The role of theoretical models explaining the relationships between brood parasites and their hosts

Modelling of the evolution of host defense

In avian brood parasitism

Brood parasite exploits parental care of the host.

Accepting parasitism usually results in the reduced reproductive success of host.

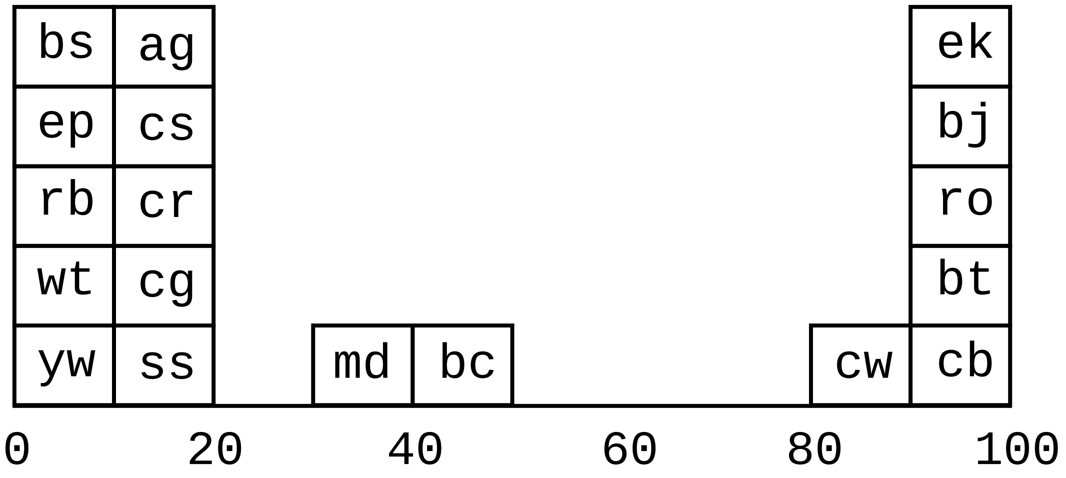
Host defense to avoid the reproductive loss is adaptive and expected to be selected in the course of interactions with parasite.

Field studies have shown that

Some host individuals have an ability to recognize and reject parasitism. The frequencies of such rejecter individuals, however, vary among species and local populations, ranging from 0% to 100%.

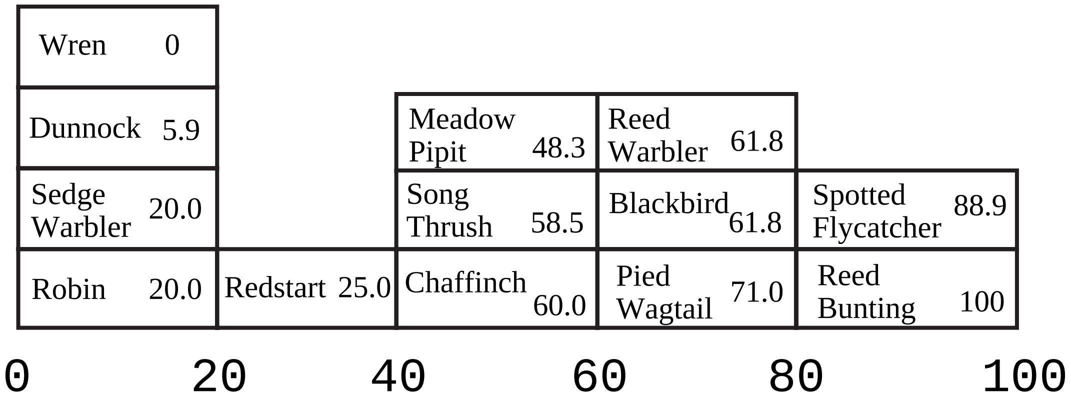
Proportion of host nests where unlike model eggs were rejected (%)

Hosts of the Brown-headed Cowbird
Molothrus ater



Rothstein (1975)

Hosts of the Common Cuckoo
Cuculus canorus



Davies and Brooke (1989a)

Theoretical models of avian brood parasitism

May and Robinson (1985)

Population dynamics of brood parasitism

Kelly (1987)

Population dynamics / genetics of host rejection and parasite mimicry

Brooker et al. (1990)

Similar to Kelly, but focuses on the intraspecific competition as a driving force of egg mimcry

Takasu et al. (1993)
Takasu (1998)

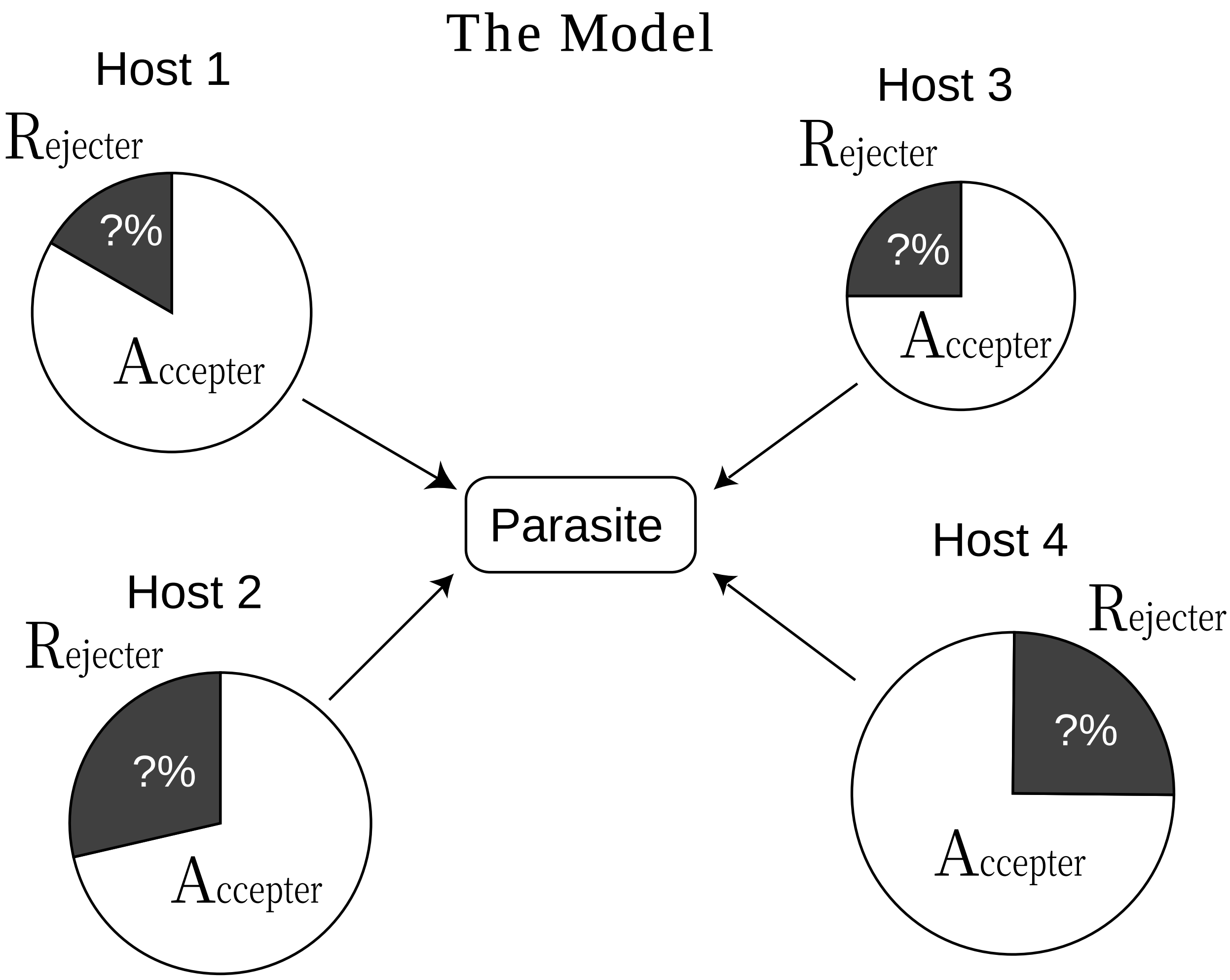
Population dynamics / genetics of host rejection

Population dynamics

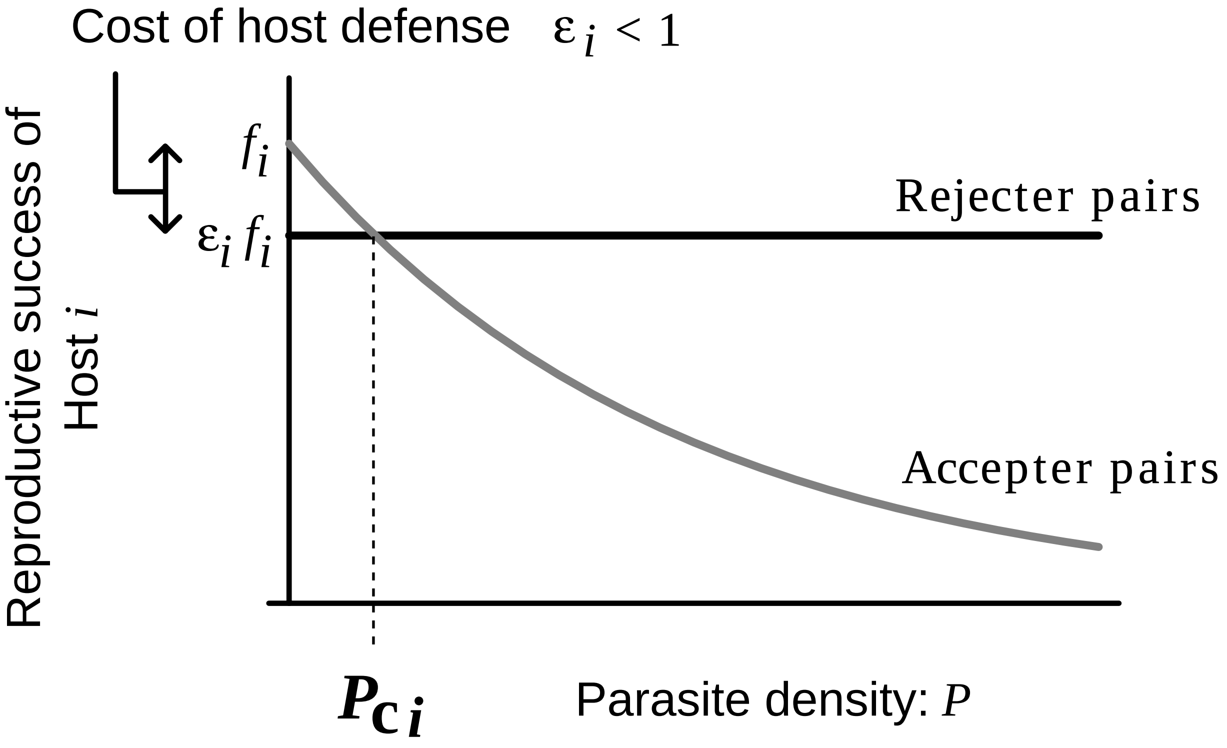
Evolution of host defense

Coevolution of parasite and its host

- How do the rejecter individuals increase in frequency in the host population?
- To what extent is the host defense established against parasitism?



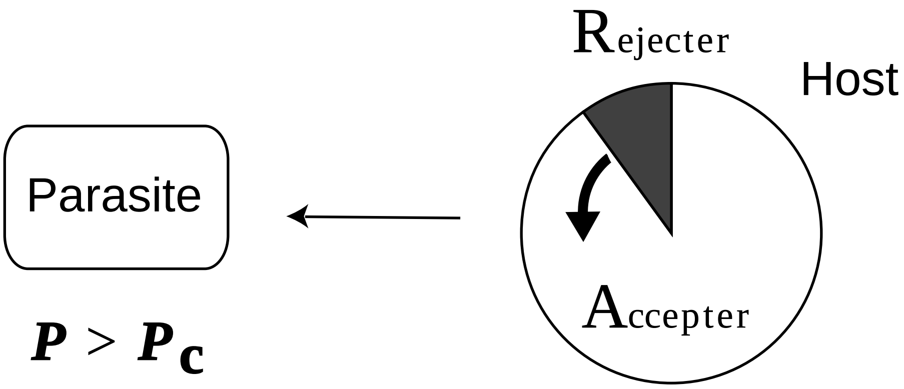
Paraisite exploits $\boldsymbol{N}$ (= 4) host populations labeled by i.



Heuristic analysis of the specialist case ($N = 1$)

Full analysis in Taksau et al. (1993)

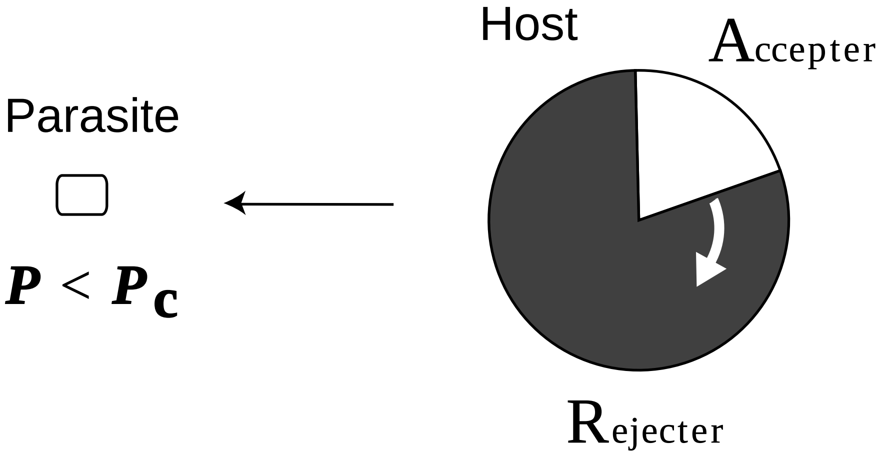
When the frequency of rejecters is low, ...



$P > P_c$

Rejecters increase in frequency.

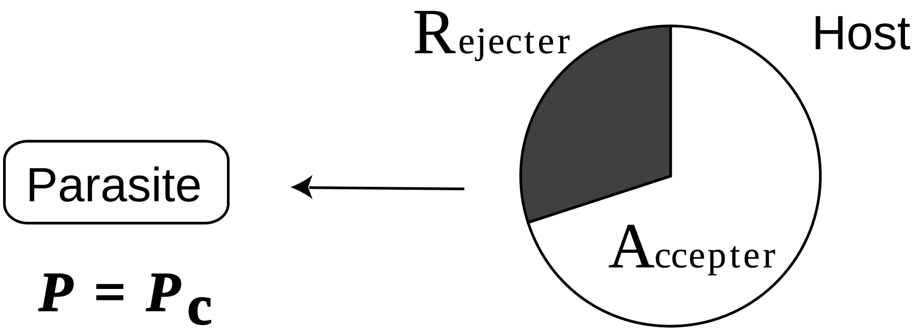
When the frequency of rejecters is high, ...



$P < P_c$

Rejecters decrease in frequency.

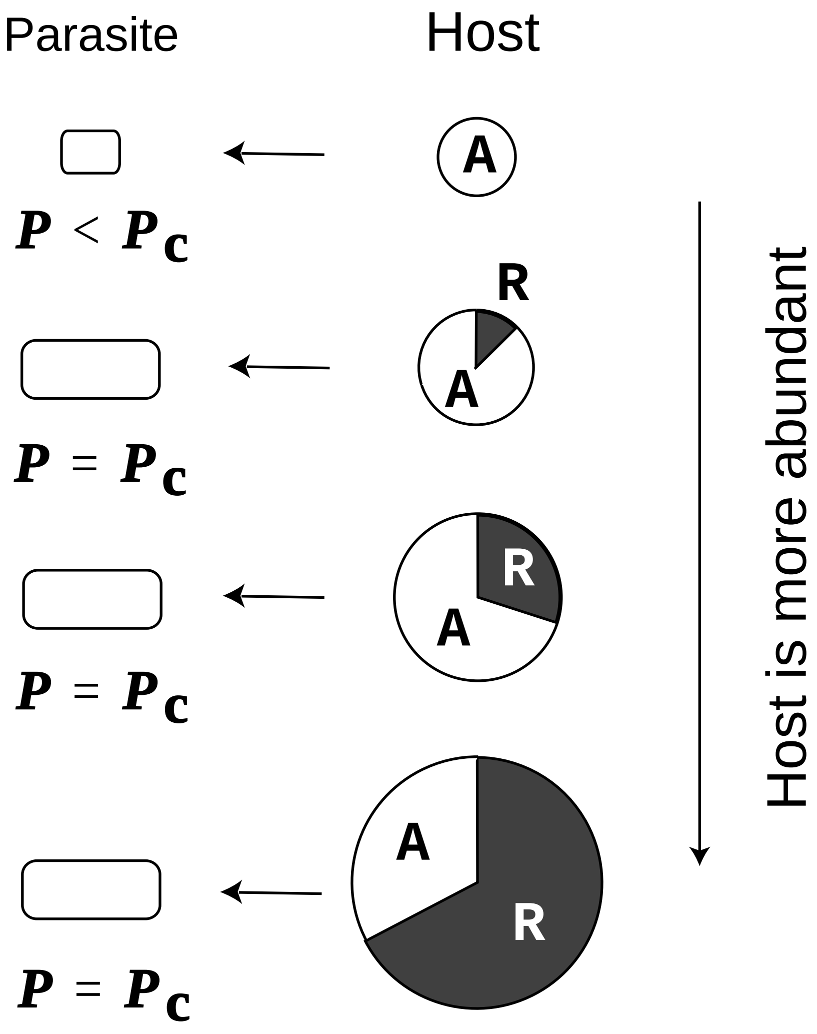
Therefore, accepter and rejecter individuals come to coexist stable with certain intermediate frequencies.

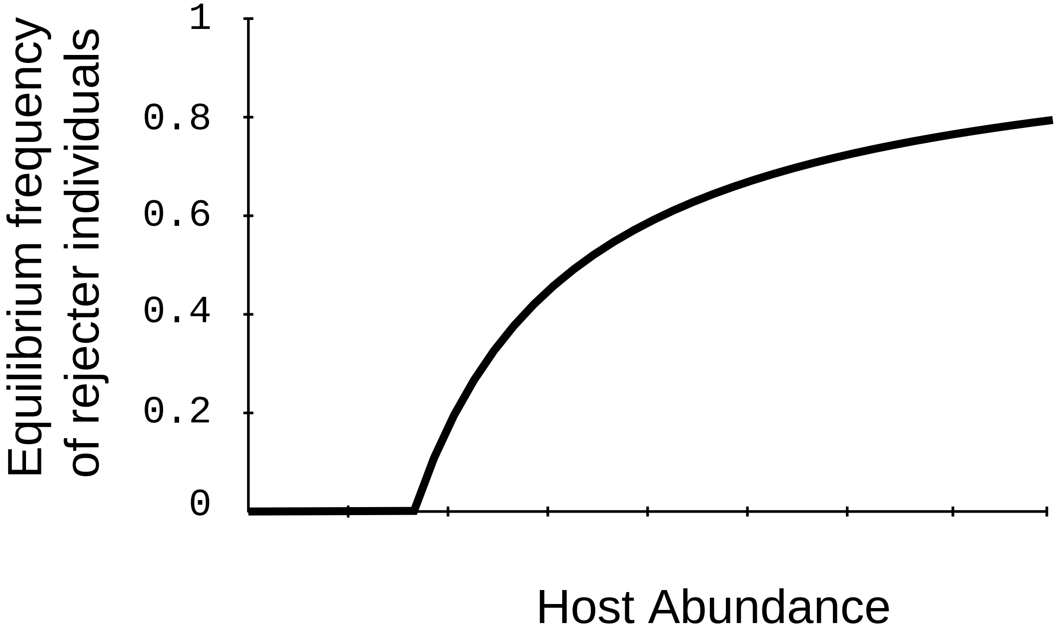


$P = P_c$

In case of specialist ($N = 1$), host population consists of accepter and rejecter individuals mixed stably with a certain frequency.

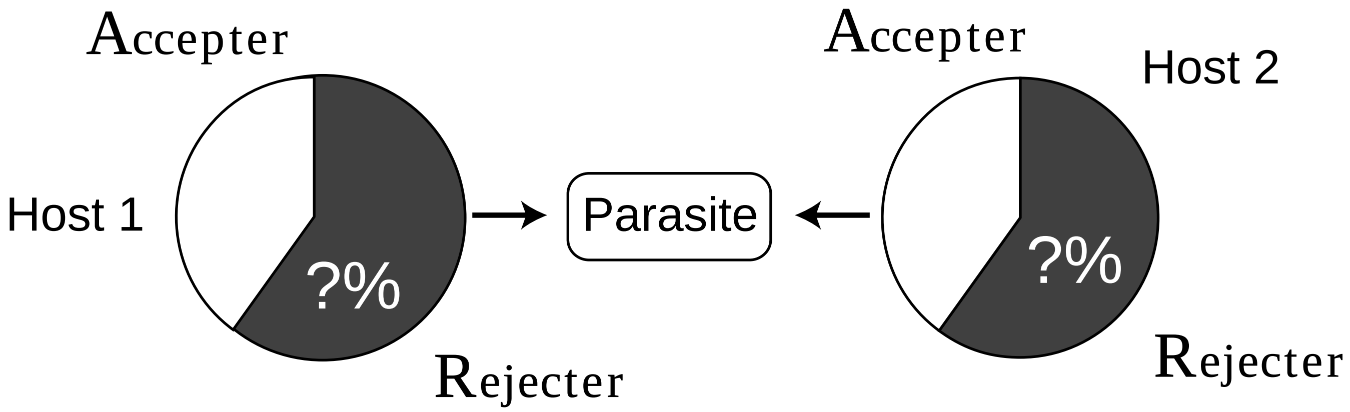
However, the equilibrium frequency depends on the host abundance.





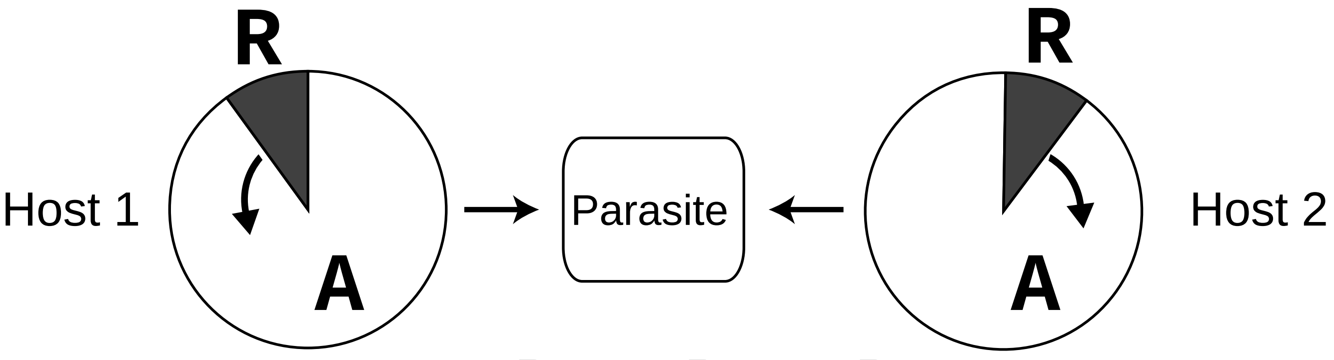
In association of specialist parasite, rejecters are not fixed in the host population.

Heuristic analysis of the generalist case ($N = 2$)



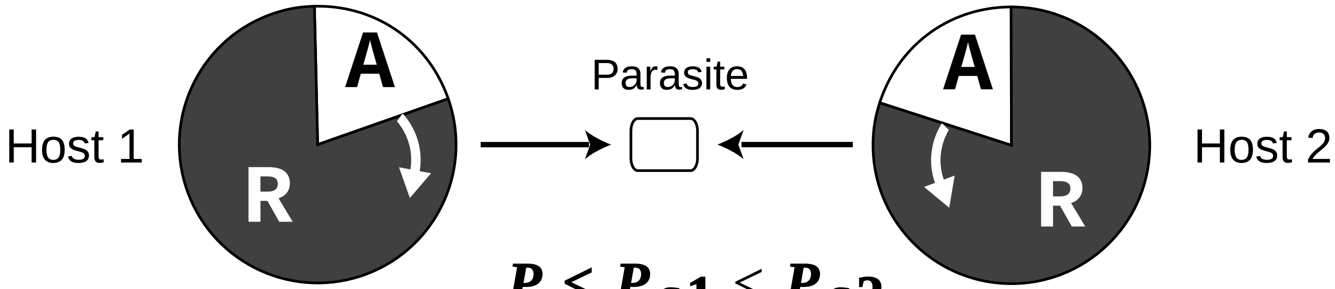
Without loss of generality, assume $\boldsymbol{P}_{\mathbf{c1}} < \boldsymbol{P}_{\mathbf{c2}}$.

When rejecters are minority in both host populations, ...



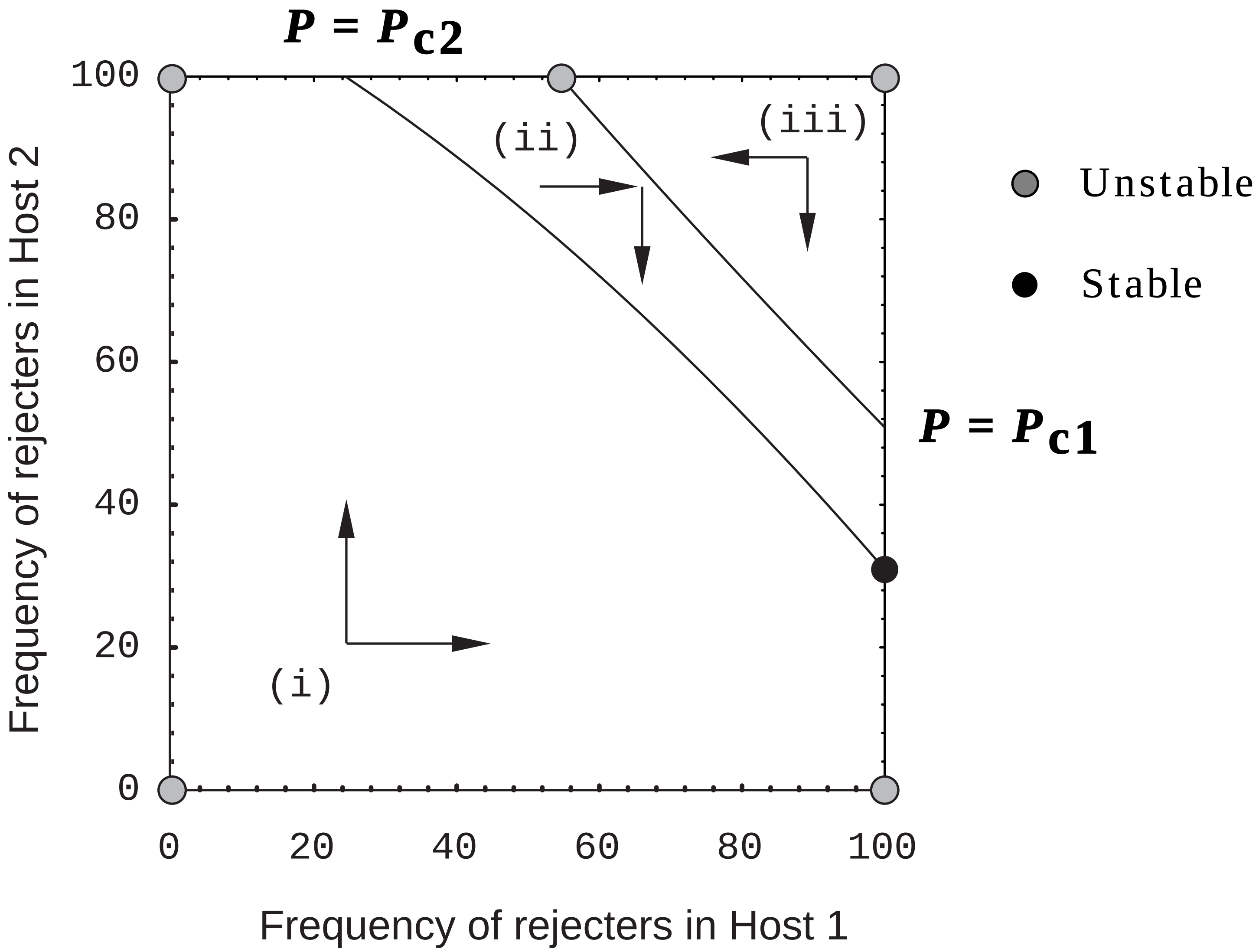
$\boldsymbol{P}_{\mathbf{c1}} < \boldsymbol{P}_{\mathbf{c2}} < \boldsymbol{P}$

When accepters are minority in both host populations, ...



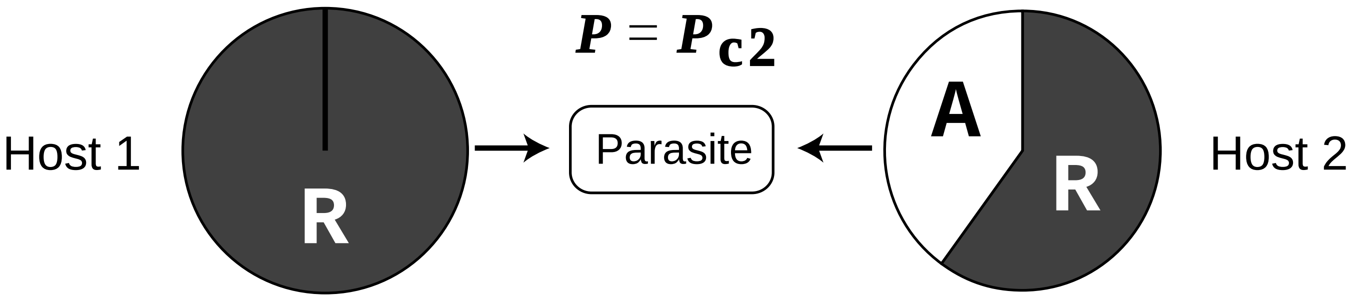
$\boldsymbol{P} < \boldsymbol{P}_{\mathbf{c1}} < \boldsymbol{P}_{\mathbf{c2}}$

Temporal changes of the frequencies of rejecters can be traced on the two dimensional phase plane.

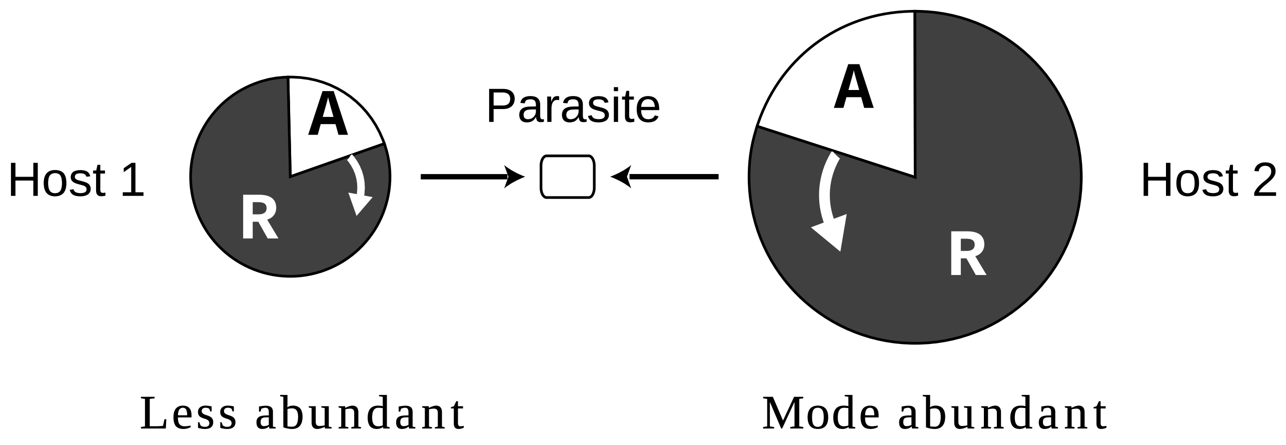


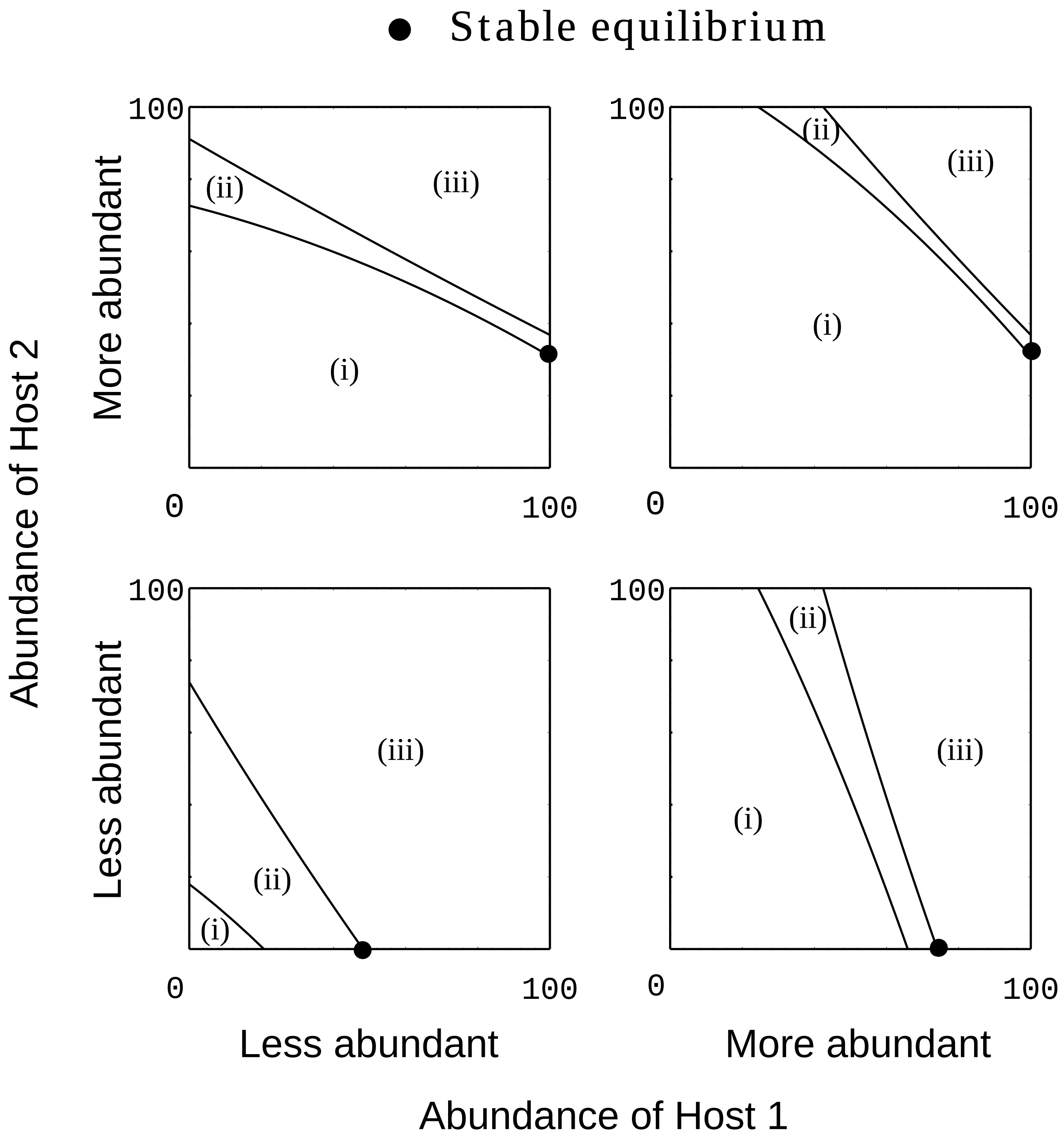
After a long run,

a stable equilibrium is attained. (shown by closed circle)

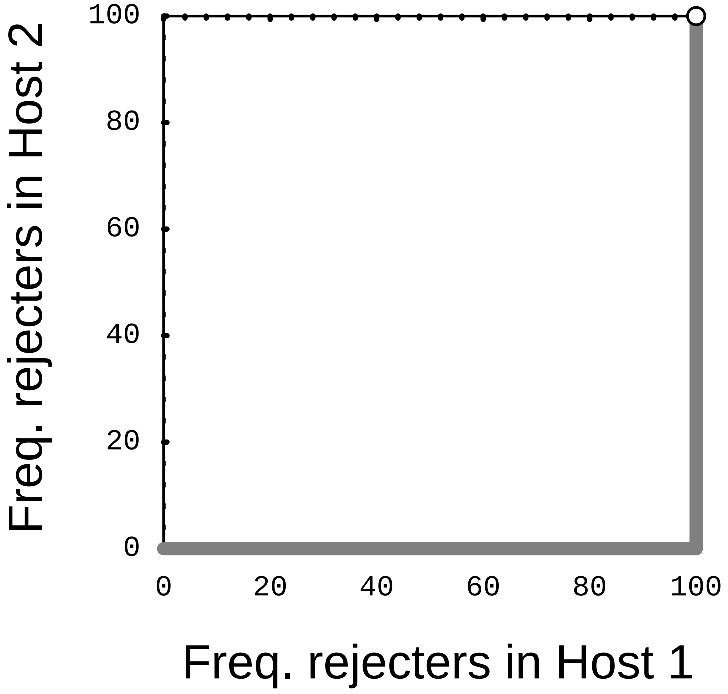


The stable equilibrium depends on the host abundances





For arbitrary combinations of host abundances,
stable equilibrium lies on the shaded line segments shown below.

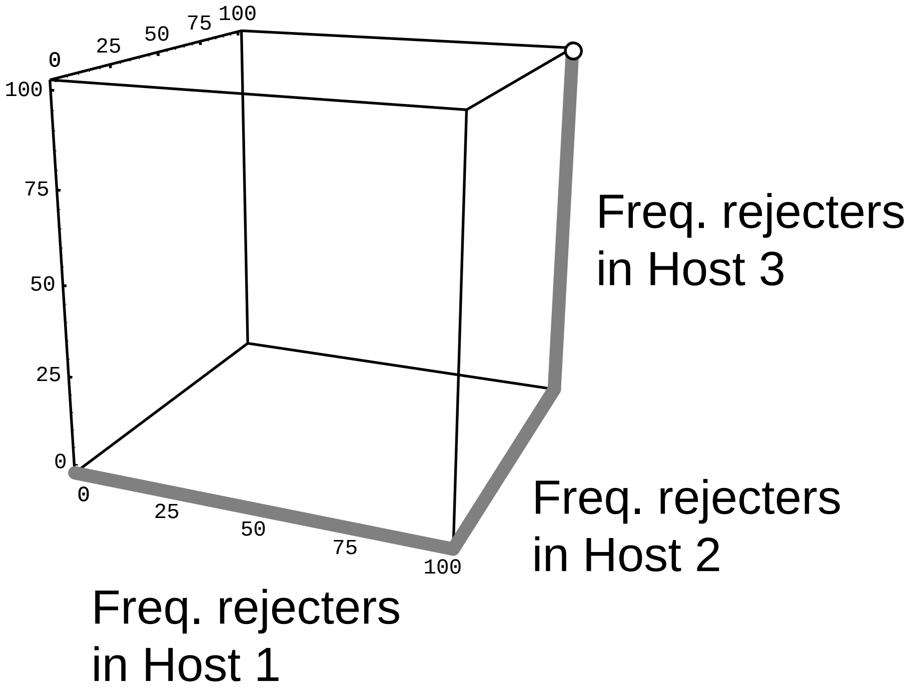


Host defense levels attained

Host 2 < Host 1

($P_{c1} < P_{c2}$)

Case $N = 3$



Host defense level attained

Host 3 < Host 2 < Host 1

($P_{c1} < P_{c2} < P_{c3}$)

Summary of the model

Full analysis in Taksau. (1998)

Host establishes the defense in the ascending order of $\boldsymbol{P}_{\mathbf{c}i}$.

Example $\boldsymbol{N} = 6$

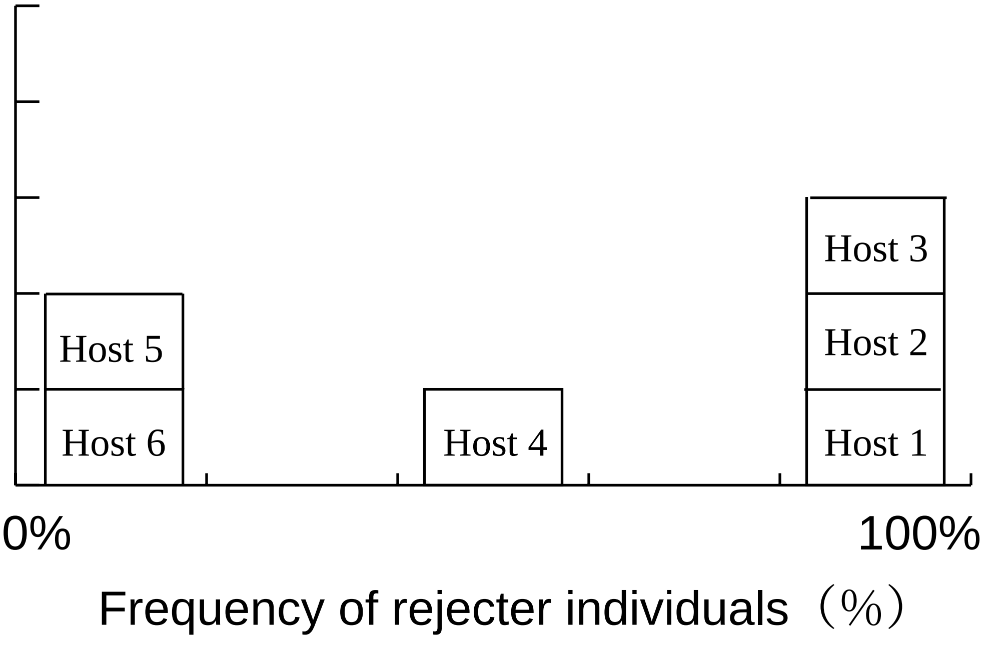
Host 6		Host 5		Host 4		Host 3		Host 2		Host 1
$\boldsymbol{P}_{\mathbf{c6}}$	>	$\boldsymbol{P}_{\mathbf{c5}}$	>	$\boldsymbol{P}_{\mathbf{c4}}$	>	$\boldsymbol{P}_{\mathbf{c3}}$	>	$\boldsymbol{P}_{\mathbf{c2}}$	>	$\boldsymbol{P}_{\mathbf{c1}}$
×		×		△		○		○		○

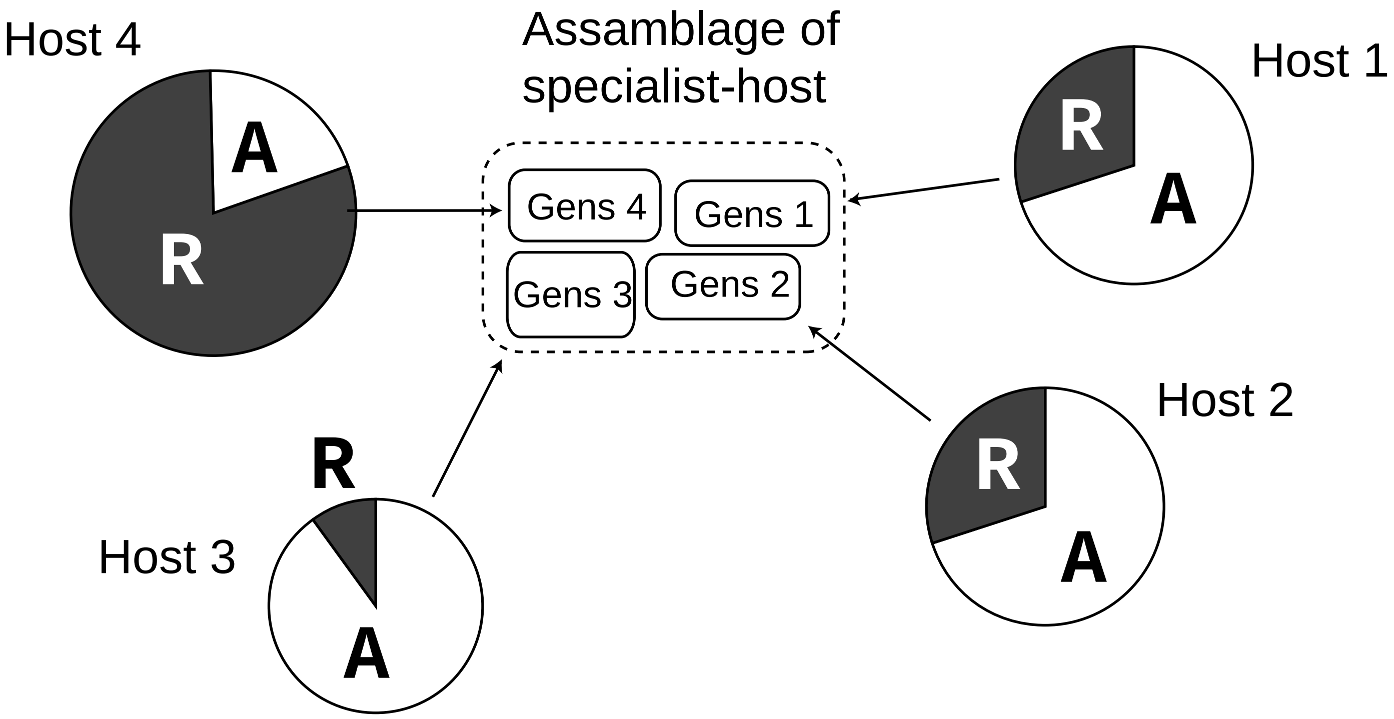
× Rejecters cannot increase. 100% accpters.

△ Rejecters and accepters coexist.

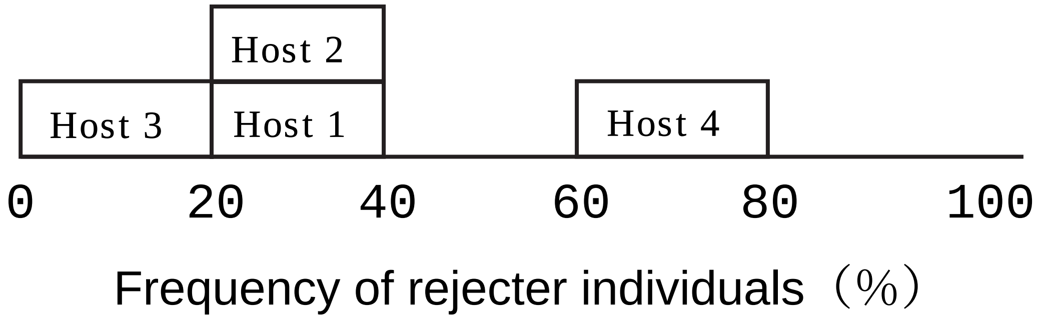
○ Rejecters are fixed. 100% rejecters.

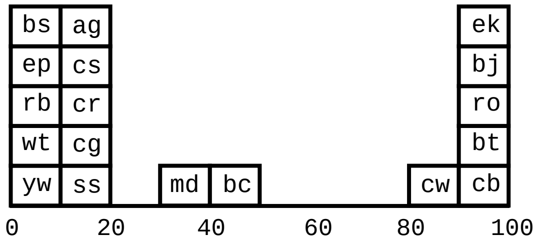
Distribution of defense level

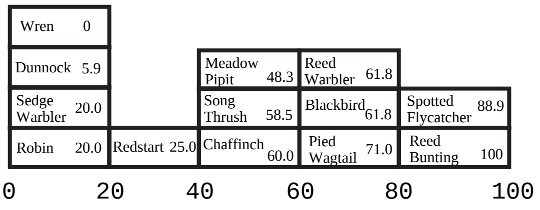




Distribution of defense level







The *bi-modal / continuous distribution* of host defense might be attributed to the parasite's breeding strategy as a *generalist or specialist.*

Summary

1) In case of specialist-host interaction, host may not establish perfect defense.

2) In case of generalist-hosts interaction, hosts establish perfect, intermediate, or no defense.
   There should be some regularity as to the order of the defense levels.

3) Parasite breeding strategy as specialist or generalist affects the distribution form of host defense levels.
   Continuous or bi-modal distribution is expected in associations of specialist or generalist, respectively.

4) Theoretical model should not be of an empty theory.
   Feedback from field study is necessary to build models that help us to understand avinan brood parasitism.

Tasks to be challenged

Extending the model to be more realistic

Heterogeneity of geographic range

Carrying out field study to collect data to test the conclusion derived from the model

The Model Equations

Parasite density: P Host i density: H_i

Genotype frequency of host i

RR: x_i
RA: y_i
AA: z_i $i = 1 \ldots N$

$$P' = \underbrace{s_{\mathrm{P}} P}_{\text{Survivor}} + \sum_{i=1}^{N} \underbrace{\left(1 - e^{-a_i P}\right) \Gamma_i H_i z_i^2}_{\text{Recruitment from Host } i}$$

$$H_i' = \overbrace{\frac{1}{1 + H_i / k_i}}^{\text{Density effect}} \left[\underbrace{s_{\mathrm{H}i}}_{\text{Survivor}} + \underbrace{\left(1 - z_i^2\right) W_{\mathrm{R}i} + z_i^2 W_{\mathrm{A}i}}_{\text{Recruitment}} \right] H_i$$

where $W_{\mathrm{A}i} = f_i \exp\left(-a_i P\right), \; W_{\mathrm{R}i} = \varepsilon_i f_i$

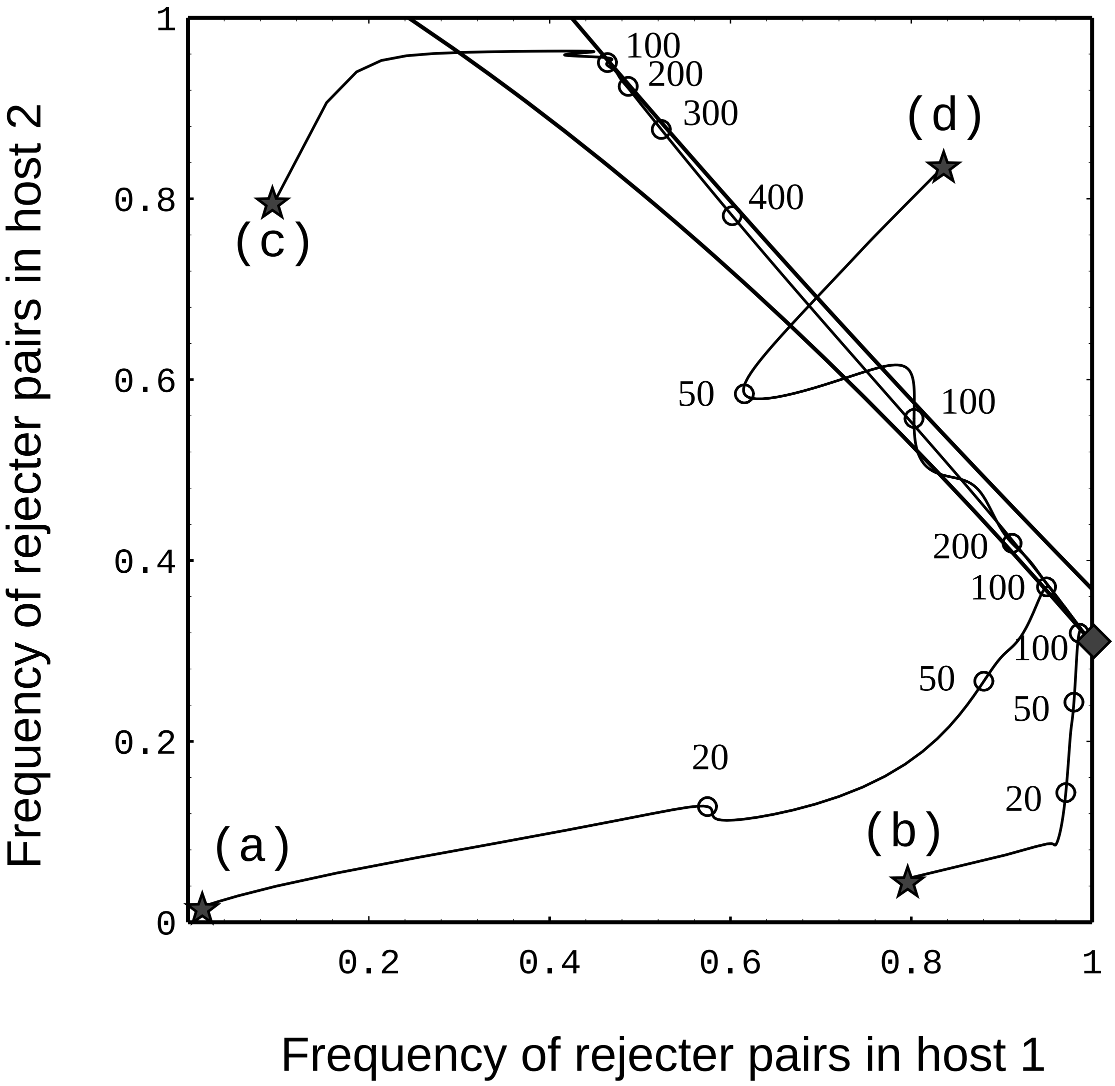
$$x_i' = \frac{s_{\mathrm{H}i} x + W_{\mathrm{R}i} \left(x_i^2 + x_i y_i + y_i^2 / 4\right)}{s_{\mathrm{H}i} + \left(1 - z_i^2\right) W_{\mathrm{R}i} + z_i^2 W_{\mathrm{A}i}}$$

$$y_i' = \frac{s_{\mathrm{H}i} y + W_{\mathrm{R}i} \left(x_i y_i + 2 x_i z_i + y_i^2 / 2 + y_i z_i\right)}{s_{\mathrm{H}i} + \left(1 - z_i^2\right) W_{\mathrm{R}i} + z_i^2 W_{\mathrm{A}i}}$$

s_{P} : Adult Survivorshi
a_i : Searching efficienc
Γ_i : Survivorship of eg
$s_{\mathrm{H}i}$: Adult Survivorshi

Example of the dynamics

Time taken for rejecters to spread (years)



★ The initial state

◆ The stable equilibrium