Characterizing a predator prey model to modelling social behavior towards a minority in a society

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Caracterizando un modelo predador-presa para modelar el comportamiento social hacia una minoría en una sociedad

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Abstract:
Key to the interaction of predator and prey is their use of space (patch use habitat use). The pattern of spatial overlap between predators and prey affects their encounters rates, predation rates, and, ultimately, predator-prey population and community dynamics. Hundreds of studies have shown that prey tend to avoid areas with more predators. Prey and predators would then, be negatively associated. Conversely, numerous studies taking a predator perspective have shown that predators tend to prefer areas with more prey –a positive spatial association. These responses clearly contradict.

Keywords: predator-prey model; community dynamics; social behavior.

INTERESTINGLY , a recent review found that, surprisingly, few theoretical or empirical studies have examined how the interplay between predator and prey behavioral responses to each other determines patterns of predator-prey spatial overlap. Instead theoretical and experimental studies on predator-prey behaviors typically hold one side fixed 8eg using cage predator or immobile prey), in order to focus on the behavior of the other. In nature, in many systems, both predators and prey are mobile and have the potential to engage in a behavioral response race. If preys win the race, the outcome is a negative spatial association between the two, whereas, if predators win, the result is a positive spatial association. The goal of this researcher is to provide an overview of factors that might influence the outcome of this race.

The key to the interaction of predator and prey is their use of space

Extant models predict that, when patches vary in resource availability, then both predators and prey should be more abundant in high-resource patches. That is, given a spatially variable resource base, predators and prey should exhibit a positive spatial association, and predator should win the race. No published behavioral study appears to address this prediction directly. Here, we present a new experimental study on the space race between predatory majority and minority prey. The key result was that predators and prey showed a significant negative spatial association: in essence, contrary to the prediction of the models, prey won the race. This result simulated a reconsideration of the logic underlying the basic prediction of the models. In brief, we suggest that, in existing models, predators win the race because prey are constrained by a "spatial anchor" which is essentially the fixed distributions of their resources, whereas predators have no corresponding spatial anchor.

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In contrast, in nature, the space use of both predators and prey might be influenced by various constraints, costs, and benefits. In the subsequent discussion, we outline ideas and predictions about how some of these factors might affect the outcome of the predator-prey space race. Finally, we suggested directions for future studies. Understanding social behavioral space use (habitat use, patch use) is a fundamental issue this kind of model. Among other things, space use influences interactions among members of a given species, competition between two social groups, and exposure to abiotic stressors. Most important, in the current context, space-use decisions by predators and prey determine the pattern of spatial overlap between the two that, in turn, affects predator-prey encounter rates, predation rates, and ultimately, predator-prey population and community dynamics.

Given the importance of predator-prey space use, it seems reasonable to expect behavioral social modeling to have a good idea about the predator and prey behavioral decision underlying their joint space use. In fact, though we know much about either predator or prey space-use decisions, we know surprisingly little about the behavioral ecology of their joint space use. This research summarizes our extant knowledge, and presents new data and ideas on the critical issue.

From the predator view, two large bodies of work address predator patch or habitat use. Optimal-patch-use studies address space use for individual predators, and ideal-free-distribution (IFD) studies examine space use for groups of competing predators. In either case, theory predicts and empirical studies show that predators generally concentrate their efforts in areas with more prey. Predator-prey population social modeling as the relationship with minorities. These bodies of work, however, assume the prey do not respond to predators. Indeed, many of the classic experimental studies examining predator patch decisions used immobile or barely mobile prey (e.g., flowers, eggs, pupae, or mealworms). In essence, what we know about predator behavioral decisions on space use comes large from situations in which only predator (not prey) are free to choose among patches.

From the prey view, innumerable studies show that prey tend to avoid areas with higher prediction risk. Theories on prey avoidance of high risk sites however almost always assume fixed predation regimes and typically feature one habitat with more food (for prey) in nature or more opportunities in social behavior [1] and more predators, as opposed to a safer, but lover food, habitat. Similarly, experimental studies on prey avoidance of areas with high risk typically use constrained predators. For example, predators are often caged to one side of an experimental arena (usually the side with more food for prey), while only prey are free to choose among patches.

In reality, in many natural situations, both predators and prey are free to exercise patch or habitat choice. Predators can respond to prey, and prey can respond to predators. The pattern of spatial coincidence between the two is an emergent outcome of behavioral response race between predators and prey. If predators win the race the outcome is a positive association between the two (i.e., more predators are found in areas with more prey; Figure 1A). If, however, prey wins the race, then the two are negatively associated (i.e., prey are more abundant in areas with fewer predators; see Figure 1A). The two counteracting responses might have canceling effects (i.e., there might be no winner). The outcome would then be no significant spatial association, despite active behavioral responses by both sides. The "winner-loser" terminology deserves some clarification. In isolation from other fitness factors, predators and prey have opposite interests. Predators do best by foraging where there are more prey, and prey do best by avoiding areas with more predators. Thus, in the absence of other considerations, it is reasonable to say that if predators and prey are found together, predators have "won" the race, whereas, if they are found apart, then prey have "won" the race. The "loser" has lower fitness than it would have had with another pattern of space use. However, if other important fitness factors are included, then either a positive or negative pattern of spatial association can arise even when both predators and prey exhibit optimal space use. For example, some sites might have an abiotic environment that is highly stressful for prey, but not for predators. The optimal prey behavior might be to stay in non stressful sites even if doing so allows predators to aggregate with them.

One view of this situation might be that, because both sides are exhibiting optimal space use, there is no winner or loser. I will take a different view. In my use of the terminology, we will say that, even if prey is exhibiting optimal space use, the external constraint.

Although the models differ substantially in details, some simple general results emerge. Notably, in a broad range of scenarios, given a patchy distribution of resources, predators are predicted to aggregate in more productive patches with more resources. Given that predators do not consume the social resources, this is a fascinating result that was called a "leapfrog effect". In contrast, although prey are also predicted to be more abundant in more productive patches, they are typically expected to be more uniformly distributed than predators The basic logic is that, without social ene-

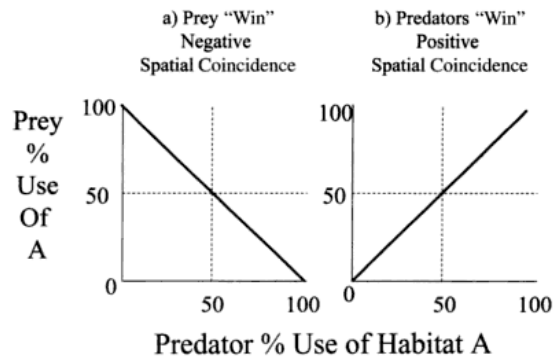

Figura 1. Spatial correlation between predators and prey as an emergent outcome of a predator-prey race (A) If prey are successful in avoiding predators (i.e., if prey win the space race between predators and prey), then the outcome is a negative association between the two. (B) if predators are successful avoiding predators (i.e., if prey win the space), then the result is a positive spatial association.

mies should prefer areas with higher opportunities to development. The majority people should tend also prefer those highly social productive sites. This preference should tend to drive social minorities out of those patches; however, given no constraints on a Social Majority's in space. Because social minorities must still feed, under a broad range of conditions, they should ultimately at least somewhat prefer the more productive sites. In turn, social majorities should prefer those sites. Note that the result is a positive association between predators and prey. Both prefer patches with more resources (social opportunities). In the terminology of contests, predators are predicted to "win" the race. Most Social Modeling researchers propose solve for the evolutionarily stable outcome, but do not address the movements of people in and out of patches that underlie the equilibrium outcome. Interestingly, models that track social movements following simple, sensible (but not necessarily optimal) rules also predict that both majorities' people and minorities' people should be more abundant in patches with greater social opportunities availability. For example, [2] derived this result with models in which all people immigrate passively into patches, but social majorities emigration rates are higher when social majorities are scarce. Social minorities' emigration rates are higher when either social majorities are more abundant, or social opportunities are less abundant.

More complex models have examined numerous aspects of reality beyond the simplest scenario, including (a) more complex and variable degrees of competition among predators or among prey [4] (b) nonlinear functional responses [4] (c) social costs [3] (d) state dependences [3] (e) two types of predators represented as social majorities [5] and intraguild social blockade [6] and (f) mobile resources that also avoid consumption [7] Finally, [8] have explicitly addressed the population-dynamic consequences of the predator-prey space race. The notion that predators should win the race is intriguing. Why should this outcome occur? My interpretation of the basic intuition is as follows: In the absence of external constraints or costs, conflict games (predator-prey games, male-female conflict games) often have no equilibrium. External constraints, however, stabilize the system If only one side has a constraint (or has a stronger constraint), then the order side wins the race In the predator-prey space race, a key type of external constraint is a spatial anchor, which is to say, essentially, any reason, outside the predator-prey race per se, for which either predators or prey should prefer some patches over others. In the models already described, prey has a spatial anchor: the spatial distribution of their resources. Predators have no spatial anchor. As a result, predators win the theoretical race.

In some existing models, predators also have a spatial anchor which considered the situation in which predators have higher inherent attack success in some patches than in others. The sites with low predator attack success then function as refuges for prey. The models predicted that, if patches differ in predator attack success (i.e., in prey safety) but not in resource value then predators and prey should exhibit a negative spatial association: prey should win the race. Most prey should hide in the social refuge sites. Because predators suffer poor attack success in refuge sites to stay save, they do not aggregate there, ever though prey are more abundant in those sites. Thus, when predators have a spatial anchor prey win the space race.

Overall, the most basic prediction emerging from most of the models is that, if patches vary only in resource value, then predators and prey should both aggregate in patches with high resource productivity. Predators and prey should exhibit a positive spatial association (i.e., predators should win the predator-prey space race). If, however, patches vary in inherent predator attack success (or, conversely, in prey safety) and not in resource productivity, then predators and prey should be negatively associated. Prey should be in social refuge sites where predators suffer low attack success, whereas predators should be in sites where they enjoy higher attack success, even though most prey are found in the other patches.

RESULTS AND SPECIFIC DISCUSSION

Figure 2 shows the proportion of predator or prey on the high-resource side in the different treatment. A one-way ANOVA showed that tadpole space use was significantly influenced by treatments (F=22.47; df=217; p¡.001). In the absence of predators, tadpoles spent about 75% of their time on the high-resource side This result differs significantly from random (50%; t=3.16. df=3, p=.05), but does not differ significantly from matching, as predicted by simple IFD theory (80%; t=0.59, p¿.50). As expected, the presence of a majority fenced into the high resource side caused a large, significant decrease in tapdole use of the high-resource side (Dunnet's test: p¡.05). In the absence of prey, a social majority use of the two halves of the tank did not differ significantly from random (t=0.83, df=3, p¿.40).

As predicted, when both kind of predators and prey were free-ranging, tadpoles showed a preference for the high-resource side (t=2.67, df=11, p=.01). However, contrary to predictions, the social majority did not aggregate on the side with high sources (and, on average, higher tadpole densities). Instead, the social majority's patch use did not significantly differ from random (t=074, df=11, p¿.40).

Figure 3 shows the relationship between the proportions of prey in the high-resource side and the proportion of predators in the high-resource side. Each point represents the mean value for a given replicate when observations are

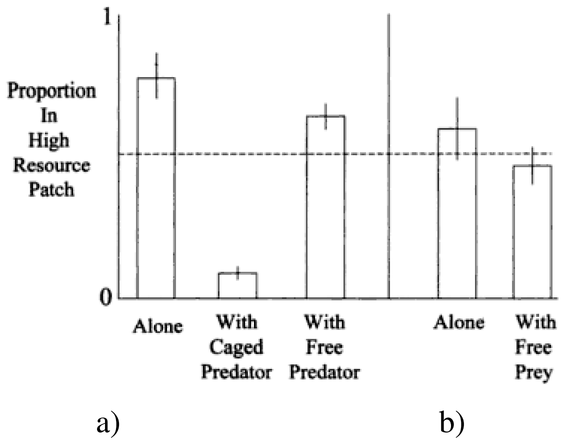

Figura 2. Proportion of predatory social majority or social minority prey in the high-resource (HR) side of an experimental arena , when prey or predators are held in single-social groups, or with the other social groups. Predators were either caged or free-ranging. Means and standard errors are shown. The horizontal dashed line is the null expectation (0.50).

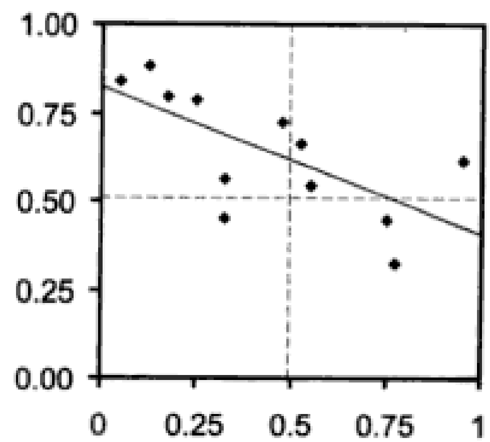

Figura 3. Proportion of a minority on HR side.

pooled over time. The y-intercept, 0.825, is the proportion of prey on the high-resource side if all predators are on the low-resource side. As expected, this value is significantly greater than random (t=4.45, p¡.01). According to the regression line, if predators are uniformly distributed (50% on each side), then, as one might expect, prey show a slight preference for the high-resource side. Most interestingly, contrary to the prediction of extant models, predator and prey distributions were negatively associated (r=-.69, N=12, p¡.001). If predators spent more time on the high-resource side, then prey spent less time on that side. Of course, this result is not entirely unanticipated. It simply means that prey avoid predators (i.e., that prey win the predator-prey space race). The result is only unexpected in the sense that existing models predict that in this experimental scenario, predators should win the race. Overall, prey behavior generally fitted adaptive expectations. In the absence of predators, prey space use matched prey resource base. When predators were present and fenced into the high-resource side, prey avoided predators. When freely roaming predators spent most of their time on the low-resource side, prey heavily favored the side that had both more resources and greater safety. When freely roaming predators spent more time on the high—resource side, prey spent less time on that side (i.e., prey avoided freely roaming predators). In contrast, predator behavior did not match adaptive expectations Predators did not tend to aggregate in areas with more prey.

For the treatment in which both predators and prey are free-ranging, the correlation between predator and prey use of the high-resource side. In Figure 3, each point shows the mean space use for one replicate. Pearson's r=0.69, p¡.001. Following the intuition outlined earlier, several types of anchors or constraints could possibly explain why prey won this race. First predatory social majority interfered with each other, thus increasing the cost of predator aggregation in areas with more prey. Second, because predators were much larger and more active than prey, prey might have had better information about predator space use than vice versa. Third, after predators had consumed a few social opportunities from prey had less social opportunities.

A Broader Look at Factors influencing the Social space race

In a broad view, we suggest that the outcome of the predator-prey space race should depend on (*a*) the relative abilities of predators and prey to respond to each other spatially, (*b*) the relative abilities of predators and prey to respond to each other spatially, (*c*) the relative costs of responding, and (*d*) the relative benefits of responding (Tabla 1).

Tabla 1. Factors that should influence the outcome of the predator-prey race.

Relative abilities to respond
Movement ability Information ability processing
Relative costs of responding
Movement costs Conflicting fitness needs- spatial anchors
Benefits of responding
"Life-dinner" principle Energy state or risk of starvation Prey or predator density

As noted earlier, in the absence of external constraints, or anchors, the race might not have a clear, logical winner. Instead patterns of spatial association might fluctuate with no stable equilibrium.

In our future research, we will implement an ubiquitous model to determine discrimination in a society and legal effects associated with this, we will implement a Brazilian Nut Effect.

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