Joint Evolution of Predator Body Size and Prey-Size Preference

Tineke Troost

Department of Theoretical Biology,
Vrije Universiteit Amsterdam, The Netherlands

Goal

To study how patterns of predator size and prey-size preference depend on ecological and environmental parameters.

Background and motivation

The range of body sizes encountered in nature is enormous. A bacterium with full physiological machinery has a volume of 0.25 x 10^{-18} m^3, while a blue whale has a volume up to 135 m^3. These body sizes are associated with the different scales in time and space in which the organisms live, and they reflect the differences in physiological processes and life histories. A similarly wide range is found in the prey-size preference of these organisms. This becomes evident when considering, for example, whales feeding on plankton and hyena eating zebra.

Although body size and prey-size preference are essential properties determining the structure of a community, general rules that relate the two are not known. Several studies have been done to find prey-size preferences and to relate these to the size of the predator. In these studies various mechanisms have been proposed that attempt to explain such size-selective prey selection patterns. These include passive selection mechanisms such as ‘prey visibility’, in which the visibility and thus the vulnerability of the prey are assumed to increase with its size (Svensson, 1997; Rincon and Loboncervia, 1995). Another passive selection mechanism is ‘gape limitation’ of the predator, i.e. the restriction on prey-size choice that is imposed by the predator’s mouth size or morphology (Karpouzi and Stergiou, 2003; Mehner et al., 1998; Rincon and Loboncervia, 1995; Forsman, 1996). In some cases also the prey abundance or availability is found to affect the predator’s selectivity (Pryor and Epifanio, 1993; Rincon and Loboncervia, 1995; Forsman, 1996).

Active selection mechanisms, on the other hand, underlie ‘optimal foraging theory’, which assumes that predators select prey sizes that provide the best energy returns. This may for example be done by avoiding prey with high evasion capabilities (Manatunge and Aseada, 1998), by preying disproportionally on young, sick, or old individuals (Husseman et al., 2003), by selecting large prey because of their higher energy or nutrient content (Kristiansen et al., 2000; Rytkonen et al., 1998) or by selecting small prey when these are more profitable due to small handling times (Turesson et al., 2002; Ellison and Gibson, 1997). The energy return, however, does not only depend on the size of the prey, but also on the size of the predator. The size of the predator is thought to positively affect properties like prey handling ability and prey encounter rate. A large body size may also increase the range of possible prey sizes, and the probability of survival in times of starvation. On the other hand, a large body implies large maintenance requirements.

Although many studies have been carried out to find relations between predator size and prey-size preference, results vary both within and between predator-prey systems. Extracting from these studies general rules explaining these differences is very difficult. In this project we therefore use a modeling approach to study how predator size and prey-size preference interact and how patterns of predator size and prey-size preference depend on environmental parameters, such as food availability, and on ecological parameters, such as encounter rate and handling time. The modeling approach provides us with the possibility to test the effects of several (combinations of) parameters, which may correspond to various predator-prey systems. Results could provide insight in the factors that determine the evolutionary outcomes of predator sizes and corresponding prey-size preferences and may explain some of the patterns observed in nature. This may lead to a better understanding of the structure of natural communities.

Research questions

We will study the evolutionary outcomes of the joint evolution of predator body size and prey-size preference. The study will focus on two questions.

First, how do patterns of predator size and prey-size preference depend on *environmental* parameters such as food availability and prey-size distribution? It is hypothesized that if food is abundant, predators will evolve to have a larger body size, as this will increase their prey handling ability, while their larger maintenance requirements will not pose a real problem under such conditions. At the same time predators will specialize on small prey, as this will decrease their handling time and thus increase their food intake rate. We denote the resulting pattern of large predator size and predator preference for small prey by L-S. If food becomes less abundant, the encounter rates rather than the handling rate will be limiting the food intake of predators, and preference will now evolve towards larger prey. For the same reason, the predators will still evolve towards larger body sizes, resulting in a pattern denoted as L-L. If food becomes really scarce, large predators will not be able to meet their maintenance requirements, which will then favor small predator body sizes; under these circumstances a preference for large prey will evolve, as this increases the encounter rate. We would thus expect a pattern denoted by S-L.

Secondly, how do patterns of predator size and prey-size preference depend on *ecological* parameters? We will focus on two ecological parameters, viz. encounter rate and handling rate, or, more precisely, the parameters that determine how these rates vary with prey and predator size and the relative importance of these two. For active predators, for example, encounter rates may depend primarily on predator size and less on prey size. This may again select for large predators and for a preference for smaller prey.

Methods and work plan

Tools. A suitable framework to study the evolution of body sizes is provided by Dynamic Energy Budget (DEB) theory. This is a modeling framework for metabolic processes with physiological rules for uptake and use of material and energy. It respects the principles of energy and mass conservation, and stoichiometric constraints on the synthesis of biomass. Biomass is assumed to consist of structural biomass and reserves, which both have a fixed chemical composition. The overall body composition of the organism can still vary through the ratio of structure and reserves.

While DEB deals with mechanisms, rules are implied for the covariation of parameter values among species. Parameters that relate to the physical design of the organism are all proportional to ultimate body size, while the rest are size-independent. The latter parameters often relate to molecular processes, which are essentially concentration- or density-based. Because such body-size scaling relationships are implicit to DEB-theory, it provides a physiologically-based modeling framework that is very suitable for studying body size preference in an evolutionary context.

Predictions of the evolutionary outcomes of a system can be made by using Adaptive Dynamics (AD) theory. Expressions for fitness, invasion criteria, and trade-offs can be derived from the DEB formulation, which gives them a physiological basis.

Model. We will develop a model of a physiologically structured population of predators feeding on a range of prey populations in a chemostat environment. The predators are described by two state variables, structural biomass and reserves, and by two evolutionary traits, their maximum size and their preference for prey size. The two evolutionary traits are constant throughout an individual's life, but may change from parent to offspring by mutation. The predators are filter feeders and reproduce by division.

The various prey populations differ only in the size of their individuals, thus providing a range of prey sizes. As a start we will assume that the preys enter the system at a constant density and with a fixed size distribution.

The state variables and the evolutionary traits of the predator, as well as the size of the prey, will affect several physiological and ecological variables. For some of these variables (growth, maintenance, and reproduction) DEB has derived in a systematic way how they relate to (maximum) body size. Other variables such as starvation follow from the energy storage dynamics which are a basic part of DEB. Remaining variables (ingestion, mortality) may also depend on body size. In the functions describing these relationships, parameter values will determine the quantitative effect of both the prey and the predator size and of their relative importance. These parameter values will then be tested for their effects on the evolutionary outcomes.

Analysis. The invasion fitness of a predator can be measured by its specific growth rate averaged over its lifetime (from birth to division). Calculations will be done numerically, using the escalator boxcar train method. Evolutionary analysis may include evolutionary trajectories, pairwise invasibility plots, and simulation studies.

Parameterization. The model can be parameterized and tested with data on Didinium feeding on Paramecium. These ciliates become considerably larger when conditioned on large prey than when conditioned on small prey (Hewett, 1988). Although this size shift is not an evolutionary change, it may have a genetic and evolutionary origin. Data is available on how mortality, handling time, encounter rate, and attack success rate depend on Didinium size, Paramecium size, and density (Hewett, 1988; Hewett, 1987; Salt, 1974).

Relevance and link to ADN's research plan

This study will apply Adaptive Dynamics methods to a Dynamic Energy Budget model. Results could provide insight into the relation between predators and their prey choice, which may lead to a better understanding of the structure of natural communities. Such information may be useful in areas such as conservation biology and fisheries management.

Expected output and publications

The study is expected to be published in a jointly authored paper in an international scientific journal, and may be integrated in one chapter of my PhD thesis.

References

Ellison, T. and Gibson, R. N. (1997). Predation of 0-group flatfishes by 0-group cod: Handling times and size-selection. Marine Ecology - Progress Series, 149(1-3):83–90.

Forsman, A. (1996). Body size and net energy gain in gape-limited predators: A model. Journal of Herpetology, 30(3):307–319.

Hewett, S. W. (1987). Prey size and survivorship in didinium nasatum. American Microscopical Society, 106(2):134–138.

Hewett, S. W. (1988). Predation by didinium nasatum: Effects of predator and prey size. Ecology, 69(1):135–145.

Husseman, J. S., Murray, D. L., Power, G., Mack, C., Wenger, C. R., and Quigley, H. (2003). Assessing differential prey selection patterns between two sympatirc large carnivores. OIKOS, 101(3):591–601.

Karpouzi, V. and Stergiou, K. I. (2003). The relationships between mouth size and shape and body length for 18 species of marine fishes and their trophic implications. Journal of Fish Biology, 62(6):1353–1365.

Kristiansen, J. N., Fox, T., and Nachman, G. (2000). Does size matter? maximising nutrient and biomass intake by shoot size selection amongst herbivorous geese. ARDEA, 88(2):119–125.

Manatunge, J. and Aseada, T. (1998). Optimal foraging as the criteria of prey selection by two centrarchid fishes. Hydrobiologica, 391(1-3):223–240.

Mehner, T., Plewa, M., Hulsmann, S., and Worischka, S. (1998). Gape-size dependent feeding of age-0 perch (perca fluviatilis) and age-0 zander (stizostedion lucioperca) on daphnia galeata. Archiv fuer Hydrobiologie, 142(2):191–207.

Pryor, V. K. and Epifanio, C. E. (1993). Prey selection by larval weakfish (cynoscionregalis) - the effects of prey size, speed and abundance. Marine Biology, 116(1):31–37.

Rincon, P. A. and Loboncervia, J. (1995). Use of an encoutner model to predict size-selective predation by a stream-dwelling cyprinid. Freshwater Biology, 33(2):181–191.

Rytkonen, S., Kuokkanen, P., Hukkanen, M., and Huhtala, K. (1998). Prey selection by sparrowhawks accipiter nisus and characteristics of vulnerable prey. Ornis Fennica, 75(2):77–87.

Salt, G. W. (1974). Predator and prey densities as controls of the rate of capture by the predator didinium nasatum. Ecology, 55(2):434–439.

Svensson, J. E. (1997). Fish predation on eudiaptomus gracilis in relation to clutch size, body size, and sex: A field experiment. Hydrobiologica, 344:155–161.

Turesson, H., persson, A., and Bronmark, C. (2002). Prey size selection in piscivorous pikeperch (stizostedion lucioperca) includes active prey choice. Ecology of Freshwater Fish, 11(4):223–233.