Finite Predation Rate: a Novel Parameter for the Quantitative Measurement of Predation Potential of Predator at Population Level

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Summary

Demography and population growth are the most important subjects of population ecology and economics. Finite and intrinsic growth rates have been used as standard parameters for describing and comparing growth potentials of populations. The predation potentials of predator populations or consumption potentials of consumer populations cannot be properly described using these growth rates alone. A standard parameter is needed for the description of the predation or consumption potential, as well as for the quantitative evaluation of a predator population in an ecosystem or biological control program. We show that the finite predation rate can be the standard parameter by linking the finite rate, the stable age-stage distribution, and the age-stage specific predation rate. The finite predation rate can be used to describe and compare the predation potentials of natural enemies used in biological control and in predicting the damage potential of different pest populations to crops.

Ecology can be defined as the scientific study dealing with the distribution and abundance of life, and the interactions between populations and their environments. Life tables provide the most detailed descriptions of the age structure, age-specific survival rate and fecundity of a population, and have become one of the most important basic tools in ecological research. The Euler-Lotka formula has been used to calculate the intrinsic rate of increase (r) for age-structured populations[1, 2], while the Lewis-Leslie matrix[3, 4] has been used to calculate the finite rate (λ). The relationship between r and λ is $e^r = \lambda$. Both r and λ represent the growth potential of a stable population[1,2,3,4], and are among the most important and widely used parameters in population ecology[5]. Ecologists, however, have lacked a scientific parameter which would enable them to take both population growth and predation rate into consideration when describing and comparing the efficiency of predators and parasitoids.

Finite Rate and Net Predation Rate

Although the finite and intrinsic rates do describe the growth potential of a stable population, they are incapable of representing the predation potential of a predator to its prey or the consumption potential of a consumer to its food resource. In other words, determining a population growth rate alone does not fully address one of the primary definitions of ecology: the interaction between populations. To precisely evaluate the effect of predation in a predator-prey system, we need not only to assess the growth potential (r or λ) of the predator, but also its predation potential. Only then, can we link the demography of predator - prey interactions with food-chain dynamics, sustainable harvesting, ecological conservation, ecosystem dynamics, etc.

Traditional female age-specific life tables[1,2,3,4] only take the female component of a population into consideration. Because they ignore the effects of male predators in biological control studies and male consumers in agricultural studies, female age-

specific life tables are incapable of accurately describing predator-prey relationships or growth in two-sex and stage-structured populations. Using the age-stage, two-sex life table[6,7] has solved these problems and is now often used in ecological studies[8,9,10,11,12]. As an example: The finite rate of the ladybird beetle *Propylea japonica* (Thunberg)[8] is 1.117 d^{-1}, for the braconid parasitoid wasp *Aphidius gifuensis* Ashmead[9] it is 1.302 d^{-1}. Both insects are natural enemies of the peach aphid and other pest aphid species. Because the finite rate is the multiplication rate of a stable population after one time (age) unit, the parasitoid population can increase 1.302 fold after a single day, while the ladybird population will only increase 1.117 fold after one day and 1.248 fold after two days. The growth potential of this parasitoid population is much higher than the ladybird population.

For an age-stage, two-sex population, the net predation rate[7] is the mean number of prey individuals killed by a predator during its life time and is calculated as

$$C_0 = \sum_{x=0}^{\infty} \sum_{j=1}^{m} s_{xj} c_{xj} \tag{1}$$

where s_{xj} is the probability that a newly laid ladybird egg will survive to age x and stage j, c_{xj} is the consumption rate (predation rate) of ladybirds of age x and stage j, m is the number of developmental stages of the ladybird. For the age-specific life table, the net predation rate is

$$C_0 = \sum_{x=0}^{\infty} l_x c_x \tag{2}$$

where l_x is the age-specific survival rate at age x, c_x is the age-specific predation rate of age x. The net predation rate of ladybird *P. japonica* is 1199 peach aphids, which is 25-times higher than the parasitism rate of 46 peach aphids by the parasitoid wasp *A. gifuensis*. Now, we face an important question. Is it justified to conclude that the

parasitoid is a more efficient natural enemy of peach aphids in comparison with the ladybird because of its higher population growth rate? Or, on the contrary, can we conclude that the ladybird is more efficient than the parasitoid based on its higher predation rate? Different parameters and methods have been used for the measurement and comparison of predation rates, e.g., prolonged survival of predator[14], numerical response[15], number of prey consumed[16], response to temperature[16], functional response[17], ELISA[18], searching hehaviour[19], etc. But all of these are incomplete due to ignorance (omission) of some of the major components of the predator population, i.e., age composition, stage structure, sexual difference, and population growth rate.

Finite Predation Rate

If the survival rate and fecundity remain constant, an age-structured population will settle to the finite rate and stable age distribution[1,2,3,4]. For an age-stage structured population, it will settle to the stable age-stage distribution (SASD)[6]. If the matrix A represents the stable age-stage structure of a predator population and its element a_{xj} is the proportion of individuals belonging to age x and stage j in SASD, it is clear that

$\sum_{x=0}^{\infty} \sum_{j=1}^{m} a_{xj} = 1$. Assuming there are far more prey individuals than the predators can kill, the total predation of population A can be calculated as:

$$\psi = \sum_{x=0}^{\infty} \sum_{j=1}^{m} a_{xj} c_{xj} \qquad (3)$$

For the non-predatory stages (e.g., egg and pupa), their predation rates c_{xj} are zero. This ψ can be defined as the stable predation rate, It is the total predation capacity of a stable population which total size is unity. Because the predator population itself will increase at the finite rate λ, the total number of killed prey will be increased at the rate $\lambda\psi$. In

other words, if the size of a predator population is unity at time *t*, it can kill ψ number of prey. After one time unit, the predator will increase to λ and kill $\lambda\psi$ number of prey. As the finite rate λ describes the growth potential of the predator, the product $\lambda\psi$ describes the predation potential of a predator population by combining its growth rate (λ), age-stage predation rate (c_{xj}), and stable age-stage structure (a_{xj}). We define the product $\lambda\psi$ as the finite predation rate and it can be calculated as

$$\omega = \lambda\psi = \lambda\sum_{x=0}^{\infty}\sum_{j=1}^{m}a_{xj}c_{xj} \tag{4}$$

The finite rate and the intrinsic rate are based on a stable population and have always being used as standard parameters for comparison of growth potential between populations. Similarly, the finite predation rate can be used for the comparison of predation potential between different predators under the same condition or same predator under different conditions. The finite predation rate takes both the increase rate of predator (λ) and the age-stage specific predation rate (c_{xj}) into consideration. In case of all $c_{xj} = 1$, i.e. each predator individual kills one prey per time unit regardless of its age and stage, then $\psi = 1$ and the predator population will kill exactly the same

number of prey as the predator population size itself, because $\sum_{x=0}^{\infty}\sum_{j=1}^{m}a_{xj}=1$. It means also that both the predator population and its predation will increase at the same rate λ, since $\omega = \psi = \lambda$. Only in this special case, the finite rate can be used as an indicator of predation potential. However, because the predation ability generally varies with age and stage[8,9,10,11], the finite predation rate is a better indicator of predation potential than the finite rate. If $\psi < 1$, then $\omega < \lambda$. In case of the parasitoid *A. gifuensis*, because only female adults are capable of laying eggs in peach aphids, all c_{xj} of immature stages (egg,

larval, and pupa) are zero, and the net predation rate is only 42. Moreover, female

adults compose only 2.4% of the SASD. The low c_{xj} and very low proportion of

predatory individuals in SASD resulted in a low value of the stable predation rate ψ

(0.396) and a low finite predation rate ω (0.305) (Table 1). On the contrary, the larvae,

male and female adults of the predatory ladybird beetles *P. japonica* can all kill peach

aphids and they compose 54% of the SASD. Moreover, its net predation rate is 1199

aphids, which is far higher than *A. gifuensis* (Table 1). All of these factors give a higher

stable predation rate ψ (8.74) and a higher finite predation rate ω (9.82) to *P. japonica*.

For the age-specific female life table, the stable predation rate and the finite

predation rate can be defined as

$$\psi = \sum_{x=0}^{\infty} a_x c_x \qquad (5)$$

$$\omega = \lambda \psi = \lambda \sum_{x=0}^{\infty} a_x c_x \qquad (6)$$

where a_x is the proportion of age x in the stable age distribution. Because female age-

specific life tables[1,2,3,4] ignore the stage differentiation and the male population, their

usefulness to two-sex or stage-structured populations is limited. In Table 1, we list the

finite rate (λ), the net predation rate (C_0), the stable predation rate (ψ), and the finite

predation rate (ω) of the predators *Propylaea japonica*, *Aphidius gifuensis*, *Harmonia

dimidiata* (a predatory ladybird), and *Aphidoletes aphidimyza* (a predatory midge).

Conclusion

If we replace the term "predation" with "consumption", the definition of finite

predation rate can also be used to compare the damage potential of different pests to a

crop, or exploitation rate of consumers on resources. Because food webs are very

complex, and there are many other factors which affect the predation potential of

predators, such as searching ability of predator, competition between natural enemies, density-dependency of predation, etc., the finite predation rate is not a parameter for all problems. The finite predation rate (ω) takes the finite rate, the age-stage structure, and the age-stage predation rate of the predator population into consideration; it thus can be used as a standard description of predation potential, just like the finite rate of increase (λ) is used for the growth potential. We suggest that both the stable predation rate and finite predation rate should be calculated and reported in all new papers involving life tables and predation rate of biological control agents.

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Table 1. Finite rate (λ), net predation rate (C_0), stable unity predation rate (ψ), and finite predation rate (ω) of a few examples

Predator-prey system		λ (d^{-1})	C_0 (preys)	ψ (preys)	ω (preys/d)
Propylaea japonica-Myzus persicae		1.125	1199	8.74	9.82
Aphidius gifuensis-Myzus persicae		1.302	46	0.305	0.396
Hippodamia variegata-Aphis fabae		1.225	1127	3.93	4.81
Aphidoletes aphidimyza-Aphis fabae		1.175	7.6	0.455	0.535
	25°C	1.096	14874	114.8	125.8
Harmonia dimidiata -Aphis gossypii	20°C	1.074	13050	108.1	116.3
	15°C	1.058	10962	58.0	61.4