Evolution of Host Defense and Parasite Counterdefense in Avian Brood Parasitism

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Brood Parasitism: Parasite exploits parental care of the host and usually reduces the reproductive success of the host

Field studies have shown that

Some host populations have an ability to recognize and reject parasitism. The degree of the host defense, however, differs from population to population.

Some parasites have counterdefense such as egg mimicry to counter the host defense.

Relationship between the parasite and its host has been thought to lead to a coevolutionary process called arms race

But a perplexing question remains to be answered ⇒

Question:

Why do not all host populations show defense against parasitism ?

Time Lag Hypotheses

The host lacks genetic variations to cause the defense against parasitism. Once a proper mutation appears, it spreads fast among the population and the host will establish the defense.

Rothstein 1975

Imperfect host defense implies that the host is currently in the process of establishing perfect defense.

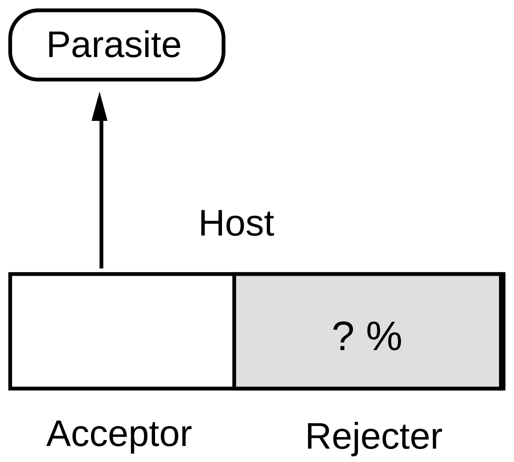
Davies and Brooke 1989

Equilibrium Hypotheses

The host accepts parasitism because it is more adaptive than rejecting parasitism.

Rohwer and Spaw 1988, Lotem et al. 1993

In order to explore how the host defense is established, I present and analyze a theoretical model, the results of which reconcile the conflicting hypotheses so far proposed and make possible new interpretations of the observed facts.



What is the final frequency of the rejecter individuals?

Suppose a population of parasite that utilizes a host population which consists of acceptor and rejecter individuals at certain frequencies.

The acceptor individual accepts parasitism, while the rejecter individual has an ability to recognize parasitism.

The probability that a rejecter individual can reject parasitism depends on the degree of the parasite counterdefense.

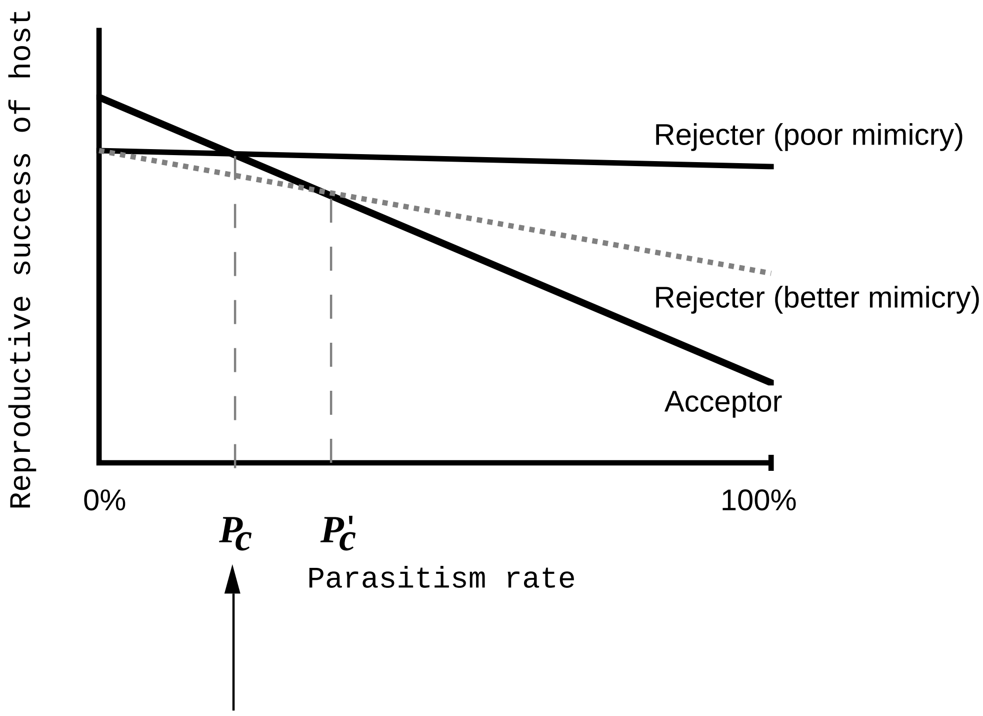
The rejecter individual can reject parasitism if the parasite has poor egg mimicry, but it may accept parasitism if the egg mimicry is nearly perfect.

The Model Assumptions

Rejecting parasitism is adaptive than acceptance when the host suffers severe parasitism.

When few parasitism occurs, acceptance is adaptive than rejection provided rejecting parasitism entails cost to perform.

The parasite counterdefense (egg mimciry) discounts the host defense.

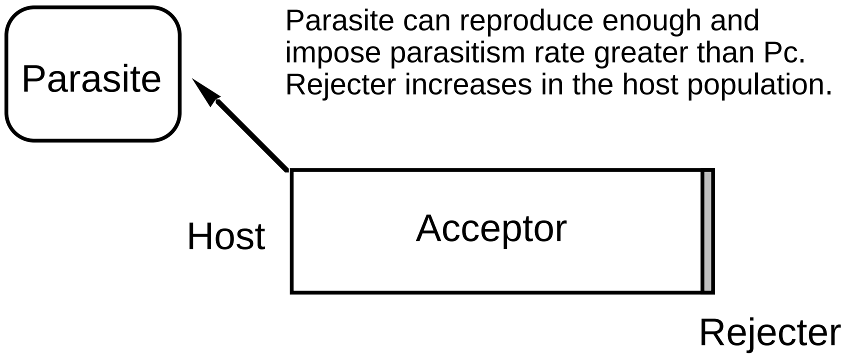


A critical parasitism rate Pc exists:
Rjection is better than acceptance under severe parasitism and vice versa

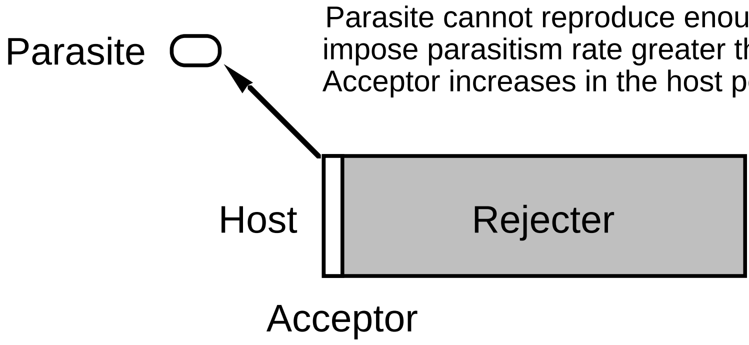
Case 1) the parasite has no counterdefense (poor egg mimicry)

Parasitism fails in nests of rejecter individual.
Only the acceptor individauls are the resource available for the parasite's reproduction.

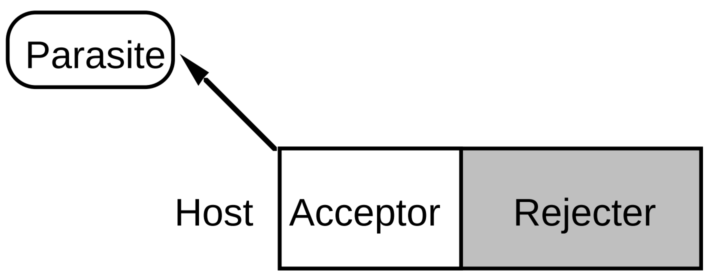
Parasite can reproduce enough and impose parasitism rate greater than Pc. Rejecter increases in the host population.



Parasite cannot reproduce enough and cannot impose parasitism rate greater than Pc. Acceptor increases in the host population.

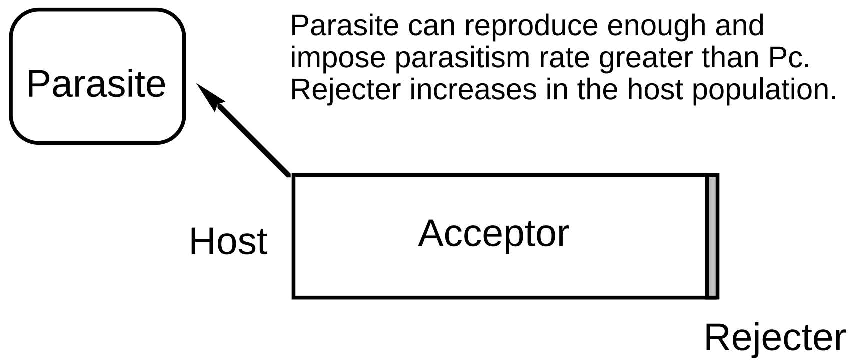


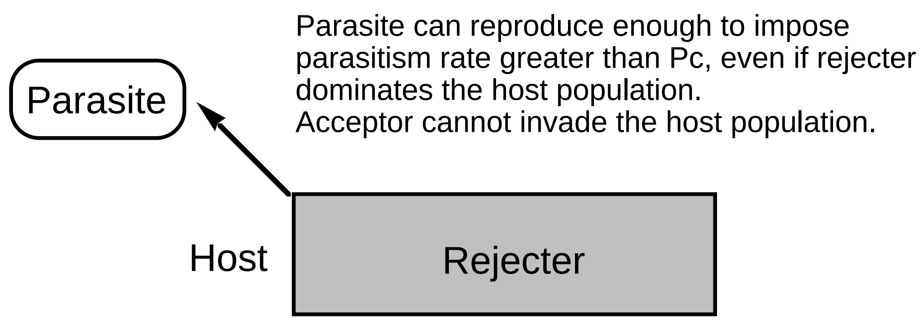
There should be a certain frequency with which the host population show dimorphism of acceptor and rejecter individuals as a stable equilibrium.

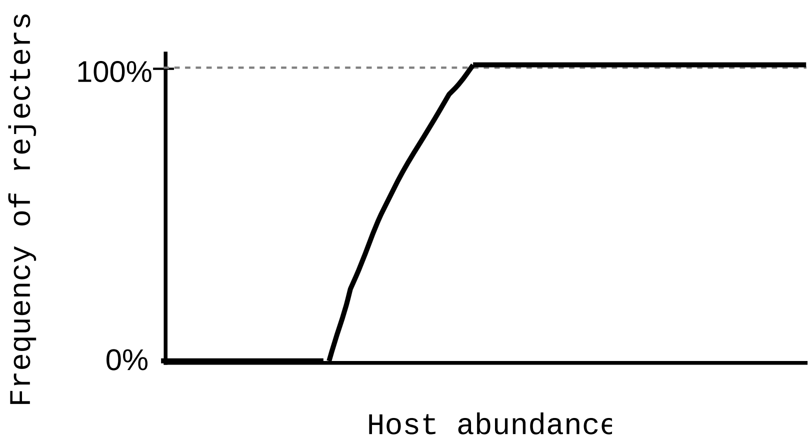


Case 2) the parasite has counterdefense (better egg mimicry)

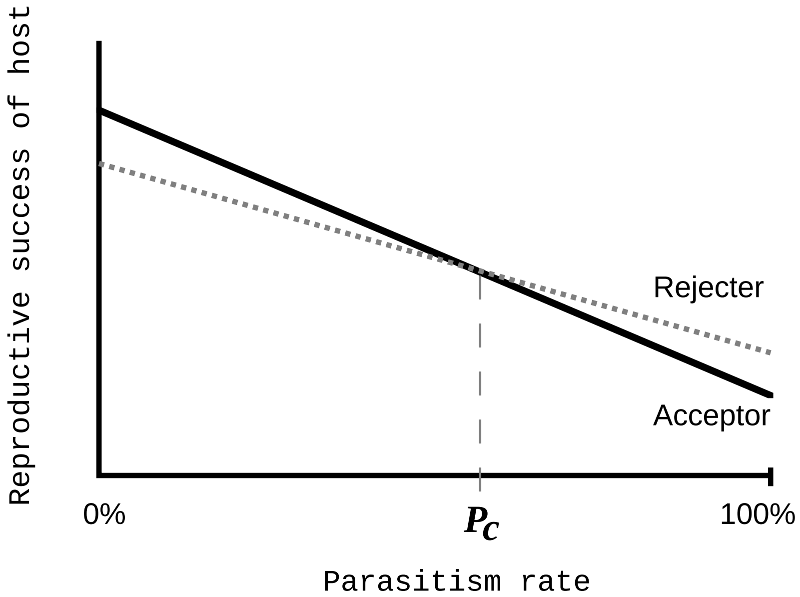
The parasite can now reproduce from nests of rejecter individual with a probability proportional to the degree of the egg mimicry





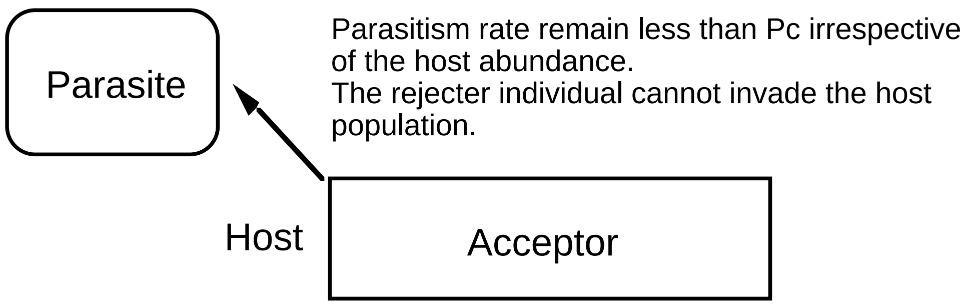


Case 3) the parasite has nearly perfect counterdefense



Host defense is discounted greatly and the parasite can reproduce enough irrespective of the frequency of rejecter individuals.

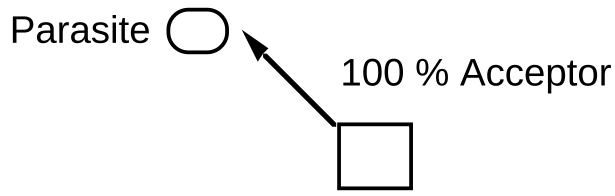
Population dynamics, however, does not allow the parasite to impose parasitism rate greater than Pc under usual breeding parameters.



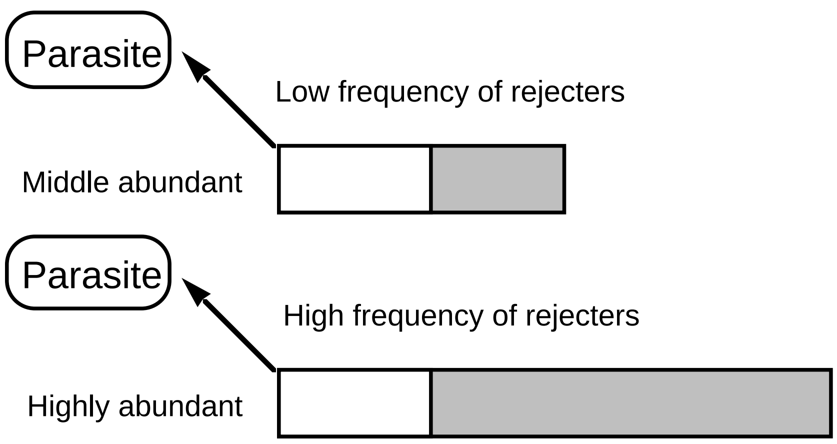
The equilibrium frequency of rejecter individual depends on the host abundance

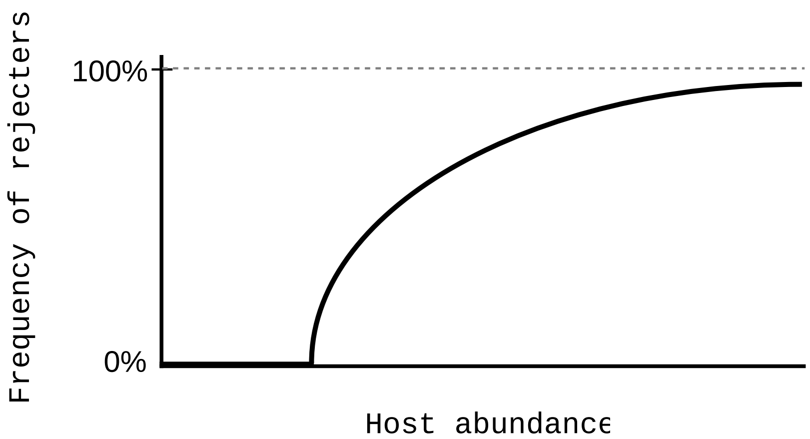
- When the host is not abundant enough...

  Parasite cannot reproduce enough and cannot impose parasitism rate greater than Pc even if the acceptor dominates the host population. Rejecter individual cannot invade the host population.

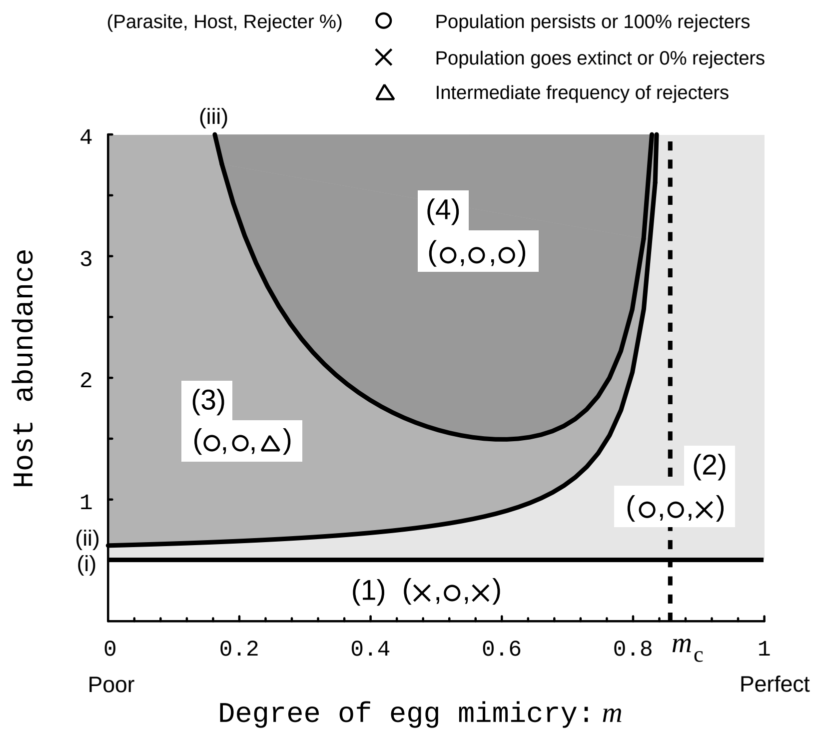


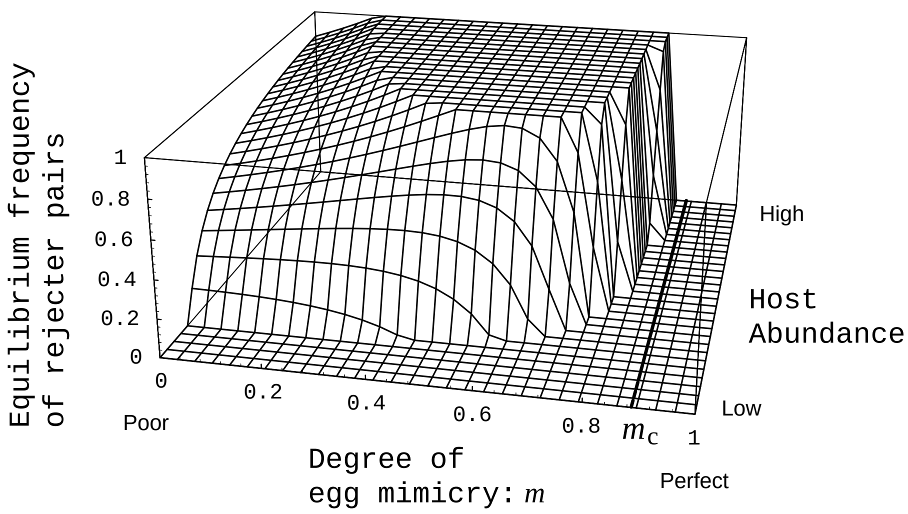
- When the host is abundant enough...



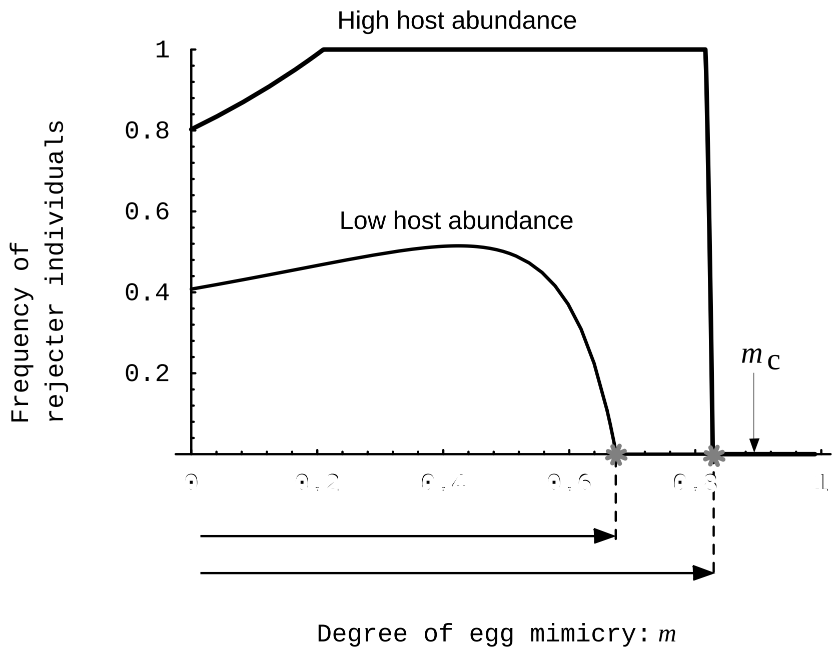


Takasu et al. (1993) Am.Nat. vol. 142. "Modeling the population dynamics of a cuckoo-host association and the evolution of host defenses"

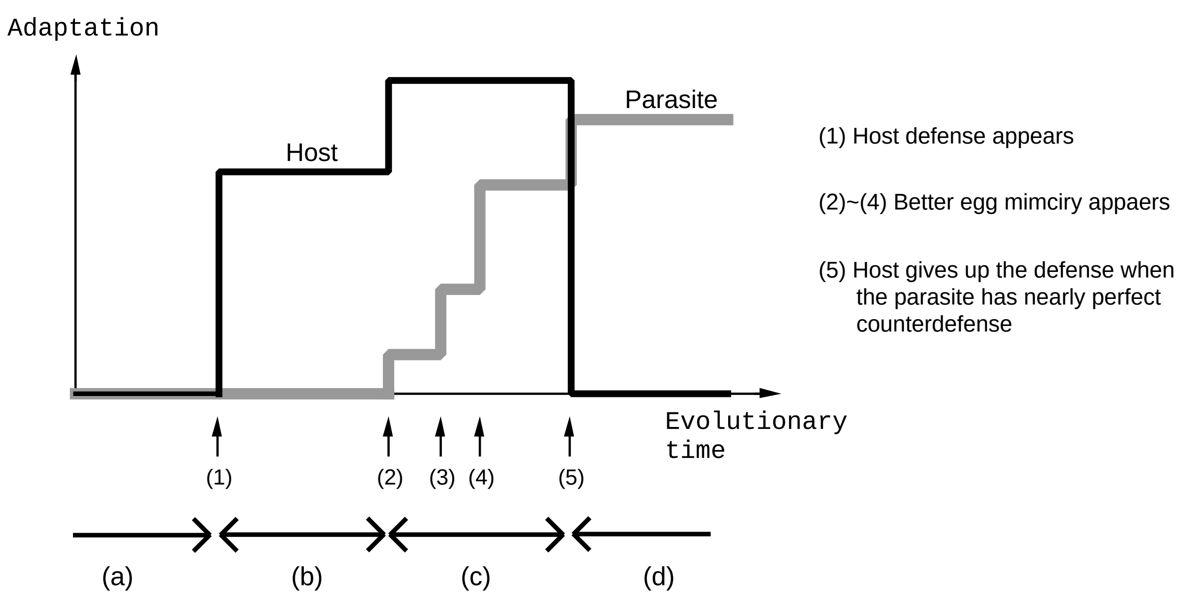

(Parasite, Host, Rejecter %)
Population persists or 100% rejecters
Population goes extinct or 0% rejecters
Intermediate frequency of rejecters
(iii)
(ii)
(i)
(4)
(o,o,o)
(3)
(o,o,△)
(2)
(o,o,×)
(1) (×,o,×)
Host abundance
0
1
2
3
4
0.2
0.4
0.6
0.8
m_c
Poor
Perfect
Degree of egg mimicry: m


Equilibrium frequency of rejecter pairs
1
0.8
0.6
0.4
0.2
0
Poor
Degree of egg mimicry: m
0.2
0.4
0.6
0.8
m_c
1
Perfect
High
Host Abundance
Low

Better counterdefense (egg mimicry) can invade in the parasite population as long as the host shows defense against parasitism



Hypothetical Pathway in the Arms Race



Summary

The host abundance influences the parasite density, which in turn affects the cost-benefit balance of parasitic burden and the host defense.

The condition for the host defense to be established depends much on the dynamic properties such as the host abundances.

Depending on the host abundance, various levels of the host defense are possible as stable equilibrium, which range from nil to perfect.

Imperfect degree of the host defense does not necessarily imply that the host is in the process of establishing perfect defense.

The model predicts that the host gives up the defense when the parasite has nearly perfect egg mimicry provided the host defense entails cost.

More attention should be paid, not only to the parasitism rate the host currently suffers, but also to the dynamic relationship between the parasite and its host.

A Mathematical Model

Density of Parasite : P

Density of Host: H

Genotype frequency: RR, RA and AA x, y, and z (x + y + z = 1)

Population densities and genotype frequencies at the next generation are given as follows

$$P' = s_P P + (1 - e^{-aP})\, \Gamma H \left\{ z^2 + (1 - z^2)\, m \right\} \qquad H' = \frac{k}{k+H}\left[s_H + (1 - z^2)\, W_R + z^2\, W_A \right] H$$

$$x' = \frac{s_H x + W_R\left(x^2 + x y + y^2/4\right)}{s_H + (1 - z^2)\, W_R + z^2\, W_A} \qquad y' = \frac{s_H y + W_R\left(x y + 2 x z + y^2/2 + y z\right)}{s_H + (1 - z^2)\, W_R + z^2\, W_A}$$

where $W_R = \varepsilon f\,(1 - m + m \exp(-aP))$ $W_A = f \exp(-aP)$

s_P s_H : Survival rate of adult parasite and host

Γ : Survival rate of parasite egg when accepted

k : Density dependent effect on host population

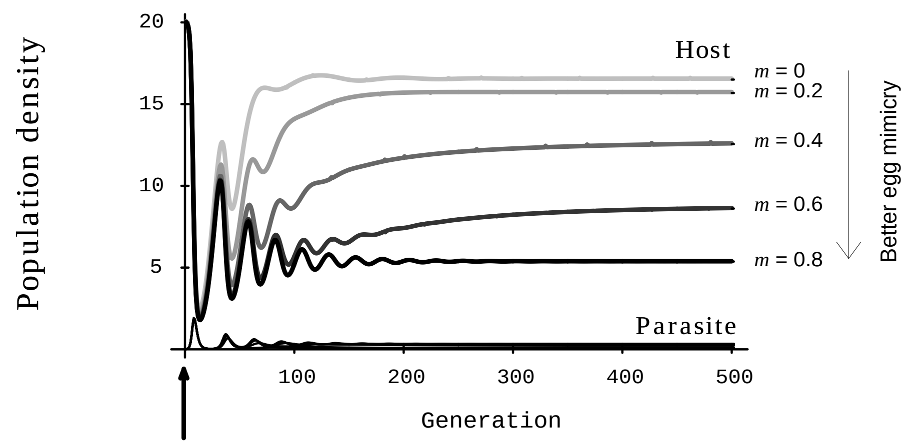
ε : Rejection cost ($\varepsilon < 1$)

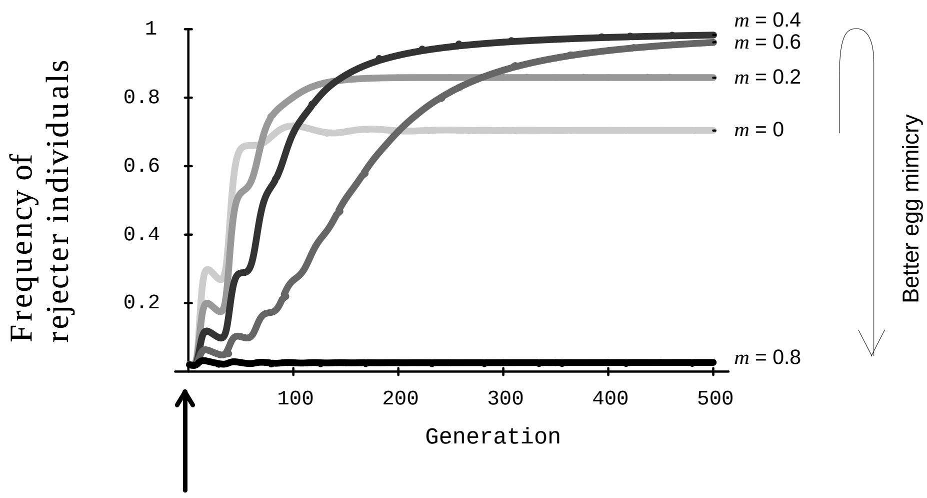
f : Host recruitment from acceptor pair's nest when unparasitized

ε f : Host recruitment from rejecter pair's nest when unparasitized

m : Degree of egg mimicry

Temporal changes in relation to degree of egg mimicry, m





Parasites begin to parasitize host population with small fraction of rejecter mutant