Theoretical study of host defense in avian brood parasitism in connection with the brown-headed cowbird and the common cuckoo

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Brood Parasitism:

Brood parasite exploits parental care of the host.

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

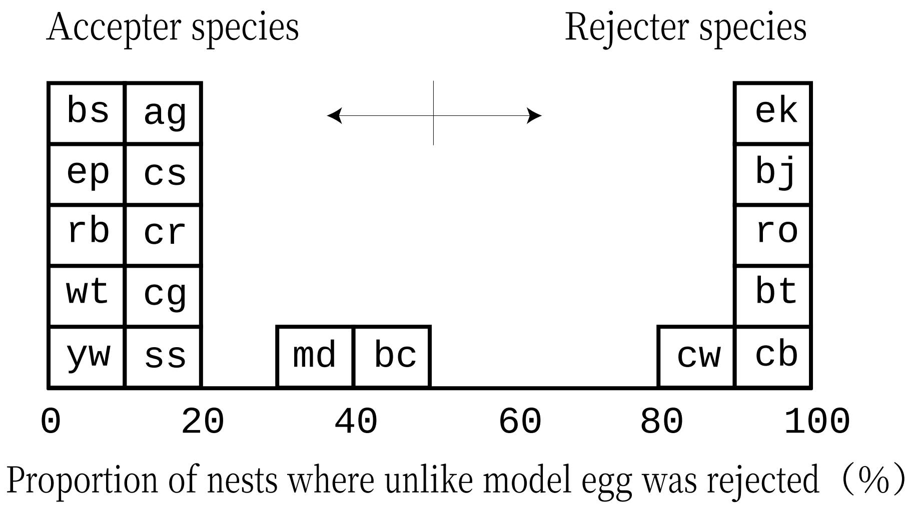
Host defense to avoid the reproductive loss is adaptive and expected to be selected for.

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 species to species and
from population to population even within the same species.

Using a model egg and observing the host behavior, Rothstein (1975, 1990) investigated the proportion of nests where unlike model egg was rejected.

Brown-headed Cowbird's Hosts



Brown-headed Cowbird, *Molothrus ater*

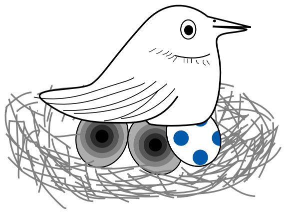
A generalized parasite that parasitizes most passerines with which it is sympatric.

Breeds in North America, but the distribution is expansing due to the opening up of forested areas and the spread of cattles over the past 150 years.

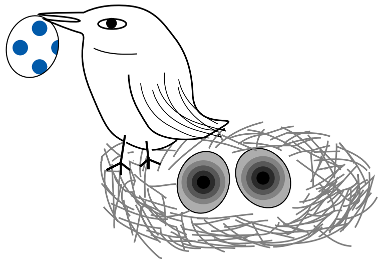
Some newly parasitized host populations have been driven nearly to extinction.

Host species parasized by the Brown-headed Cowbird can be grouped into two categories

Accepter speices that
almost accepts parasitic egg



Rejecter speices that
almost rejects parasitic egg



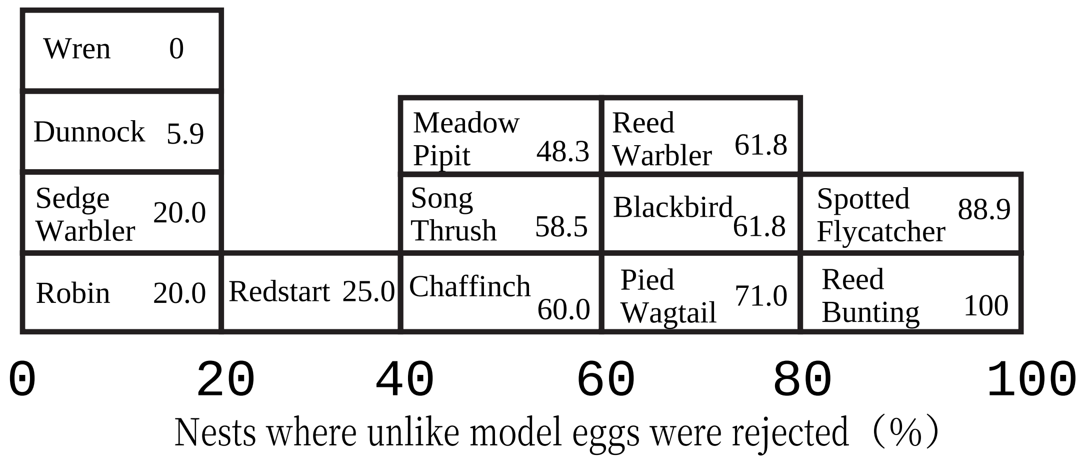
Common Cuckoo, *Cuculus canorus*

It has been suggested that the cukoo population consists of several strains, called gentes, each of which is specialized on a particular host speceis.

It parasitizes many host species, but it has been thought that each gens stands independent with respect to the host usage, by means of 1) the chick's imprinting on the foster and 2) egg markings inherited by daughter from the mother.

Breeds widely in Eurasia. Defense level of the host differs from species to species. Even within the same species, the defense level differs locally.

Davies and Brooke (1989a)
Common Cuckoo's Hosts



The continuous distribution of the host defense level is also demonstrated by Mosknes et al. (1990), Soler and Møller (1990), and Lotem et al. (1992, 1995).

The cuckoo's hosts show defense, the extent of which varying continuously from none to perfect

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The aim of this study is to investigate and to answer

Why is the *constrasted difference* between the cowbird and the cuckoo observed?

What is the cause of the difference?

Basic assumptinos of the model

Parasite uses $\boldsymbol{N}$ host populations labeled by i

Host defense entails cost to perform

The rejection behavior is adaptive when parasitized much, but disadvantageous when few parasitized due to the cost

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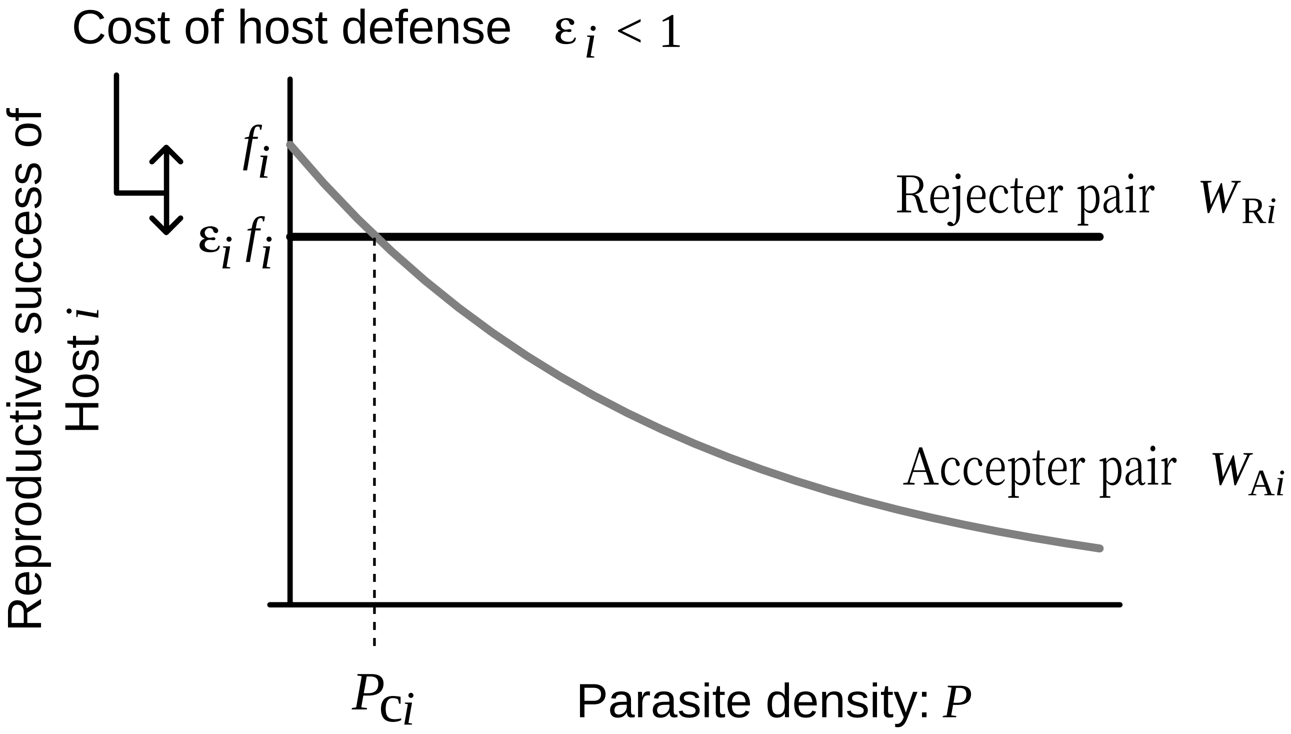
Reproductive success of "Host i" is then given as follows.

$i = 1 \ldots \boldsymbol{N}$



$\boldsymbol{P}_{Ci}$: Threshold parasite density of Host i

$\boldsymbol{P}_{Ci} < \boldsymbol{P}$ Rejecter individuals increase in frequency in Host i

$\boldsymbol{P} < \boldsymbol{P}_{Ci}$ Rejecter individuals decrease in frequency in Host i

Without loss of generality, assume $\boldsymbol{Pc1} < \boldsymbol{Pc2} < \boldsymbol{Pc3} < \ldots < \boldsymbol{PcN}$

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

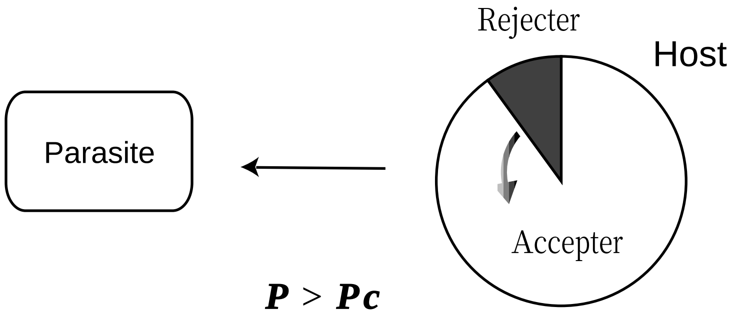
Full analysis in Taksau et al. (1993)

Parasite uses one host population, and can reproduce only from nests of accepter individuals

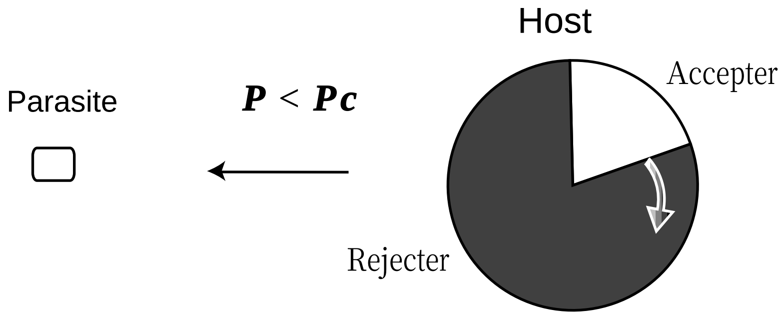
Rejecter individuals, if any, increase in frequency because their reproductive success is greater than that of accepter.

To what extent do the rejecters increase?

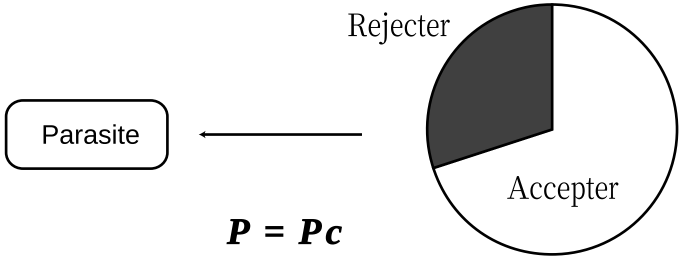
When the frequency of rejecters is low, parasite can reproduce enough from nests of accepters. Parasite density P is great, and rejecters increase in frequency under the strong parasitic pressure.



When rejecters dominate the host population, parasite cannot reproduce enough and its density is low. Accepters increase in frequency because the parasitic pressure is very weak and rejecter is disadvantageous.



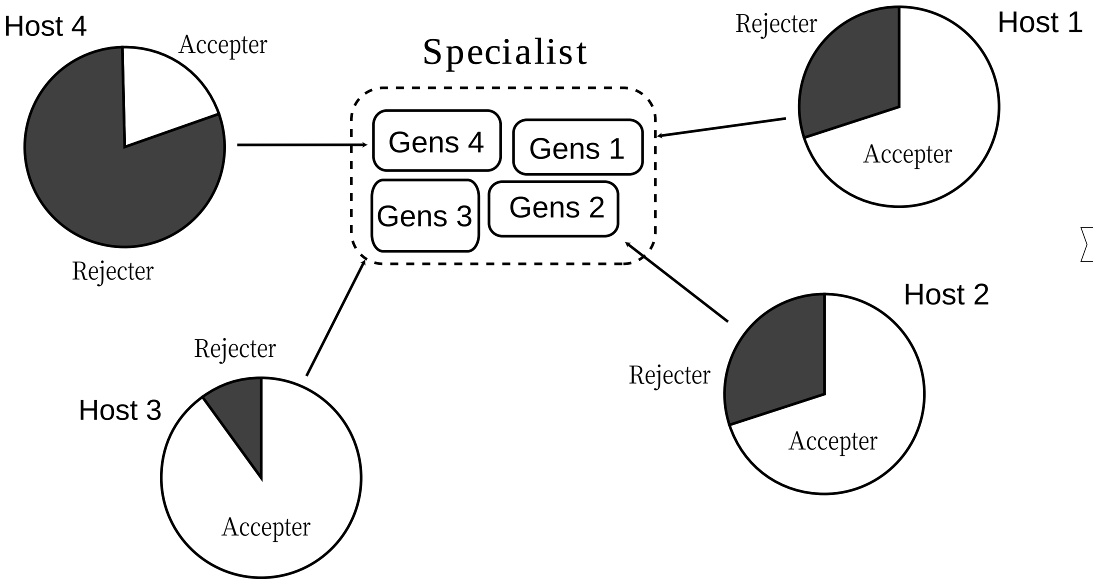
Therefore, accepter and rejecter individuals come to coexist with a certain intermediate frequency as stable equilibrium

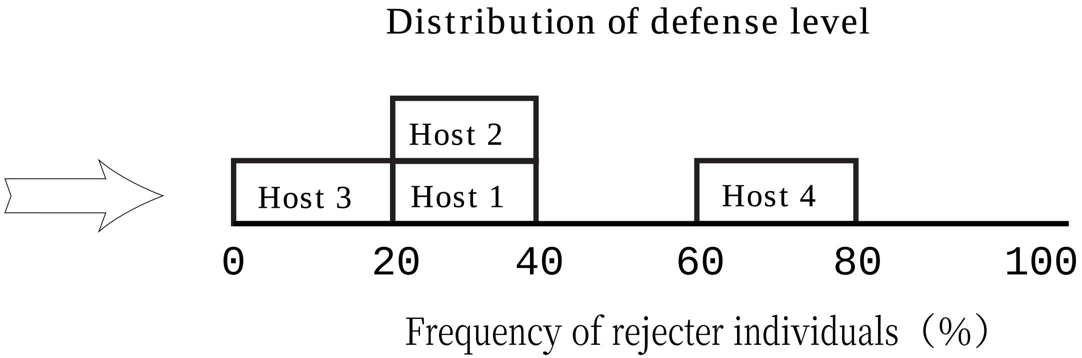


Summary of the specialist case ($N = 1$)

Each interation between a parasite gens and its corresponding host population converges to a stable equilibrium. The equilibrium frequency of rejecters depend on several biological parameters, such as the host carrying capacity and will differ from each other.

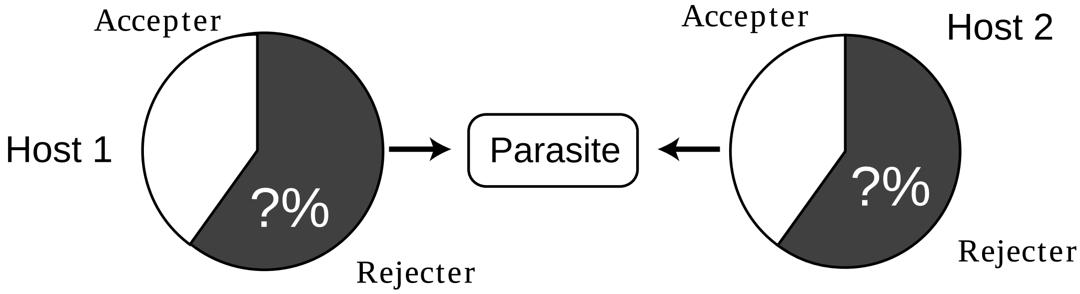
Superimposing the defense levels on one spectrum yields a contiuous distribution of host defense levels as Davies and Brooke (1989a) demonstrated.



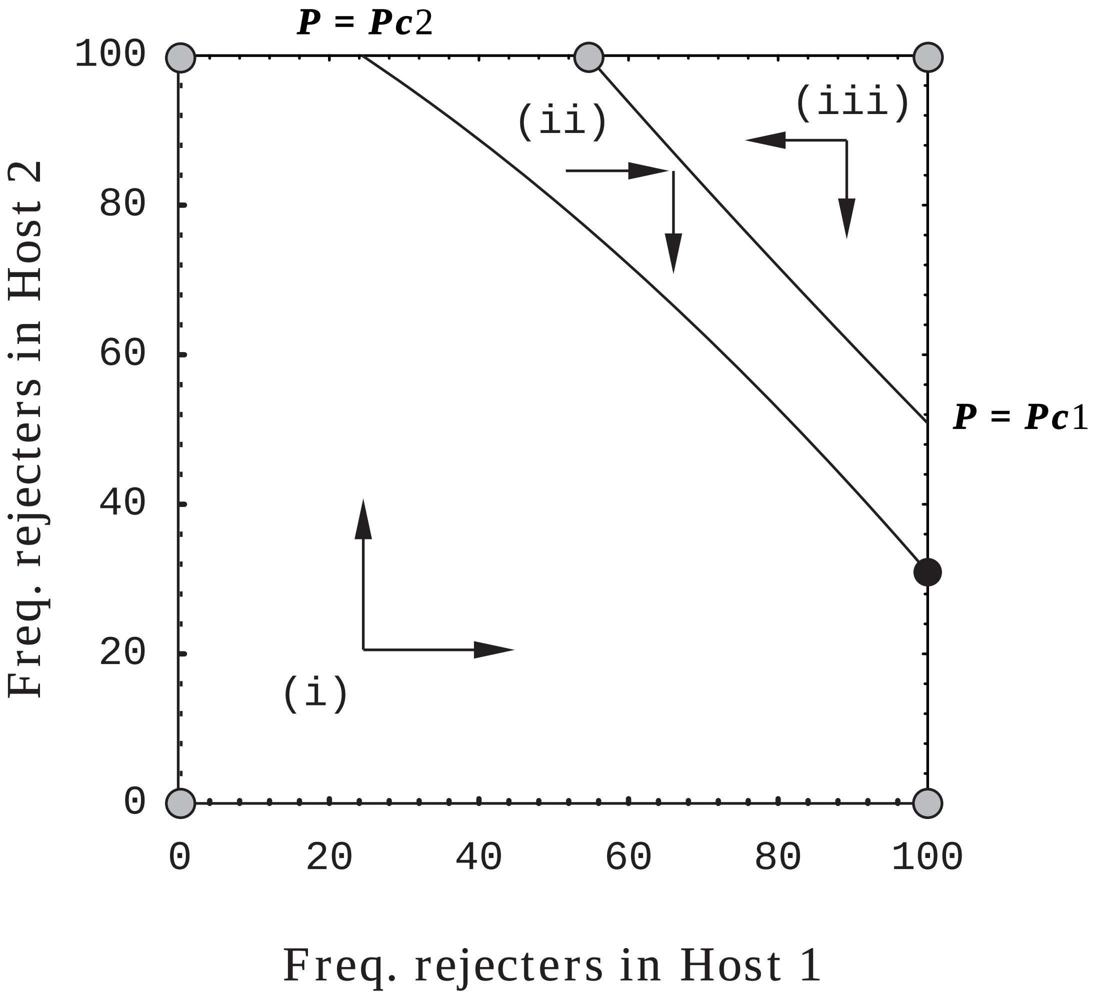


The *continuous distribution* of host defens can be attributed to the cuckoo's breeding strategy as a *specialist* (Takasu in press)

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



1) Take the frequency of rejecters of Host 1 as abscissa, and that of Host 2 as ordinate.
2) Parasnte density ***P*** is given as a function of these frequencies of rejecter individuals.
3) ***P*** takes greater value when both the frequencies are low, while ***P*** approaches 0 as they become higher, because parasite can reproduce only from accepter nests.
4) Then, we have two contour curves that ***P*** = ***Pc***1 and ***P*** = ***Pc***2, in the phase plane.



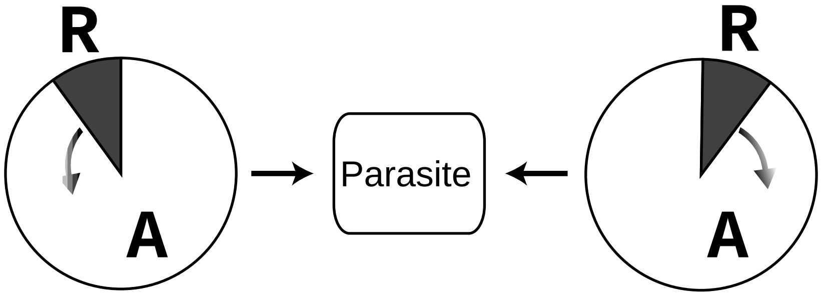
○ Unstable

● Stable

See the next poster for explanation of arrows and stable and unstable equiibria.

In region(i): $Pc1 < Pc2 < P$

Parasite can reproduce enough because accepters predominate both in Host 1 and 2



Rejecter individuals increase
in frequency both in Host 1 and 2

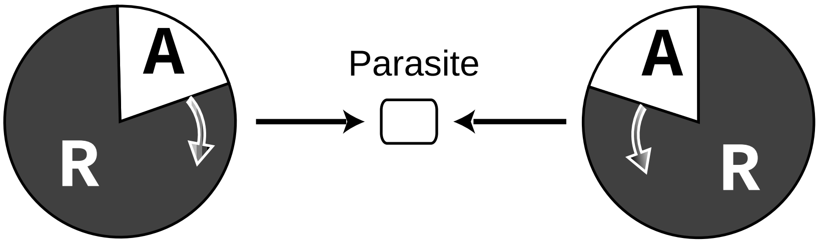
The direction flow of the change in rejecter frequencies
is drawn as arrow in the phase plane.

In region(ii): $Pc1 < P < Pc2$

Accepter individuals increase in frequency in Host 1, but decrease in Host 2

In region(iii): $P < Pc1 < Pc2$

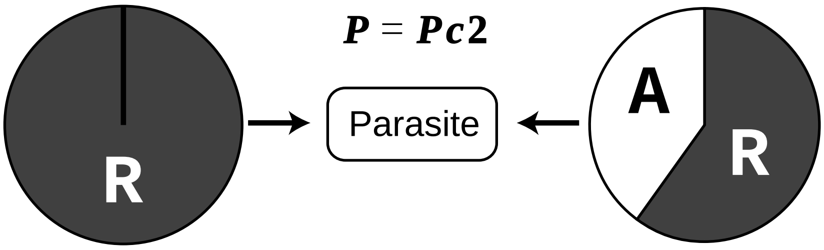
Rejecters predominate both in Host 1 and 2 and parasite cannnot reproduce enough.



Accepter individuals increase
in frequency both in Host 1 and 2

After a long run,

a stable equilibrium is attained (shown by closed circle)

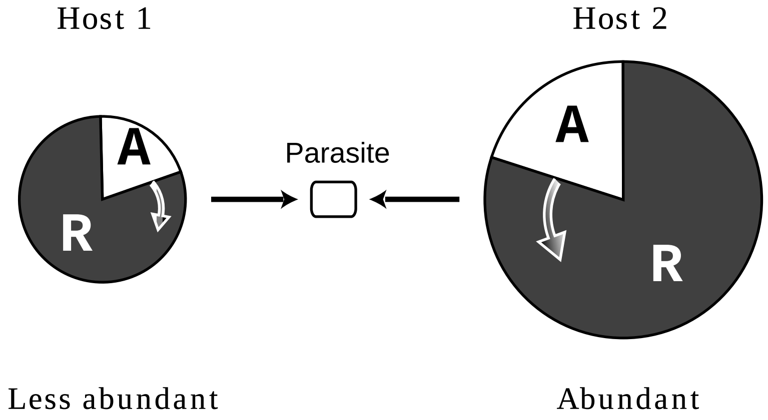


Rejecter is fixed in Host 1, but
rejecter and accepter coexist in Host 2

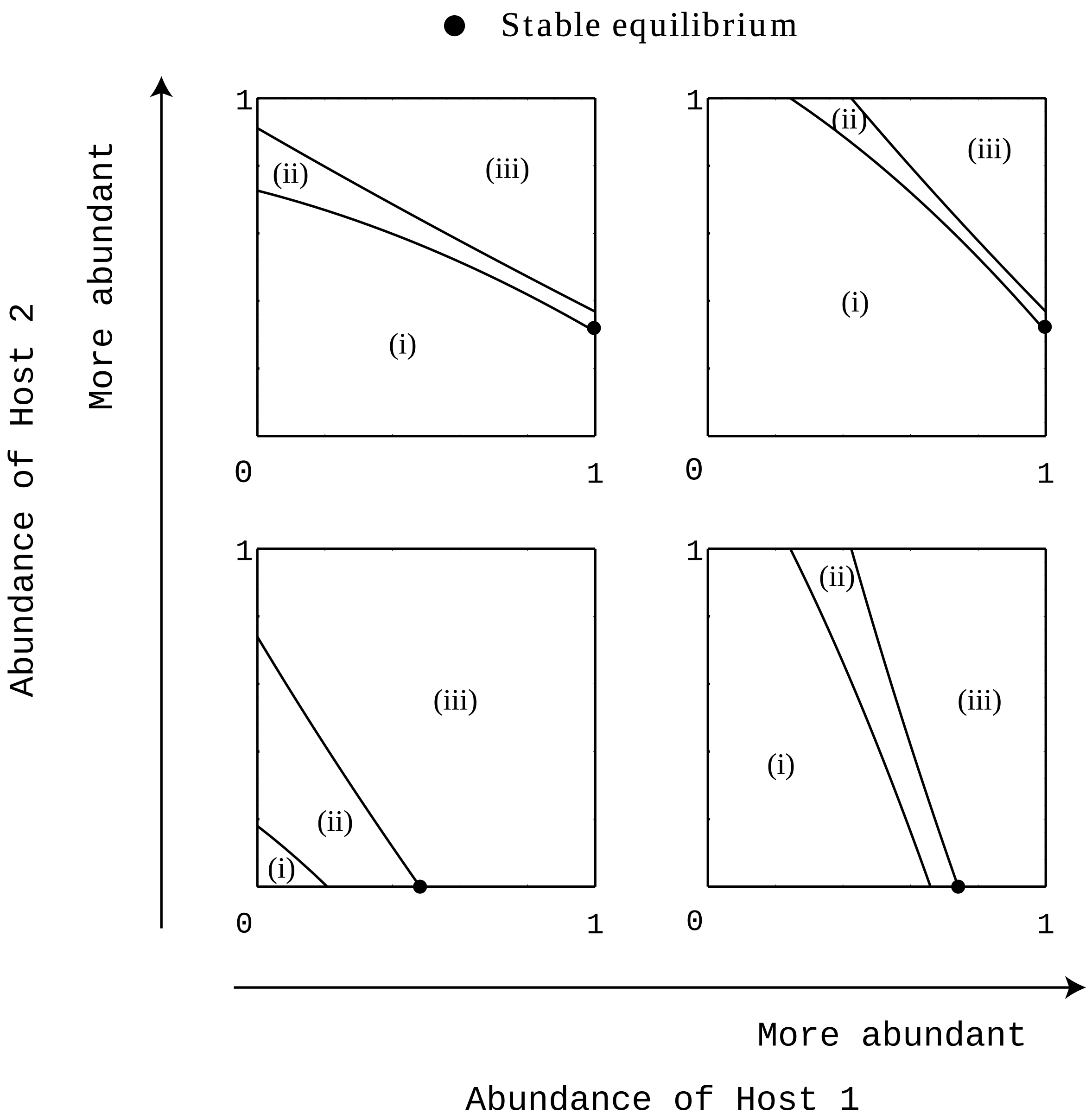
Stable equilibrium depends on the host abundances

The amount of resource available for the parasite repduction is given as the product of the host abundance and the frequency of nests of accepters.

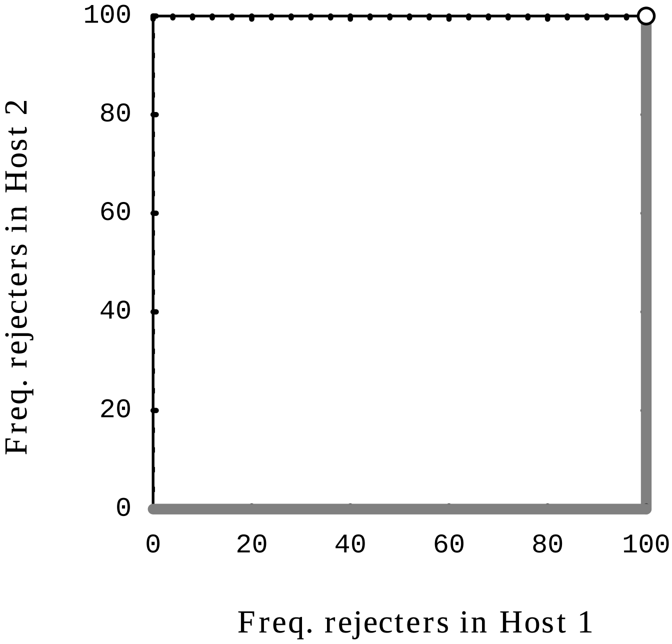
Therefore, the equilibrium state shold depend on the host abundances.



Depending on the host abundances,
the phase diagram looks like either one of the following figures.



For arbitrary combinations of host abundances, the stable equilibrium comes to lie on the following line segments



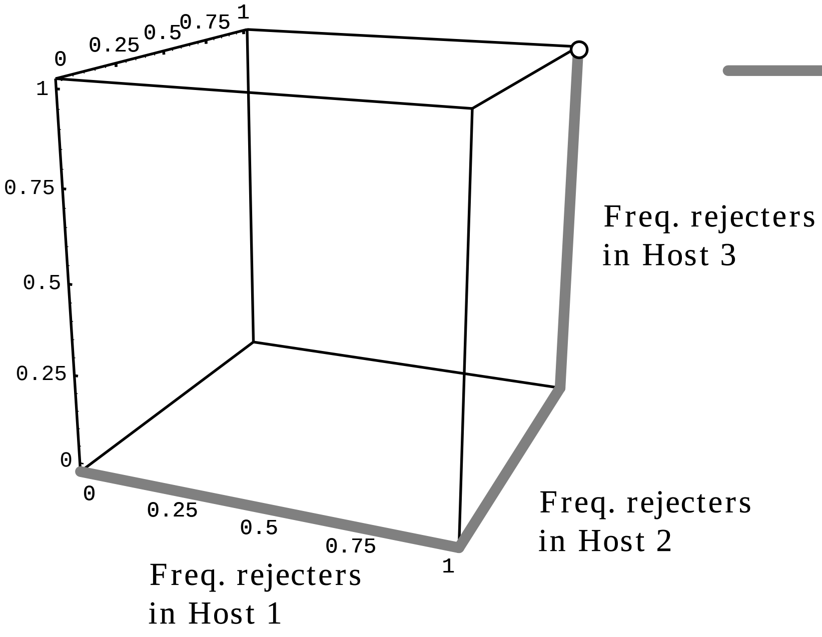
▬ Stable equilibrium is realized on here

Host defense level attained

Host 2 < Host 1

($\boldsymbol{Pc1} < \boldsymbol{Pc2}$)

Using the same techniques, it is shown that the stable equilibrium is attained on the following line segments for any combinations of host abundances for $N = 3$.



▬ Stable equilibrium comes on here

Host defense level attained

Host 3 < Host 2 < Host 1

($\boldsymbol{Pc1} < \boldsymbol{Pc2} < \boldsymbol{Pc3}$)

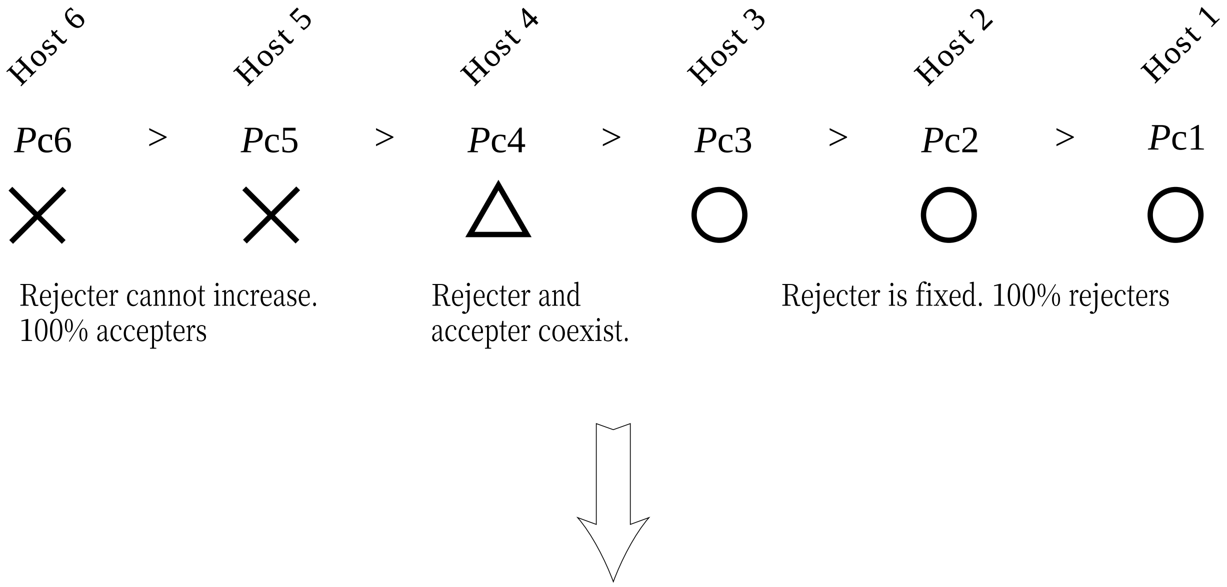
Summary of the generalist case

All the host populations establish none or perfect defense, except for one population that shows an intermediate level of the defense.

Which population exibits a mixture of accepter and rejecter depends on a set of the host abundances as a whole.

In general, host with smaller ***Pci*** establishes the defense at higher level.

Example ***N*** = 6

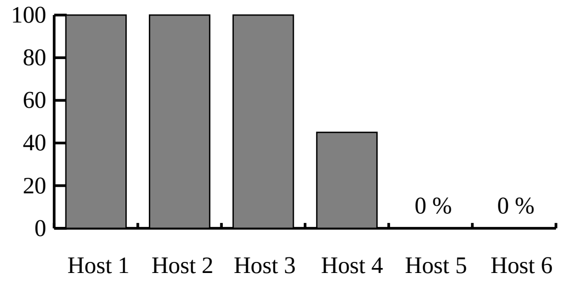


Rejecter cannot increase. 100% accepters

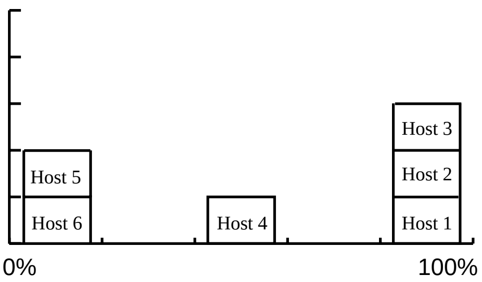
Rejecter and accepter coexist.

Rejecter is fixed. 100% rejecters

Equilibrium frequency of rejecter individuals (%)



Distribution of defense level



The *bi-modal distribution* of the cowbird hosts can be attributed to the cowbird's breeding strategy as a *generalist* (Takasu, submitted)

In this poster, I derived the results heuristically without explicit mathematics. Although I belive that the heuristic and intuitive analysis suffices to grasp the eccense of the model, here I list the original equations for those interested in mathematical models. Analyzing these, of course, results in the same conclusion.

The Mathematical Model

Parasite density: P

Host i density: Hi

Genotype frequency of Host i

RR: xi
RA: yi
AA: zi

$i = 1 \ldots N$

Frequency of accepter pairs (available for parasite reproduction) zi^2

Frequency of accepter pairs (not available for parasite reproduction) $1 - zi^2$

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

s_{p} : Adult Survivorship

a_i : Searching efficiency

Γ_i : Survivorship of egg

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

$s_{\mathrm{H}i}$: Adult Survivorship

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

Densities of offspring with genotype RR, RA, and AA are derived as follows.

RR $H_i W_{\mathrm{R}i} \left(x_i^2 + x_i y_i + y_i^2 / 4\right)$

RA $H_i W_{\mathrm{R}i} \left(x_i y_i + 2 x_i z_i + y_i^2 / 2 + y_i z_i \right)$

AA $H_i W_{\mathrm{R}i} \left(y_i^2 / 4 + y_i z_i \right) + H_i W_{\mathrm{A}i} z_i^2$

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

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

Discussion

Parasite breeding strategy as Specialist or Generalist can greatly affect the distribution form of the host defense level. The model has shown that in associations of specialist, degree of the defense level might be continuously distributed with most falling between none and complete, while it might be bi-modal (either none or perfect) in those of generalist.

Few quantitative studies have been available about associations of avian brood parasitism other than the cowbird and the cuckoo. I encourage further studies that pay attention to the host defense levels in connetion with the parasite breeding strategy to test this idea.

This model does not target avian associations only. It could be applied to arthropod parasite (parasitoid) system where a parasitoid population parasitizes patchy distributed host populations. Variance of local host defense level (degree of resistance against parasitism) might well be explaned by this model.

This model does not take into account the spatial structure (no migration). The conclusion, however, would not change quantitatively even with spatial structure (Takasu, submitted). But, modeling such a case (C.A. model or else) is certainly intriguing and I will (hopefully) present the model analysis somewhere else in future.

References

Davies, N. B., and M. de L. Brooke. 1989a.
An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts:
I. Host egg discrimination. Journal of Animal Ecoogy 58:207-224.

Lotem, A., H. Nakamura, A. Zahavi. 1992.
Rejection of cuckoo eggs in relation to host age: a possible evolutionary equilibrium.
Bebavioral Ecology 3:128-132.

Lotem, A., H. Nakamura, A. Zahavi. 1995. Constrains on egg discrimination and cuckoo-host coevolution. Animal Behavior 49:1185-1209.

Moksnes, A., E. Røskaft, A. T. Braa, L. Korsnes, H. M. Lampe, and H. C. Pedersen, 1990.
Behavioral responses of potential hosts towards artificial cuckoo eggs and dummies.
Behavior 116:64-89.

Rothstein, S. I.. 1975. Evolutionary rates and host defenses against avian brood parasitism.
American Naturalist.109:161-176.

Rothstein, S. I.. 1990. A model system for coevolution: avian brood parasitism.
Ann. Rev. Ecol. Syst. 21:481-508.

Soler, M., and A. P. Møller, 1990. Duration of sympatry and coevolution between the great spotted cuckoo and its magpie host. Nature 343:748-750.

Takasu, F., K. Kawasaki, H. Nakamura, J. E. Cohen, and N. Shigesada. 1993.
Modeling the population dynamics of a cuckoo-host association and the evolution of host defenses.
The American Naturalist 142:819-839.

Takasu, F.. 1997 (in press). Modeling arms race in avian brood parasitism. Evolutionary Ecology.

Takasu, F.. submitted.
Why do not all host species show defense against avian brood parasitsm - evolutionary lag or equilibrium?