipulating both predator density and experiment duration, it is possible to separate the effects of exploitation and interference. The separation is made possible by the method of multiple linear regression and examination of the interaction term between predator density and experiment duration. We test our method by using an individual-based model and analysis of an experimental dataset of gerbils foraging for seeds in artificial food patches located in the field. The method is explained in more detail in the next two sections of the paper.

The model

To evaluate predator feeding rates (or encounter rate with prey items), we designed an individual-based simulation in which simulated animals searched for prey items in a continuous space (50 \times 50 length units), and the cumulative number of prey items each predator encountered was recorded. Two hundred prey items were randomly distributed, and predators searched for prey using correlated random walk (velocity of two length units per turn). To simulate exploitation competition, caught prey items were not replaced. Interference was simulated as follows: each time the distance between two predators was less than the predator detection distance (hereafter, PDD), both stopped searching for prey for two time units, after which they resumed searching from random points in the arena, using correlated random walk. This is a common method of simulating interference among foragers (e.g., Moody and Ruxton 1996; Lerman and Galstyan 2002), although other methods are acceptable too (i.e., interference occurs only when a prey item is discovered; Stillman et al. 1997). Clearly, the decision on which method to use is systemdependent and may be related to the type of interference involved.

We varied the interference magnitude by increasing the PDD from 0 (i.e., no interference) to 7.5. We ran the model at five different predator densities (3, 6, 9, 12, and 15) for a fixed time (100 time units), although we refer only to each simulation beginning. For simplicity, we assumed that predators had no handling time. However, in some cases, especially when prey density is high, handling time may reduce interference, since predators are mostly occupied with handling the prey instead of searching (Van der Meer and Ens 1997). Nevertheless, including handling time in our model should not affect the results because during each simulation run many prey items are captured by each individual predator; incorporating handling time simply lowers the long-run capture rate (or alternatively rescales the time axis).

Our study centered on the change in the cumulative number of prey items caught per individual over time (Fig. 1a, b) and under two different scenarios, with and without interference. As can be seen in Fig. 1, the cumulative number of prey items caught by a single predator initially increased linearly and then gradually leveled off to an asymptote due to exploitation. The higher the predator density the faster the depletion and the earlier the curve approached the asymptote. Our analysis focused on the initial part of each experiment, when the capture curve was still in the linear phase and during which less than 10% of the prey was caught. Identifying this linear phase can be done using several methods. For example, one can locate the breakpoint using a segmented piecewise regression or a robust locally weighted scatter plot smoothing. We illustrate this point below with the field data, which are more noisy and where finding the breakpoint is not as straightforward as with the simulation results. Based on such a small percentage of caught prey, we assumed that in this phase the effect of depletion on the analysis was negligible (Fig. 1c, d). The strength of interference was assumed to be constant across the experiment.

Testing for interference competition

We recorded the number of prey items captured from t = 1 to 11, while varying the predator density (N = 3, 6, 9, 12, and 15). This is because when using the highest density (N = 15), 10% of the prey was caught after 11 time steps. In the analysis, we used the same time units (i.e., up to t = 11) for all densities. This procedure was replicated 50 times for each of the five different predator densities.

We used multiple linear regression to test for the effects of density, time, and their interaction $(N \times t)$ on the number of prey items caught. A significant interaction term 321

indicated that slopes of different densities were significantly different and therefore interference existed; insignificant interaction implied insignificant differences between the slopes and therefore, that there was no interference. The interaction was indeed significant when the PDD was 7.5 (P < 0.0001) and insignificant when the PDD was 0 (P = 0.241). Figure 2 presents the natural logarithm of the feeding rate (i.e., prey items caught divided by time or slopes of Fig. 1b) versus the natural logarithm of the predator density. The negative slope indicates that density negatively affected capture rate before exploitation came into play [i.e., the interaction term $(N \times t)$ is significant]. In case there was no interference, the slope of this figure would have been close to zero. Consequently, we conclude that this method is capable of resolving whether interference exists in an experimental system.

Next, we were interested in the relationship between interference and predator density. We thus estimated the regression slope for each density when the PDD was 7.5. These slopes represent the average feeding rate of an individual predator at different predator densities. Previous work (e.g., Sutherland and Koene 1982; Stillman et al. 1996) demonstrated that feeding rate vs. predator density is described by a monotonically decreasing curve (either linear or curvilinear in log-log scales). The slope of this curve measures the (negative) marginal effect of increasing predator density on feeding rate. Our graph (Fig. 2) is similar to those of previous studies (e.g., Sutherland and Koene 1982); however, in contrast to these studies, it describes a decrease in feeding rate that is solely due to interference competition, rather than the combined effect of interference and exploitation. Additionally, Fig. 2 suggests a diminishing marginal effect of density on individual feeding rate as predator density increases (because the decreasing linear relationship in log-log translates into a hyperbola in the original axes of feeding rate vs. predator

Fig. 1 The cumulative number of prey items caught per predator from the start of simulation without (a, c) and with (**b**, **d**) interference, for five different predator densities. The main difference is during the first time steps of the simulation. When interference exists (d vs. c), the functional response starts to level off earlier, even when most prey items have not yet been found. Note that Fig. 1c, d are an enlargement of the first time steps of Fig. 1a, b





Fig. 2 The natural logarithm of predator densities vs. the natural logarithm of the prey capture rate (prey items found as a function of the searching time) in the first time steps, estimated by linear regression. A *straight line* ($R^2 = 0.912$, n = 6, P = 0.003) with a negative slope indicates that the marginal effect of density on the slope decreases as predator density increases. The following predator densities were used to create this graph: 3, 5, 6, 9, 12 and 15

density; not shown). Finally, this relationship between predator density and feeding rate (in logarithmic scale) is often curvilinear as has been recently shown (e.g., Moody and Ruxton 1996; Stillman et al. 1996; Van der Meer and Ens 1997). However, such additional considerations and the exact shape of the curve are beyond the scope of this paper (we only wish here to demonstrate that our method is capable of identifying interference, regardless of whether it increases linearly with predator density).

Testing a dataset of foraging gerbils

We used a dataset taken from a previous experimental study on *Gerbillus andersoni allenbyi* during which direct observations were made to study its foraging behavior (Ovadia et al. 2001; Ovadia and zu Dohna 2003). *G. a. allenbyi* is a small desert rodent inhabiting a wide range of sandy areas in the western Negev Desert in Israel. This gerbil species has long served, together with its congener *G. pyramidum*, as a model system to investigate different aspects related to competition and habitat selection.

Gerbils were stocked, at varying densities, into 1-ha fenced plots located in the sandy areas of the western Negev Desert. Their foraging behavior was monitored using thermal imaging cameras and seed trays $(45 \times 60 \times 2.5 \text{ cm} \text{ deep})$ each filled with 5 L of sifted sand into which 3 g millet seeds were thoroughly mixed. The direct observations indicated that individual *G. a. allenbyi* collected and delivered the seeds to their burrows or to surface caches for later consumption (Ovadia et al. 2001). It is important to note that although these seed trays were exploited by several gerbils, only a single gerbil could forage in a seed tray at a time.

The total foraging time in such an artificial food patch was calculated by summing-up all foraging bouts observed until the foraging session was stopped and the sand was sifted to recover the remaining millet seeds. In our analysis, we used only the foraging time until the curve of seeds collected over total foraging time started to level off. The exact point was determined using two independent methods. First, we used an Excel toolbox for segmented piecewise regression (O'Day 2007) to determine the breakpoint at which the curve started bending (Neter et al. 1996). Segmented piecewise regression can identify the trend changes in a nonlinear curve and divide the curve into a series of segmented linear curves.

The best overall R^2 was obtained within a range of t = 1,200-1,400 s ($R^2 = 0.332-0.323$). This suggests that when exceeding the upper limit of this range, exploitation comes into play (see exact regression equations in Fig. 3a). Similar results were obtained when we used robust locally weighted scatter-plot smoothing (defined as LOWESS in Systat 11.0). Therefore, we considered only the data up to t = 1,350 s as the linear phase during which exploitation plays a negligible role in determining seed consumption.

Because these data were collected for another purpose, replications were not uniformly distributed across densities. Therefore, we collapsed the data into three density groups: gerbil density <6 (average density = 4, n = 9), gerbil density = 6 (n = 64) and gerbil density > 6 (average)density = 10, n = 11). Figure 3b presents the number of seeds collected per gerbil as a function of total foraging time at different densities. We used the method described above to test for the effect of predator density, time and the interaction term (density \times time) on the seeds collected gerbil. The interaction term was significant per (P < 0.001), indicating that the rate at which seeds were collected at high densities was lower. Furthermore, it suggests that interference is a dominant force affecting gerbil foraging behavior (Fig. 3c). The decrease in feeding rate as a function of increasing densities was difficult to calculate because we had only three densities. Nevertheless, the regression coefficient was -1.49 ($R^2 = 0.96$, n = 3, P = 0.033; Fig. 3c). It may imply that interference increases at a decreasing rate with density, at least for the density range tested, but a more comprehensive study is needed for that purpose.

Final words

We propose an experimental design and a statistical analysis that are capable of distinguishing the effect of interference from that of exploitation. According to this design, searches for prey by predator groups of varying densities should occur during several periods of short



Fig. 3 a Seeds (in g) collected per gerbil, as a function of total foraging time (s). Two segmented linear regression lines are fitted to the data, according to the breakpoint (t = 1,350) identified by the segmented piecewise regression (for the whole model: $R^2 = 0.151$, $F_{1,171} = 30.32, P < 0.001$). The equations are $Y = 3.73 \times 10^{-4}$ $t + 2.09 \times 10^{-2}$ ($R^2 = 0.498$, $F_{1,77} = 76.36$, P < 0.001) and $Y = -7.83 \times 10^{-5} \times t + 6.24 \times 10^{-1}$ ($R^2 = 0.028$, $F_{1,93} = 2.67$, P = 0.106) for the first and second segment, respectively. The next analyses refer only to the first segment of the data where exploitation can be abstracted. b Seeds (in g) collected per gerbil for three different densities, as a function of total foraging time (s), up to t = 1,350. The slopes of the regression lines are 6.13, 3.57, and 1.57×10^{-4} (g/s) for N < 6, N = 6 and N > 6, respectively. Multiple linear regression $F_{3,81} = 206$, P < 0.001; $Y = 3.18 \times 10^{-3} \times N$ $(R^2 = 0.881,$ + 7.88 × 10⁻⁴ × t - 6.75 × 10⁻⁵ × N × t) indicates that there is a negative effect of density on seed collection rate (a significant $N \times t$ interaction term; P < 0.001). c The natural logarithm of gerbil densities vs. the natural logarithm of per-capita rate of seed collection (only for total foraging time <1,350 s). A straight line ($R^2 = 0.997$, n = 3, P = 0.033) with a negative slope indicates that the marginal effect of density on the slope decreases as predator density increases

duration (until 10% of the prey is caught). A multiple linear regression is then applied to test for the interaction between the effect of density and time. Significant results are indicative of the existence of interference competition.

Contrary to most previous studies that examined the relationship between competition and predator density without distinguishing between interference and exploitation, we suggest examining only the initial phase of such an experiment when exploitation is negligible, and thus it is possible to directly scrutinize the connection between interference and predator density.

The model we used to test the suggested experimental design and statistical procedure incorporated only basic properties of animal behavior, and clearly it does not resemble more complicated systems. It assumes that interference is relatively constant throughout the experiment and that exploitation can be neglected during the initial phase before significant reductions in prey numbers occur. Additional simplifying assumptions are homogeneity of the landscape, no phenotypic differences among predators, predator movement via correlated random walks, each predator consuming much more than a single prey item, handling time is relatively short, and predators do not change their behavior during the experiment. Furthermore, our method addresses mechanisms of interference that involve loss of foraging time, such as aggressive interactions or displays among individual predators. There may be other (albeit less common) types of interference (such as kleptoparasitism) that may not involve such loss of foraging time. In that respect our method may not point on the existence of interference.

Despite these assumptions, the described method may also be productive in field experiments and not only in controlled lab experiments. The most notable difficulty might be keeping the predator density fixed through the experiment. However, this can be easily done using field enclosures or an aviary, similarly to the gerbil experiment. This is a common method often incorporated in field studies on small mammals involving competition or foraging (e.g., Abramsky et al. 2001). Moreover, when such an experimental system does not exist or when it is not applicable to the study species (e.g., birds with large territories), one can simply document the number of predators that were involved in the experiment. When replicating this procedure several times, predator density will naturally vary. Then, mean predator number in each replication may be a sufficient estimate for predator density. Finally, food items can be artificially supplemented and later counted to calculate the predators' feeding rate.

In addition to the simulation model, we used a dataset taken from an empirical study on gerbils foraging for seeds in artificial food patches under field settings. Although this dataset was collected for another purpose, we could successfully isolate the effect of interference. Designing a similar experiment with more density levels should provide better understanding of interference competition in that system. Together, the suggested experimental design and statistical analysis distinguish between exploitation and interference in a novel and simple manner that ultimately may contribute to our understanding of the relationship between interference competition and predator density.

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