

On the Prudent Predator: Individual-based Modeling of Multilevel Selection and the Evolution of Predatory Restraint

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Abstract

Individual selection favors that predator which can most efficiently turn its prey into increased reproductive capacity. But any species that becomes too successful in this game sows the seed of its own demise; for its progeny may be delivered into an environment where prey populations are depleted, and starvation a danger. From this derives a compensatory evolutionary pull toward moderation. The latter effect derives from a cost that is shared generally by the community that claims a common prey population. A widely accepted argument from classical evolutionary theory holds that the selective force of such group effects is likely to be weak and slow-acting compared to the efficiency of individual selection. We offer a numerical simulation in defiance of this wisdom, demonstrating how under general assumptions and a wide range of parameter values, predatory restraint may evolve as a group adaptation.

1 Introduction

Do animal populations self-regulate for the sake of demographic stability? Over-exploitation of food resources may threaten the viability of the species on which a predator depends, leading to extinction of both predator and prey. But maintaining consumption within sustainable limits requires cooperation, explicit or implicit, as individual fitness may be diminished by any moderation of consumption. Classical population genetics, based on the maximization of individual reproductive potential, supports the conclusion that the evolution of population limits as an adaptation is improbable. Field studies and the experience of wildlife managers suggest that population regulation may be a reality, though clean tests of group adaptation are rare. We report the results of simulation studies, indicating one mechanism by which predator restraint and population regulation may evolve.

Population control is a stark example of strong conflicting interests, setting the individual against the group. It is not surprising that this issue has played a key role in a historical debate concerning the viability of group selection as an evolutionary force. Evidence for the thesis was first described comprehensively by Wynne-Edwards [1962],

but a new breed of quantitative evolutionary theorists met his claims with skepticism bordering on derision [Williams 1966, Ghiselin 1974, Maynard Smith 1976a]. Williams argued persuasively that populations with large numbers of altruistic individuals would be susceptible to invasion by selfish individuals. Maynard Smith noted that the high extinction rate required for limiting the spread of selfish individuals from invaded populations would be unlikely to attain in nature.

But even as the concept of group selection lost currency in circles of theoretical evolution, minority theorists were already suggesting ways that nature might find paths to those adaptations that would succeed at higher levels of organization, over longer periods of time. Multilevel selection theory, developed by Wilson [1975, 1983] on the foundation of the Price [1970] Equation, seeks to predict the outcome when selection at the individual and the group level are at odds. But a key parameter in this calculation is the relatedness (or genetic covariance) within groups [Hamilton 1964], which is difficult to measure or to predict. Numerical simulations provided a complementary way to explore a variety of assumptions about population dynamics within and among groups. An early simulation by Gilpin [1975] made the most of limited computer resources, to demonstrate ways that predatory restraint might evolve, and predator-prey population dynamics might be damped.

Gilpin's model consisted of predator-prey populations in spatially distributed patches connected by predator migration. He used difference equations to track the frequencies of two genes, for restrained and unrestrained predation, across an ensemble of patches. Gilpin's model successfully evolves prudent predation, and he argued in his monograph that his assumptions were conservative and generally applicable, his results realistic. Nevertheless, few evolutionary theorists of the era were ready to accept his conclusions.

There is abundant evidence from field and experimental studies indicating the reality of population self-regulation. Fruitflies and nematodes appear to suppress their fertility in response to crowding, even with abundant nutrition [Kenyon and Guarente, 2000]. Observations in the wild suggest that rabbits exhibit the same response [Bittner & Chapman 1981]. Arctic caribou in a fragile tundra environment breed less frequently than animals of the same species further south [Wynne-Edwards 1962]. When deer are plentiful, wolves kill more deer and consume less of each [Kolenosky 1972]. And the accumulated anecdotal experience of wildlife managers has created in that culture a belief that predator populations self-regulate [Nudds 1987]. For each of these examples, evidence is not clean enough to rule out explanations from individual self-interest, which are deemed theoretically more conservative.

Recent computer simulations suggest a renewed examination of the theoretical issue. Pepper and Smuts [2001] have modeled competing populations of restrained and unrestrained foragers, interacting in an environment where the only group structure is imposed by isolated patches of available food. Like Gilpin, they report a range of parameter values under which the restrained foragers can prevail. Rand et al [1995] have modeled a generic host-pathogen system using a simple CA model. They evolve a gene for pathogen transmissibility, and find that above a critical value, the pathogen experiences local extinctions, creating a void that is re-filled from the boundary by

pathogens with lower transmissibility. Haraguchi and Sasaki [2000], and Rauch et. al. [2002] each report similar results, with enriched detail. These models are conceptual kin to our own, but with simpler rules and a map that allows a maximum of one predator per grid site. Most recently, models by Pels et al [2002] have sought to characterize environments under which predator evolution does not lead to global extinction.

2 The Model

We have implemented an individual-based model that features competition among predators within each site on an $n \times n$ viscous grid. Sites are statistically identical and adjacent grid sites are connected by slow, random migration of both predators and prey, allowing for between-group competition in exportation of migrants. *Migration* rates (the same for predators and prey) control the probability that each individual would migrate to a von Neumann neighbor in a given time step. Within each site, predators reproduce in proportion to the prey that they capture. Their ability to capture prey is controlled by a single gene, inherited with the chance of mutation.

Prey are programmed individually so as to conform collectively to a logistic population dynamic. In each time step, they acquire *maturity* points, with probability inverse proportion to the current prey population at the site. When a fixed number of points is accumulated, the prey reproduces, simply turning into two prey, each with zero points. Except for point count, preys are indistinguishable. Prey interact in each time step with each predator at the same grid site, and the interaction carries a risk of death for the prey in proportion to the predator's *appetite*. This is the only manner in which prey may die.

A single gene, an integer variable controlling their *appetite*, characterizes predators. Predators are programmed to keep track internally of an *energy* reserve. A fixed quantity of energy (*cost-of-living*) is lost in each time step. If *energy* falls to zero, the predator dies; if *energy* reaches a *threshold* value, the predator reproduces, passing half its *energy* to an offspring. The *appetite* gene is inherited, with a small *mutation* probability that it will be increased or decreased by one unit. There is also a fixed probability per time step that each predator might experience *accidental-death*.

We hypothesize that local extinction and migration serves as a tempering influence on the individual selection pressure for unbounded *appetite*. This is because within each grid site, predators with higher *appetite* reproduce at a faster rate. But as *appetite* evolves to values that are unsustainably high, the prey population is depleted and the predators starve. This site may await prey migration from a neighboring site before it can support predators that migrate in from a neighboring site. The migrants are likely to come from a site that has not yet reached unsustainable levels of *appetite*. Thus, local extinction and migration serves as a tempering influence on the individual selection pressure for unbounded *appetite*.

3 Relationship of model to the Lotka-Volterra equations

Our model has a direct relationship with the Lotka-Volterra equations. The relationship to Lotka-Volterra equations has informed our exploration of parameter space for our model. The commonly accepted generalization of the Lotka-Volterra equations constituting three dynamic variables, x - the prey population, and y -the predator population and t -time, can be written as:

$$\frac{d \ln(x)}{dt} = r(1 - x/K) - cy \quad \frac{d \ln(y)}{dt} = bcx - d \quad (3.1)$$

Here, the five parameters are: r - the exponential growth rate of the prey population, capped by a logistic population ceiling, K - the population scale of prey species, c - the capture rate per individual predator-prey encounter, b - the predator population growth associated with each capture event, d - the predator death rate, conventionally taken as constant and independent of other conditions.

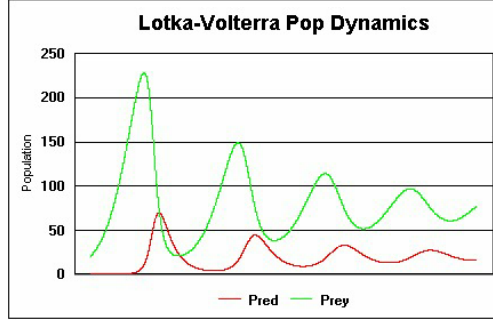


Figure 1: Lotka-Volterra population dynamics, with damping due to the logistic limit K to prey population growth.

With the added parameter K , the L-V dynamic variables follow a damped version of the familiar periodic curves, relaxing exponentially toward their steady state values x_o and y_o with a decay time of Q cycles (Figure 1), given by:

$$x_o = \frac{d}{bc} \quad y_o = \frac{r}{c} \left(1 - \frac{d}{bcK}\right) \quad Q = \frac{K}{x_o} = \frac{bcK}{2d}$$

Although our model is individual-based, a correspondence can be seen between the model parameters and the L-V parameters. The crowding factor K that inhibits prey reproduction in our model corresponds closely to the logistic K , which is also the K of the L-V equation. *Maturity* is the doubling time for deer population, and should relate to r of L-V simply by $r = \ln(2)/maturity$

The *appetite* variable, which is the target of evolution in our model, corresponds closely to the capture rate c of L-V. Since the accumulation of $threshold/2$, is sufficient to create a new predator, we take this as an equivalent to the L-V parameter b , related by: $b = 2 * meal / threshold$.

A predator may die due to *accidental-death* kills, one predator at a time, and this takes away the energy accumulated toward creating another. A reasonable estimate is to call this a loss of $3/2$ predators. In addition, *cost-of-living* is the energy that is subtracted from each predator in each time step, so the fraction of a predator lost is $2 * cost-of-living / threshold$. Putting these together, we have a relationship to the parameter d in equation 4.1: $d = 3/2 * accidental-death + 2 * cost-of-living / threshold$.

4 Experiments

Gilpin's major result was that "over a wide range of parameter values and initializations, group selection can prevail against individual selection and send gene a , the less efficient exploitation gene, to fixation throughout an ensemble of predator populations." In the present model, selection is not restricted to an either-or choice, but is permitted a

range of the *appetite* gene corresponding to exploitation efficiency. We find that over a wide range of parameter values, group selection can compete effectively with individual selection to temper the pressure toward an unsustainable level of exploitation, and establish a steady state that is (globally) stable over many generations and many site extinction times.

4.1 Effect of varying migration rate

Interaction among groups is mediated by the migration rate. For values of the migration parameter that are too high, inter-site differences are washed out, so there can be no effective competition between groups. The result is that *appetite* increases without bound, and the entire predator population is driven to extinction. Typically, a few prey

survive to regenerate full population of the grid. In our model, *migration* levels higher than ~0.03 led to this scenario. (This represents the probability of a given predator emigrating from the site in a given time step.)

If the migration parameter is too low, the sites are effectively isolated. One site may evolve an unsustainably high level of *appetite*, and disappear; before it can be reseeded, its neighbor sites may also evolve to extinction. Again, in our model a few prey escape and survive to repopulate the grid. This scenario prevailed for *migration* values less than ~0.0002. a few runs, we allowed the two species to have separate *migration* rates. High prey migration rates posed a substantial danger to stability, and selection for a moderate *appetite*; predator *migration* rates were associated with runaway *appetite* only at levels an order of magnitude higher. Some results for a range of *migration* rates are plotted in Figures 2a - 2d.

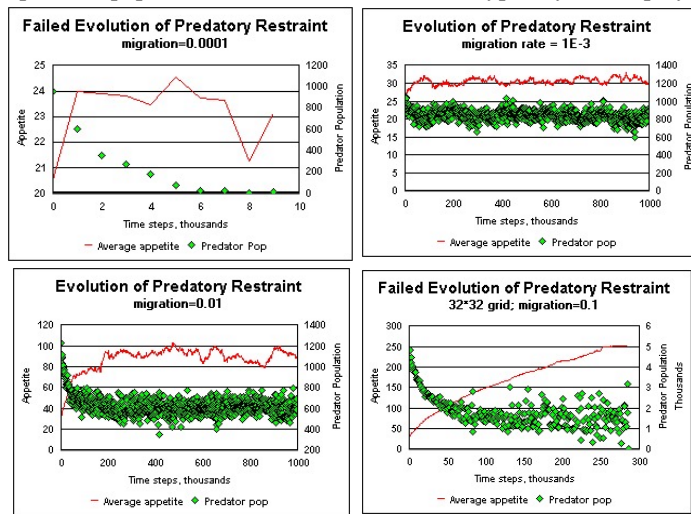


Figure 2: Evolution of predatory restraint with migration

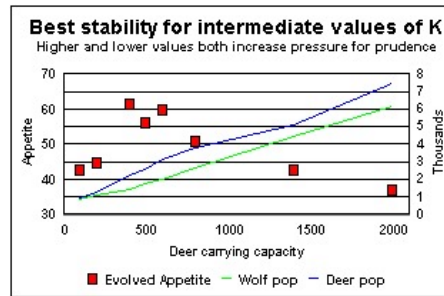


Figure 3: Appetite and crowding

Thus we find *appetite* remains stably enough within bounds over two orders of magnitude in the *migration* parameter. More complex and realistic scenarios in which migration rates are sometimes within and sometimes outside this range are explored in Section 5.5 below.

4.2 Effect of varying per-site carrying capacity

The parameter K controls the maximum number of prey that can be supported at a site in the absence of predation. Both total predator and prey populations increase quasi-linearly with K . (Figure 3.) Selection pressure for moderating *appetite* is lowest for intermediate values of K . When K is low, the prey population is vulnerable to extinction via random fluctuations; but large values of K correspond to insufficient damping of the wide population swings characteristic of Lotka-Volterra dynamics. Predator population maxima increase linearly with K , but population minima actually decrease exponentially for large values of K . Hence group selection pressure for moderating *appetite* increases for larger sites. The case of mixed high- and low- K ensembles is explored below in Section 4.5.

4.3 Relative time scales of predator and prey life histories

There are two parameters of the L-V equations that scale time evolution: r is the time scale for exponential increase of the prey population in the absence of predation, and d is the time scale for exponential extinction of the predator population in the absence of food. Together, these two rates determines the time scale on which L-V dynamics unfolds. The ratio of $r:d$ is also important. The dynamic is stabilized by a large ratio corresponding to a prey life cycle that is shorter than the predator; as the ratio decreases, evolved *appetite* becomes smaller and smaller to compensate; for ratios $r:d \ll 1$, the dynamic is unstable, and will not support a steady-state at all.

4.4 Variable mutation rate

Mutation rate itself may be an object of evolution. With a high mutation rate, *appetite* values can only be stabilized by an ongoing tension between within-group selection and between-group selection, a conflict which exacts a cost in over-predation and local extinctions. We added a second predator gene that controls the rate of mutation in the *appetite* gene. (The mutation rate gene itself is inherited with a fixed mutation rate.) After a stable *appetite* value was established, the mutation rate controlled by this gene evolved to much lower values, with concomitant benefits for the predator population: *appetite* stabilized at a slightly lower value, leading to higher prey populations, which supported higher predator populations; *appetite* values and population levels were both more stable; there were fewer local extinctions.

4.5 Allowing parameters to vary randomly across the grid

In seeking to apply model results in the real biosphere, the question arises whether qualitative results depend critically on parameters choices, or whether the results are

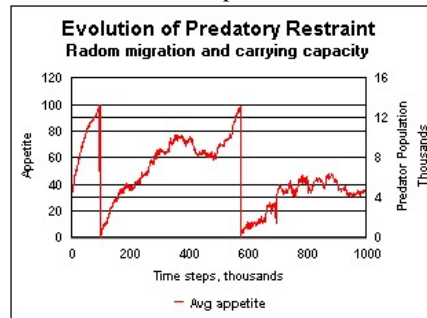


Figure 4: Evolution of predatory restraint

more robust and likely to apply more generally. To aid in addressing this question, we have run the model with random values of two key parameters, assigned site-by-site across the grid. First, carrying capacity K was assigned random values at different sites, following a logarithmic distribution from a minimum of 10 to a maximum of 1000, on a 32*32 site grid. *Appetite* was found to evolve to a sustainable value and fluctuate within limits about that value. In another series of experiments, the *migration* connections between adjacent sites were programmed to random values, varying (log distribution) from a minimum of 10^{-5} to a maximum of 10^{-1} per time step. (In order to keep migration from emptying some sites and accumulating population at others, random migration was kept symmetrical for forward and reverse paths between the same pair of sites.) *Appetite* values fluctuated more widely than in the previous experiment, varying K , but population fluctuations were a little less wide. A broader range of random values, 10^{-6} to 1, produced runs in which K climbed out of control, then a population crash brought K values back to a sustainable range, which was relatively stable through hundreds of thousands of time steps. We also ran cases in which both K and *migration* varied randomly across the grid, and results were comparable to those just described (Figure 4).

5 Summary and conclusions

The entire corpus of population genetics is founded on the principle of differential reproduction: that the allele with the highest reproductive potential will spread through a population, eventually to the exclusion of all others. Our results, like the work of Gilpin a generation ago, call that fundamental assumption into question. If individual reproductive potential is not maximized, a great part of the body of evolutionary theory will have to be reconsidered. Our model is considerably more general and more explicit than that of Gilpin (1975), but our conclusions are similar. We simulate situations in which group selection is able to temper individual selection, keeping individual reproductive potential from rising so far as to threaten demographic stability.

We also have uncovered hints of two intriguing connections between model results and field studies: First, in our simulations, it appears that population dynamics are stabilized when the fundamental time scale of the prey species is shorter than that of the predator. This suggests a connection to the observation that predator life spans are typically somewhat longer than those of their prey. Second, it is intuitively expected that small population numbers can lead to fluctuations that cause statistical extinctions; our results indicate that large, unstructured populations may also lead to unstable population dynamics. The mechanism for this unexpected phenomenon is best understood in terms of the parameter we have called Q (section 3) which plays the role of a damping constant for the amplitude of L-V population cycles. Roughly speaking, the dynamic is driven by too large a difference between the steady-state prey population levels in the presence and in the absence of predators.

Results from the experiment with variable mutation rate illustrate the principle that any allele established via group selection faces constant challenge from individual selection, and this process carries a cost which is borne by the population. There will generally be a selective advantage (again, requiring group selection) in preventing reverse mutations toward alleles that are advantageous to the individual at the expense of the group.

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