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 danger 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.

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.

Historic context

Population control is a stark example of strong conflicting interests, pitting 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). Williams argued persuasively that populations with large numbers of altruistic individuals would be susceptible to invasion by selfish individuals. Maynard Smith (1964, 1976) 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, 1997) 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 used difference equations to track the frequencies of two genes, for restrained and unrestrained predation, across an ensemble of patches, linked by random migration. He found that this system was robust in its ability to evolve prudent predation, and 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.

Field evidence

There is abundant suggestive evidence from field and experimental studies indicating the reality of population self-regulation. Fruitflies and nematodes appear to sup-

press their fertility in response to crowding, even with abundant nutrition (Guarente & Kenyon 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 models of predator restraint

Recent computer simulations suggest a renewed examination of the theoretical issue. Pepper and Smutts (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 refilled from the boundary by pathogens with lower transmissibility. Haraguchi and Sasaki (2000), and Rauch and Bar-Yam (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.

Description of Our Model

We have implemented an individual-based model that features competition among predators within each site on an $n \times n$ viscous grid. Within each site, predators reproduce in proportion to the prey that they capture. Their rate of prey capture is controlled by a single gene (*appetite*). Adjacent grid sites are connected by slow, random migration of both predators and prey, allowing for between-group competition in exportation of migrants.

Prey and predator behaviors

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, prey 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.

Predator behaviors

Predators are characterized by a single gene, an integer variable controlling their *appetite*. 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*.

Global aspects of the ensemble

Sites are statistically identical, and are arrayed on a cartesian grid, typically 16×16 or 32×32. *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.

Heuristic dynamics of the model

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. The site may have a small residual population of prey, or it may have to await prey migration from a neighboring site. Once a prey population is established, the site can again support predators that migrate in from a neighboring site. The migrants are likely to come from a site which has not yet reached unsustainable levels of *appetite*, so local extinction and migration serves as a tempering influence on the individual selection pressure for unbounded *appetite*.

Relationship to Lotka-Volterra Equations

The Lotka-Voltera equations can be written

$$\begin{aligned}
\frac{d\ln(x)}{dt} &= r(1 - x/K) - cy \\
\frac{d\ln(y)}{dt} &= bcx - d
\end{aligned} \tag{1}$$

The three dynamic variables are:

x, the prey population

y, the predator population

t, time

and the five parameters are:

r**,** the exponential growth rate of the prey population, capped by a logistic population ceiling, K

K**,** the population scale of prey species. Though it was not originally part of Lotka or Voltera's formulation, it has become accepted as a common modification, because it is a realistic generalization that allows for solutions that oscillate less wildly.

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

Relationship of individual behaviors to population behaviors in Lotka-Voltera

The present model is individual-based, so our parameters relate to individual behaviors; nevertheless, a correspondence can be seen between the model parameters and the L-V parameters. Our parameters are:

maturity, the quantity of points accumulated by a prey that triggers reproduction

threshold, the quantity of energy accumulated by a predator to trigger reproduction

accidental-death, the probability per time step of a predator dying when he is not starving

cost-of-living, an amount of energy lost by each predator in each time step, meal, the quantity of predator energy credited to each successful act of predation

K**,** crowding factor, inhibiting prey reproduction

Some of the connections between our individual-based parameters and the population dynamic parameters of L-V are clear; others are less obvious. 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 prey 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.

The other correspondences are more subtle. The L-V variables are numbers of organisms; our model also tracks internal energy of the predators. How much energy is equivalent to one animal? An accumulation of *threshold/2*, is sufficient to create a new predator, so we

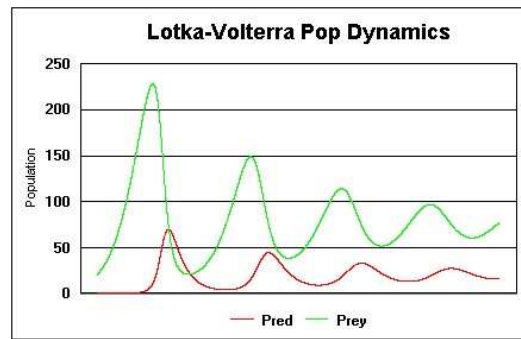

Figure 1: Lotka-Voltera population dynamics, showing the familiar predator and prey cycles, with damping due to the logistic limit K to prey population growth. Both predator and prey populations tend to steady-state values over time.

take this as an equivalent. Then the L-V parameter b, which controls what fraction of a predator is created each time a prey is consumed, may be related to our parameters by

$$b = 2 \times meal/threshold$$

Corresponding to the L-V death rate, the parameter d, we have two ways in which a predator may die; *accidental-death* kills one predator at a time, but also takes with him the energy he may have 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 $2 \times cost - of - living/threshold$. Putting these together, we have

$$d = 3/2 \times accidental - death + 2 \times cost - of - living/threshold$$

Lotka-Voltera dynamics

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).

The values x_o and y_o can be found algebraically by setting both logarithmic derivatives of Eqn 1 to zero:

$$
\begin{aligned}
x_o &= d/(bc) \\
y_o &= (r/c)(1 - d/(bcK))
\end{aligned}
$$

The damping parameter Q is given by

$$Q = K/x_o = bcK/2d$$

This analysis has informed our exploration of parameter space for the model. x_o and y_o should simply scale the predator and prey population sizes, while Q should
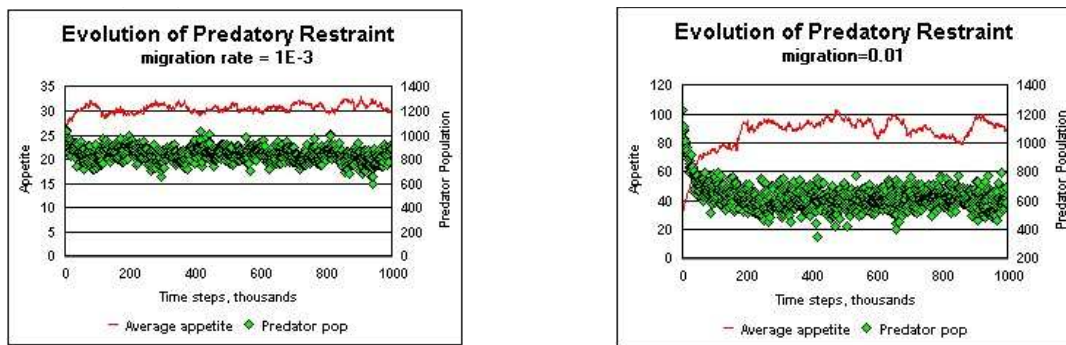
Figure 2: For intermediate values of the migration parameter, the appetite gene is found to stabilize at a moderate value, and populations fluctuate within limits.
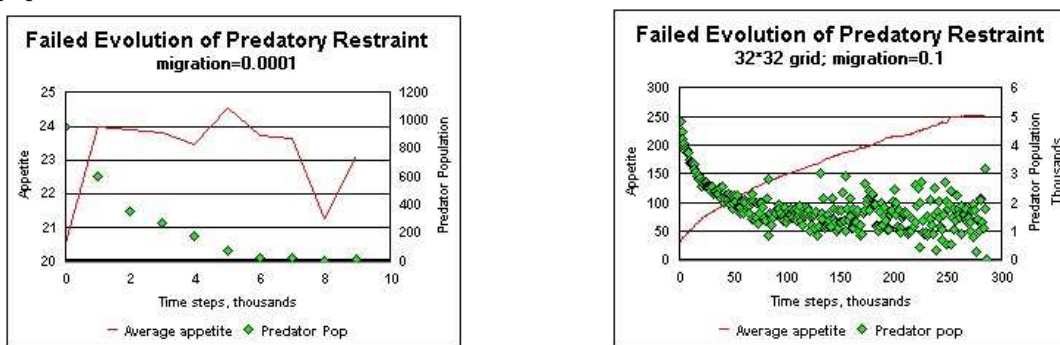

Figure 3: For values of the migration parameter that are too low, the population quickly drives itself to extinction; for values that are too high, the appetite gene increases without bound, in a grid that is dense with prey but mostly empty of predators.

control the dynamic stability; large Q (high K) leads to an unstable dynamic, in which predators must be more conservative to avoid extinction. We have also explored the response to r and d, the dynamic time scales associated with prey and predator populations, respectively; the ratio of these two time scales is a dimensionless parameter that also has an interesting effect. (The other variable which we have explored in our analysis is migration rate, which is a property of the ensemble rather than the site dynamics, and hence has no analog within L-V.)

Confirming the viability of group selection

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 with bounded appetite that is (globally) stable over many generations and many site extinction times.

Effect of varying migration rate

Interaction among groups is mediated by the migration rate. For values of the migration parameter that are too high, the entire ensemble behaves as a single population. 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 re-seeded, 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.

In a few runs, we allowed the two species to have separate *migration* rates. High prey migration rates posed a
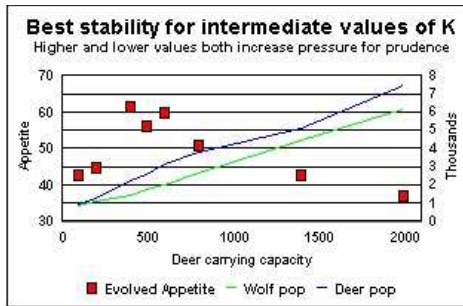
Figure 4: The carrying capacity per site, K, controls steady-state prey population linearly, as we would expect. But evolved appetite exhibits a surprising response, declining for values that are either too high or too low. Low K is inherently unstable because small numbers may fluctuate to zero; high K implies high Q, which decreases the stability of L-V population dynamics.

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 2 – 3.

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 below.

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 4) 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-Voltera 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.

Relative time scales of pred 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 determine 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 $r/d \lesssim 1$, the dynamic is unstable, and will not support a steady-state at all.

Territoriality

Territoriality is one mechanism by which predators in nature limit their numbers. To the extent that the owner of a site successfully keeps his competitors at bay, the mechanism is adequately explained by individual selection; but to the extent that the disenfranchised passively accept the system, it can only be supported by group selection.

We modified the model to include the rule that predator migration would proceed only into sites that had no existing predator population. The result was that appetite stabilized at a value about half of that which evolved when territoriality was not included. Total predator and prey populations were both increased by territoriality.

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.

Letting parameters 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 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
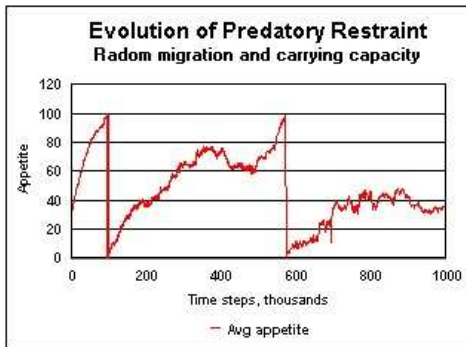
Figure 5: With randomly varying values of both carrying capacity K and migration rate in the ensemble, we find that appetite can evolve dangerously high, causing population crashes that allow appetite to climb once more from low values.

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. *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 begin another climb. We also ran cases in which both K and *migration* varied randomly across the grid, and results were comparable to those just described (Figure 5).

Summary and conclusions

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. Evidence concerning the extent to which this happens in nature is both equivocal and controversial. To a field biologist, it may seem obvious that populations are regulating themselves in the interest of long-term stability; however mechanisms that involve individual self-interest in an indirect way are difficult to exclude. Most field biologists have heard that group selection is out of favor among evolutionary theorists; but few have a basic appreciation for the way in which the short-term interest of the individual can be deeply at odds with the long-term survival of the species (Nudds 1987, for instance).

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 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. In real biological systems, there is evidence that chromosomes are structured so as to suppress certain mutations and enhance the frequency of others, and evidence that mutation rate may be subject to stabilizing selection (Sniegowski, Gerrish, & Lenski 1997).

Generality and scope of application

Abrams (2000) emphasizes that most animals are predators in that they depend for nourishment on the culling of animal or plant populations. Every living thing is part of a local ecosystem, and its short-term interest in maximally exploiting that ecosystem is balanced by the long-term interest of its relatives and its progeny in maintaining the productivity of that ecosystem. Thus it is possible that the results of our model could find application that is nearly universal in scope.

Acknowledgements

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