Interactions between parasites and hosts

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Interactions between exploiters and victims can result in various forms of adaptations and counter-adaptations

Exploiters try to make use of their victims while the victims try to escape from being exploited

Models of avian brood parasitism

What is avian brood parasitism?

Avian brood parasite exploits parental care of host and usually reduces the reproductive success.

Host defense against brood parasitism is adaptive and some host have evolved an ability to recognize and reject parasite eggs in response to parasitism.

The host defense, in turn, should select for egg mimicry by parasite.

The relationship between host and parasite is expected to result in coevolutionary arms race.

The common cuckoo

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Other cuckoos

ホトトギス

ジュウイチ

ツツドリ

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The brown-headed cowbird

http://www.mbr-pwrc.usgs.gov/id/framlst/i4950id.html

http://animaldiversity.ummz.umich.edu/site/accounts/information/Molothrus_ater.html

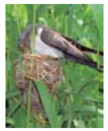
And others

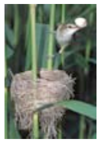
About 1% of 9672 bird species are obligate brood parasites

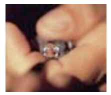
Inter-specific and intra-specific brood parasitism

Adaptations and counter-adaptations

Host adaptive behavior/trait	Parasite adaptive behavior/trait
Attack toward parasite nearby nest	Cryptic & quick behaviors when parasitizing
Egg recognition and rejection	Egg mimicry
Chick recognition and rejection	Chick mimicry







Rothstein and Robinson 1998, Davies 2000

Evolution of host defense

Field studies have shown that

Suitable hosts of the Common Cuckoo, *Cuculus canorus*, show in general an ability to recognize and reject unlike model eggs.

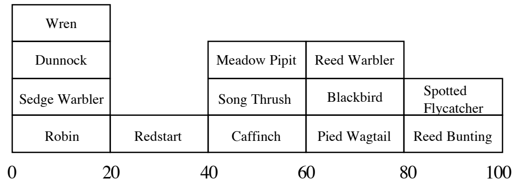
Hosts unsuitable for breeding cuckoo chicks show no such behavior.

Thus, host's ability to recognize and reject unlike egg in nest has evolved in response to brood parasitism.

However, the frequency of host individuals that reject parasitism differs from population to population. Why?

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

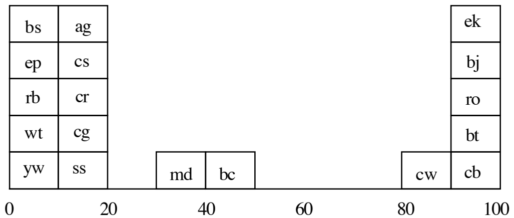
Suitable hosts of the Common Cuckoo, *Cuculus carnorus*



Davies and Brooke 1989

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

Suitable hosts of the Brown-headed Cowbird, *Molothrus ater*



Rothstein 1975

How a cuckoo egg looks

Some cuckoo lays eggs that do not match host eggs. Such eggs would be rejected by hosts

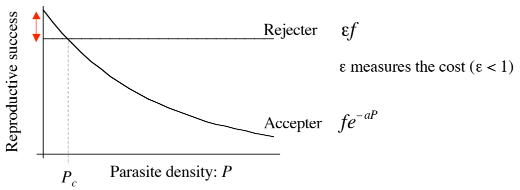
Cuckoo egg in the nest of great reed warbler
An example of poor mimicry

Model assumptions

- Host behavior toward parasitism is genetically determined.
- Host population consists of accepter and rejecter individuals.

Genotype RR, RA : Rejecter
AA : Accepter

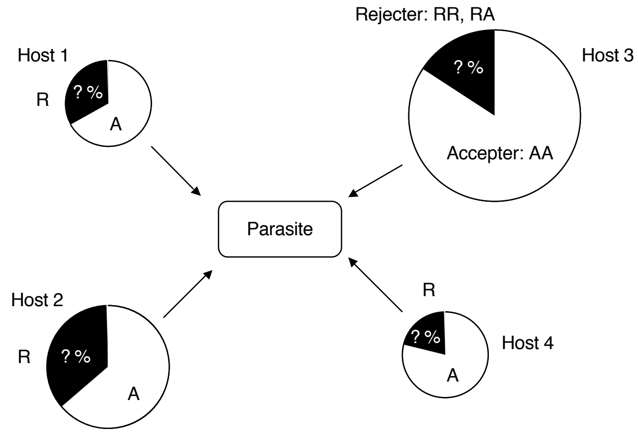
- Recognizing and rejecting parasite egg entails cost to perform.



Rejecting parasitism is more adaptive when severely parasitized ($P > P_c$), while accepting parasitism is more adaptive when no or few parasitism occurs ($P < P_c$).

Model diagram

Parasite exploits N host populations ($N = 4$)



Model equations

Parasite density: P Host i density: H_i $i = 1 \ldots N$

Frequency of genotype RR of Host i: x_i

RA of Host i: y_i AA of Host i: $z_i = 1 - x_i - y_i$

$$P' = s_P P + \sum_{i=1}^{N} (1 - e^{-a_i P}) H_i z_i^2 \Gamma_i$$

$$H_i' = \frac{k_i}{k_i + H_i} \left[s_{Hi} + (1 - z_i^2)\varepsilon_i f_i + z_i^2 f_i e^{-a_i P} \right] H_i$$

$$x_i' = \frac{s_{Hi} x_i + \varepsilon_i f_i (x_i^2 + x_i y_i + y_i^2/4)}{s_{Hi} + (1 - z_i^2)\varepsilon_i f_i + z_i^2 f_i e^{-a_i P}}$$

$$y_i' = \frac{s_{Hi} y_i + \varepsilon_i f_i (x_i y_i + 2 x_i z_i + y_i^2/2 + y_i z_i)}{s_{Hi} + (1 - z_i^2)\varepsilon_i f_i + z_i^2 f_i e^{-a_i P}}$$

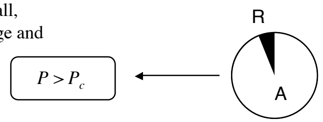
s_P: Parasite survival rate
a_i: Searching efficiency of host i
Γ_i: Survival rate of parasite egg
k_i: Density effect of host i
s_{Hi}: Host i survival rate

Specialist case: $N = 1$

There is a stable equilibrium frequency of rejecter individuals. that is always less than 1 (<100%). Host rejection is never fixed in the population!

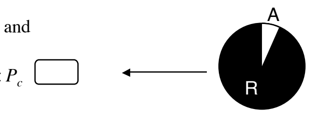
When freq. of rejecters is small,
parasite density becomes large and

freq. of R increases.



When freq. of rejecters is large,
parasite density becomes small and

freq. of A increases. $P < P_c$



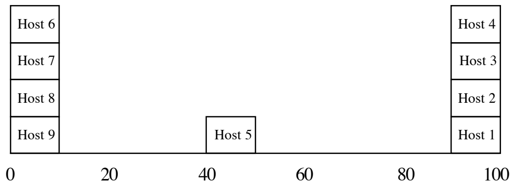
After a long run, the frequency of R reaches an equilibrium state.

The equilibrium frequency critically depends on the host abundance.

Generalist case: $N > 1$

Among N host populations, there exists a unique population that exhibits stable coexistence of rejecter and accepter individuals at equilibrium.
All the other populations consist either of only rejecter or accepter individuals.

Example of the distribution of host defense level at stable equilibrium derived from the model

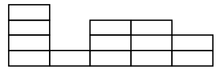


N hosts are distributed in the ascending order of the critical parasite density P_{ci}

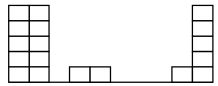
The equilibrium distribution depends critically on the N host abundances.

Real world

Cuckoo hosts show various levels of defense against unlike model eggs

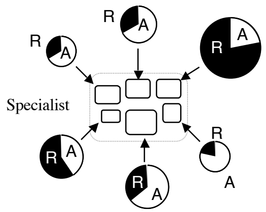


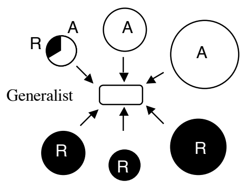
Cowbird hosts show a bi-modal distribution of 100% acceptor and 100% rejecter



Suggestion from the model

Breeding strategy of parasite – specialist or generalist – reflects the difference in the distribution of host defense level





The various defense levels the cuckoo's hosts show and
the bi-modal distribution the cowbird's hosts show can be stationary.