

Models of co-evolution in host-parasite interactions

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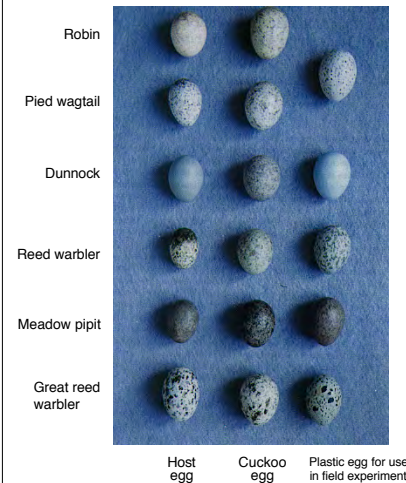


Common Cuckoo *Cuculus canorus*

In avian brood parasitism,

- Parasites exploit parental care of their hosts.
- Accepting parasitism reduces the reproductive success of hosts.
- Some hosts have evolved defense against parasitism - rejection of unlike eggs.
- The host defense selects for egg mimicry by parasites.

Brooke and Davies, 1988, Nature 335:630-632.



In general, common cuckoos have evolved good mimicry.

Parasitic interaction can act as a selective force for co-evolution of egg appearance.

Questions

Hosts that lay eggs looking different from those of the parasites are more adaptive. This will destabilize egg mimicry by parasites.

Hosts lay egg type A and parasites lay egg type A (perfect mimicry).

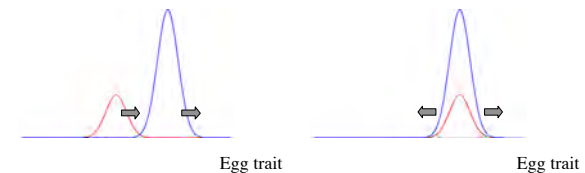
A host that lays egg type B ($B \neq A$) has greater reproductive success because this makes easier recognition and rejection of parasite egg A.

If egg appearance of both hosts and parasites can co-evolve in response to each other, what is the consequence of the arms race concerning egg appearance?

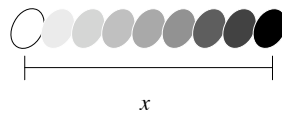
Egg mimicry is a quantitative trait measured in relative scale to host eggs.

Arms race concerning egg patterns

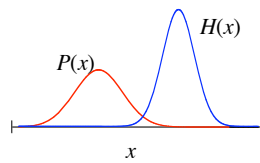
Hosts are shown in blue
Parasites in red



Model assumptions



Egg appearance is one dimensional quantitative trait x .



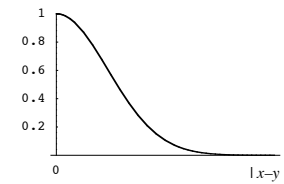
$P(x)$: Population density of parasites x

$H(x)$: Population density of hosts x

Egg trait is asexually inherited from mother to daughter.

Hosts accept or reject parasite's egg according to the difference in the traits.

The probability that a parasite egg y is accepted by a host x , $A(x, y)$, is a decreasing function of the absolute difference $|x - y|$.



$$A(x, y) = \exp[-\gamma(x - y)^2]$$

γ : Sensitivity of host discrimination

The Model (asexual)

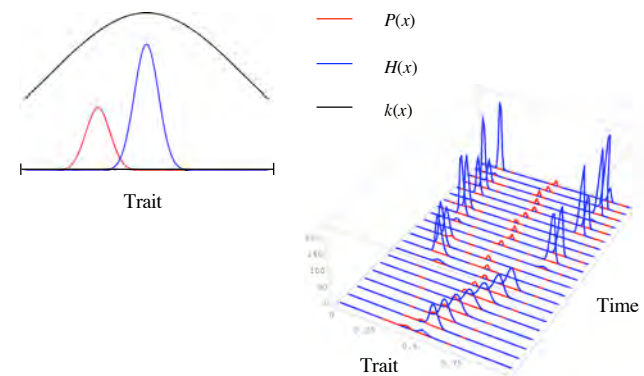
$$P'(y) = \underbrace{s_p P(y)}_{\text{Survival}} + \underbrace{\left\{1 - \exp(-a \int P(y) dy)\right\}}_{\text{Reproduction from host nests}} \frac{P(y)}{\int P(y) dx} \int H(x) A(x, y) dx \Gamma$$

$$H'(x) = \frac{k(x)}{k(x) + \int H(x) dx} \left\{ \underbrace{s_H H(x)}_{\text{Density effect}} + \underbrace{W_{\text{From_not_parasitized}}}_{\text{Survival}} + \underbrace{W_{\text{From_parasitized}}}_{\text{Reproduction from unparasitized and parasitized nests}} \right\}$$

$$W_{\text{From_not_parasitized}} = \int \exp(-a \int P(y) dy) H(x)$$

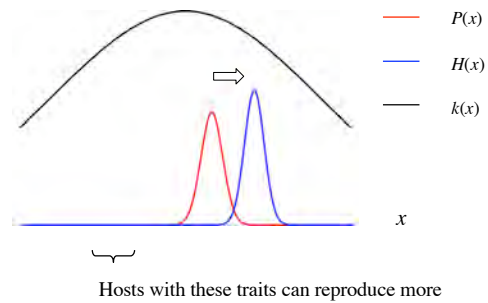
$$W_{\text{From_parasitized}} = \int \left\{1 - \exp(-a \int P(y) dy)\right\} \frac{\int P(y) \{1 - A(x, y)\} dy}{\int P(y) dx} H(x)$$

The dynamics (asexual)

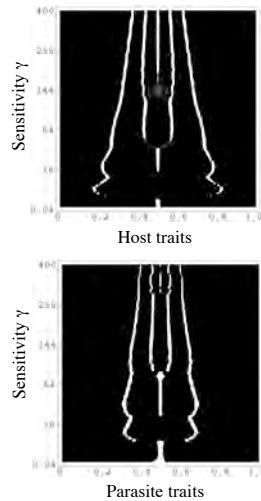
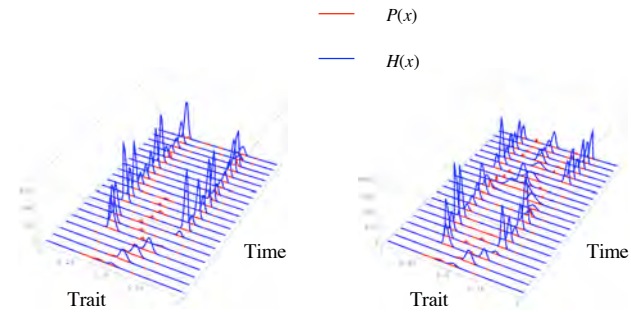


Discrete polymorphism can occur (asexual)

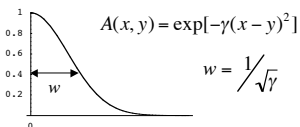
As parasites chase their hosts to one extreme, hosts that lay eggs of the opposite types become more adaptive and begin to increase.



The dynamics (asexual)



Traits are placed discretely in the trait space. The greater the sensitivity γ , the larger the number of traits that survive.



Summary asexual

If egg appearance is asexually inherited to offspring,

- Discrete polymorphism of egg patterns easily emerges.
- As hosts have higher sensitivity against unlike eggs, the number of the discrete traits increases.
- Perfect mimicry is not always realized.

The deterministic model has produced an unrealistic behavior of sudden appearance of traits in the opposite side. Comparison with stochastic individual-based model would be useful.

Trait is sexually inherited

Assume that the trait of an offspring, z , is distributed around the mid-point value of its parents, $(x + y)/2$.

Given a frequency distribution of parent trait x , $f(x)$, the frequency distribution of offspring trait z is given as

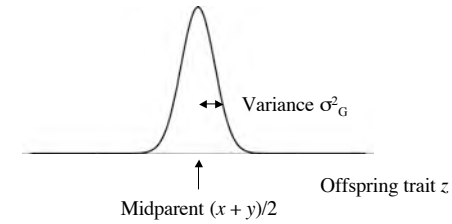
$$f'(z) = \iint f(x)f(y)k(z, x, y)dx dy$$

where $k(z, x, y)$ is the distribution of offspring trait z from a pair of parents x and y , e.g.,

$$k(z, x, y) = \frac{1}{\sqrt{2\pi}\sigma_G} \exp\left[-\frac{\left(z - \frac{x+y}{2}\right)^2}{2\sigma_G^2}\right]$$

$$k(z, x, y) = \delta(z - x) \text{ if trait is asexually inherited}$$

Distribution of offspring trait (hypothetical)



Variance σ_G^2 is assumed to be constant and take a different value for hosts and parasites.

The Model (sexual)

$$P'(z) = s_P P(z) + \left\{1 - e^{-aP_T}\right\} \frac{1}{P_T^2} \int P(x) \underbrace{\int H(y) A(x, y) dy}_{\text{Offspring of } P(x) \text{ accepted}} \underbrace{P(y) k_P(z, x, y) dy dx}_{\text{Prob. of mating with } y \text{ to produce offspring } z}$$

$$H'(z) = \frac{k(z)}{k(z) + H_T} \left\{ s_H H(z) + W_{\text{From_no_parasitized}} + W_{\text{From_parasitized}} \right\}$$

$$W_{\text{From_no_parasitized}} = f e^{-aP_T} \frac{1}{H_T} \int H(x) \int H(y) k_H(z, x, y) dy dx$$

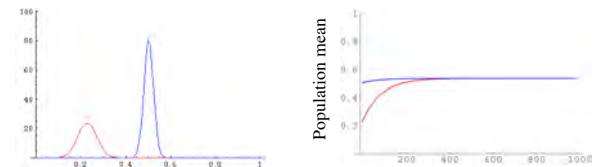
$$W_{\text{From_parasitized}} = f \left\{1 - e^{-aP_T}\right\} \frac{1}{P_T H_T} \int H(x) \int P(y) \{1 - A(x, y)\} dy \int H(y) k_H(z, x, y) dy dx$$

$$P_T = \int P(y) dy \quad H_T = \int H(x) dx$$

The dynamics (sexual)

$$\sigma_{GP} = 2\sigma_{GH}$$

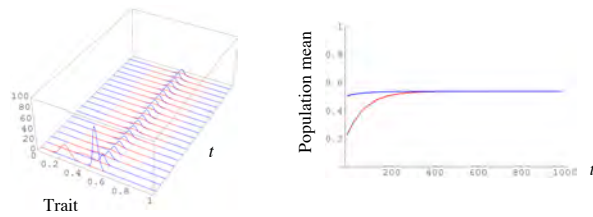
Parasite
Host



The dynamics (sexual)

$$\sigma_{GP} = 2\sigma_{GH}$$

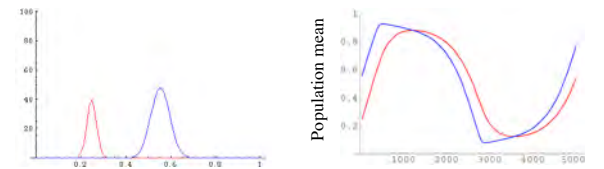
— Parasite
— Host



The dynamics (sexual)

$$\sigma_{GP} = \frac{1}{2}\sigma_{GH}$$

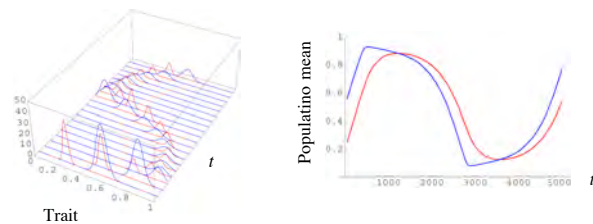
— Parasite
— Host



The dynamics (sexual)

$$\sigma_{GP} = \frac{1}{2}\sigma_{GH}$$

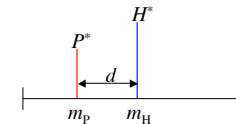
— Parasite
— Host



The threshold ratio $\sigma_{GP}^2/\sigma_{GH}^2$

There exists a threshold ratio of the genetic variances $\sigma_{GP}^2/\sigma_{GH}^2$.

$$\frac{\sigma_{GP}^2}{\sigma_{GH}^2} = \frac{fP^*}{(1 + H^*/k)H^*} = \theta$$



If $\sigma_{GP}^2/\sigma_{GH}^2 > \theta$ ---> converges to a stable state

Wider distribution of parasites' eggs acts as stabilizing force to keep the host distribution fixed in the trait space.

If $\sigma_{GP}^2/\sigma_{GH}^2 < \theta$ ---> oscillates in the trait space

Wider distribution of hosts' eggs makes possible for hosts to evade always from parasites.

Summary sexual

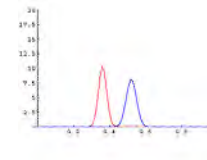
If egg appearance is sexually inherited (distributed around mid-parent)

- Polymorphism does not occur.
- There exists a threshold for the ratio of variances of parasites and hosts traits.
- The system either converges to a stable state where parasite distribution acts to stabilize host distribution, or shows oscillation in the trait space where hosts can always evade from parasites.

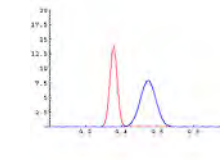
The deterministic model might produce an unrealistic behavior.
Comparison with stochastic individual-based model would be useful.

Sexual hosts and asexual parasites

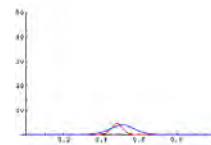
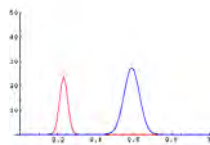
Parasites' mutation rate high or
Hosts' variance low



Parasites' mutation rate low or
Hosts' variance high



Asexual hosts and sexual parasites



Conclusions

If egg trait of both hosts and parasites can evolve, the co-evolutionary consequences are very different depending on the mode of egg trait inheritance.

When egg trait is asexually inherited both in hosts and parasites, discrete polymorphism can be a stable state where perfect egg mimicry is not necessarily achieved.

When egg trait is sexually inherited either in hosts or parasites or in both, co-evolutionary cycle can occur. The maintenance of egg trait variance is crucial for the cycle.

Comparison with individual-based models would be useful to validate these conclusions derived from deterministic population dynamics models.

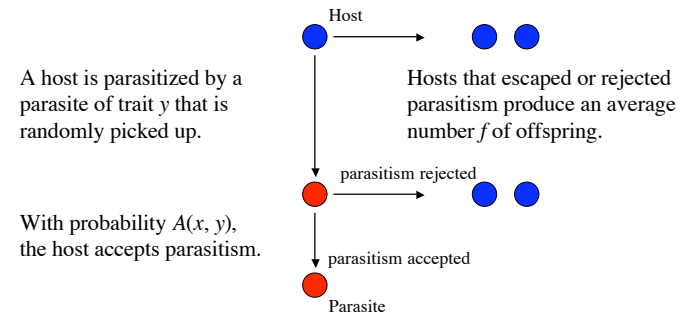
Real world

1. We may observe co-evolutionary change of egg appearance of both parasites and hosts in the field.
2. In some host species, there exist distinct types of egg within a population. This could be maintained by parasitic interaction.
3. Red-chested cuckoo *Cuculus solitarius* lays eggs of at least three different types, none of which matches those of the most commonly used host species.

Quantitative measurement of egg trait, the genetic mode of the inheritance, and comparative study in areas with various history of parasitism are needed to test co-evolution in action in brood parasitism.

Individual Based Model (asexual)

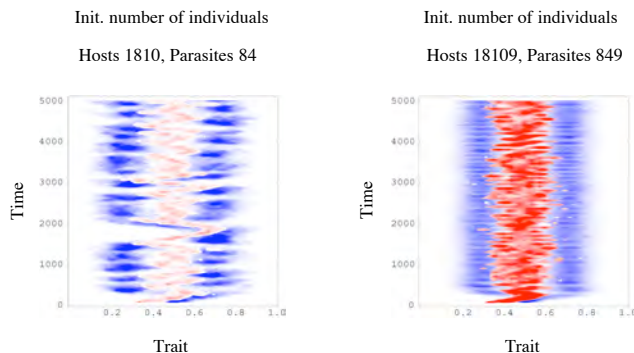
Each individual is assigned a trait value x .



Offspring trait is distributed around the parents' trait value.

Adult individuals survive with s_P and $k(x)/(k(x) + H_{\text{total}}) s_H$.

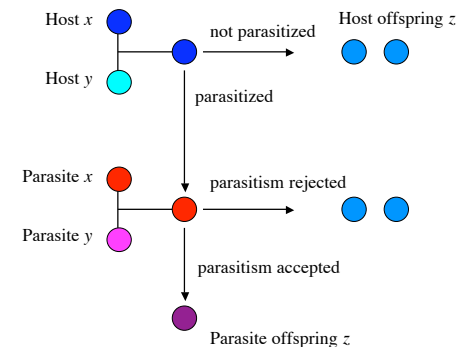
Simulation (asexual)



Individual Based Model (sexual)

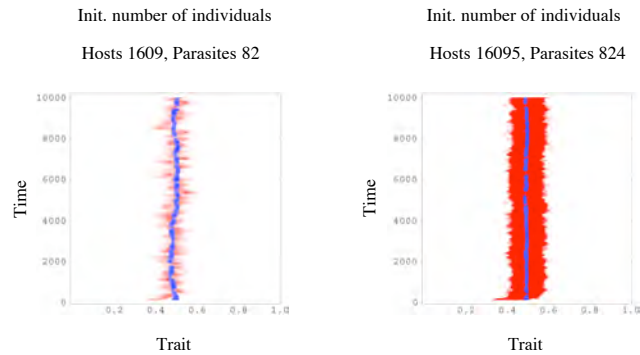
For each individual, pick up a mate randomly.

For each individual, pick up a mate randomly.

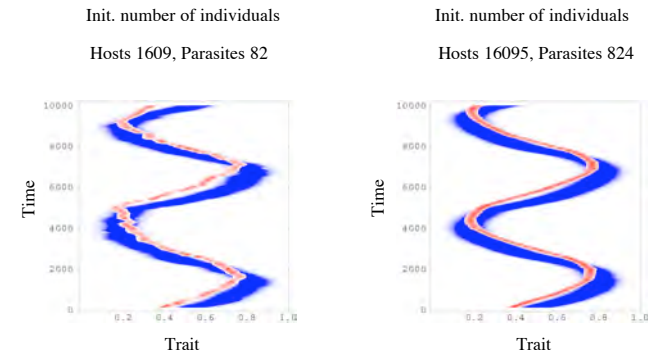


Offspring trait z is distributed around the mid-parent value.

Simulation (sexual)



Simulation (sexual)



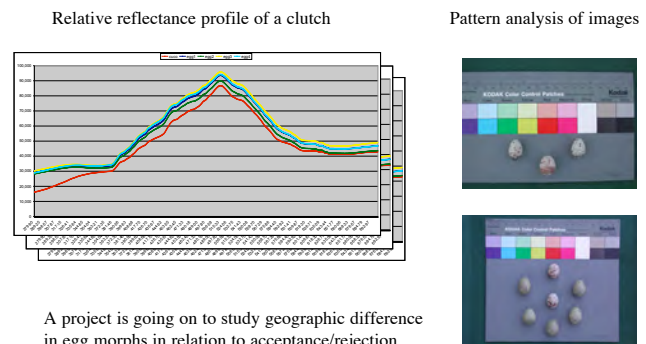
Conclusion

If egg trait is asexually inherited to offspring both in hosts and parasites,
discrete polymorphism easily emerges but
stochasticity might hinder the realization of polymorphism.

If egg trait sexually inherited both in hosts and parasites
(distributed around parent midpoint),

blending of trait makes discrete polymorphism difficult and
coevolutionary cycle can occur.

Quantitative measurement of egg morphs



A project is going on to study geographic difference
in egg morphs in relation to acceptance/rejection
Muñoz, Barta, Moskat, Nakamura and Takasu

Avian brood parasitism

Conspecific avian brood parasitism

- Laying of eggs in the nest of another individual of the same species
- Observed in many bird species in various taxa
- Could be a strategy to increase the fitness of the actor
- The actor shares the risk of being parasitized

At least 185 species out of about 10,000 birds are conspecific brood parasite

Almost all conspecific brood parasites are facultative parasites

About 100 species are obligate brood parasites like the common cuckoo

A puzzle

Jackson 1992, 1993, 1998

The Northern Masked Weaver *Ploceus taeniopterus*, a conspecific brood parasite, has remarkably variable eggs. Between-female variation is very high.

They discriminate and reject eggs of unlike color from their own.

Egg pattern specific to each female probably works as a signature to discriminate parasitic eggs. But this should select against behaving as parasite.



Northern Masked Weaver
<http://www.kenyabirds.org.uk/weaver-nm.htm>



Eggs of the Village Weaver *Ploceus cucullatus*
Photo from Collias E.C., 1993, Auk 110: 683-692

IBM Assumption

I) An individual is assigned a set of three adaptive traits.

- 1) allocation rate of eggs as parasitic, p ($0 \leq p \leq 1$)
- 2) rejection rate as the probability to behave as rejecter, r ($0 \leq r \leq 1$)
- 3) egg appearance as a quantitative trait, e ($-\infty < e < \infty$)

An individual with (p, e, r)

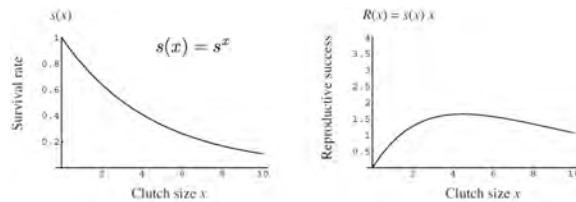
distributes pN eggs parasitically one by one in a randomly chosen nest and the rest $(1 - p)N$ in own nest. The number of total eggs N is fixed.

behaves as rejecter with probability r . It actually rejects parasitic egg e' with probability $R(e, e')$. $R(e, e')$ is an increasing function of $|e - e'|$ and $R(e, e) = 0$.

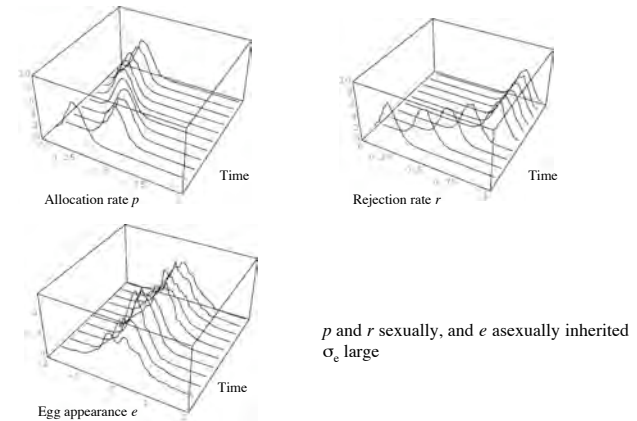
Assumption 2

II) Potential to rear a clutch is limited.

The survival rate of an egg in a clutch, $s(x)$, decreases as the clutch size x increases.

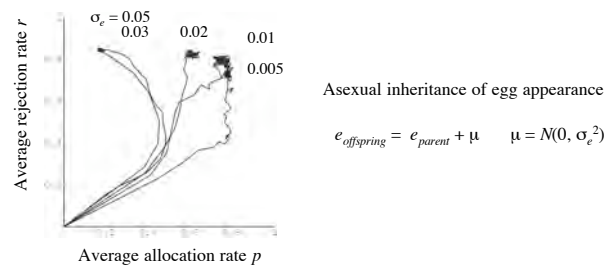


An example



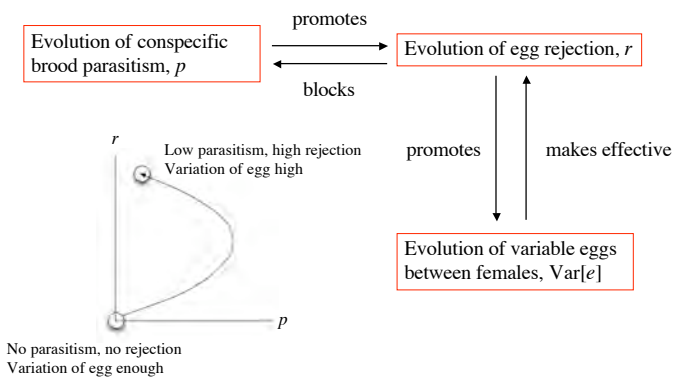
Evolutionary trajectories

Trajectories of the mean p and r for various mutation rates of egg appearance e



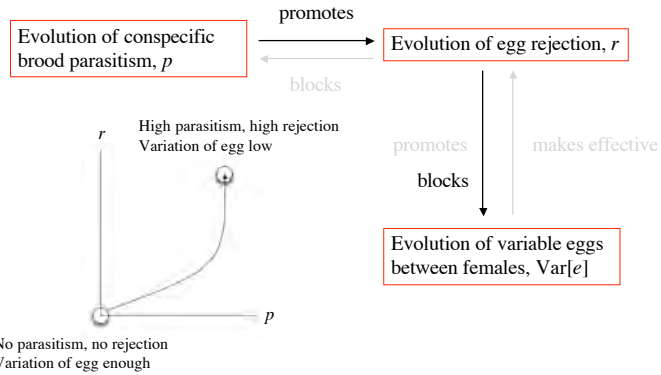
IBM: Summary 1

If enough variation of egg appearance is assured



IBM: Summary 2

If the variation of egg appearance is kept low



From IBM to analytical model 1

Let $n_t(p)$ be the density of individuals with trait p at time t ($0 \leq p \leq 1$)

Reproductive output from own nest

$$s((1-p)N + N_{para}) \times (1-p)N$$

Reproductive output from other nests

$$cpN \int s((1-p')N + N_{para} + 1) \frac{n_t(p')}{\int n_t(p)dp} dp'$$

$$N_{para} : \text{Poisson with mean } \lambda = N \frac{\int p n_t(p) dp}{\int n_t(p) dp}$$

c : Cost of behaving as parasite ($0 \leq c \leq 1$)

Analytical model 1

Assume p is asexually inherited and derive i -state distribution of p .

$$n_{t+1}(p) = s_H n_t(p) + E[s((1-p)N + N_{para})(1-p)N] n_t(p) + cpN \int E[s((1-p')N + N_{para} + 1)] \frac{n_t(p')}{\int n_t(p)dp} dp' n_t(p)$$

If $s(x) = s^x$, expanding expectation $E[*]$ gives

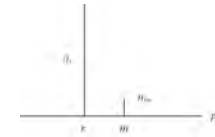
$$n_{t+1}(p) = s_H n_t(p) + (1-p)N s^{(1-p)N} s^{\lambda(s-1)} n_t(p) + cpN \int s^{1+(1-p')N} e^{\lambda(s-1)} \frac{n_t(p')}{\int n_t(p)dp} dp' n_t(p)$$

Adaptive dynamics of p

Assume monomorphic resident and mutant populations.

$$n_t(p) = n_r \delta(p-r) + n_m \delta(p-m)$$

$$n'_m = s_H n_m + (1-m)N s^{(1-m)N} e^{\lambda(s-1)} n_m + cmN \frac{n_r s^{1+(1-r)N} + n_m s^{1+(1-m)N}}{n_r + n_m} n_m$$



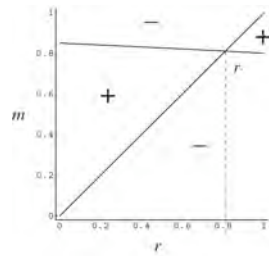
Fitness of the mutant in the resident population, $F_r(m)$, is

$$F_r(m) = \lim_{n_m \rightarrow 0} \frac{n'_m}{n_m} = s_H + (1-m)N s^{(1-m)N} e^{\lambda(s-1)} + cmN s^{1+(1-r)N} e^{\lambda(s-1)}$$

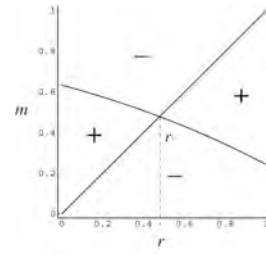
$$\lambda = rN$$

Pairwise invasibility plot

No cost of behaving as parasite $c = 1$



$c = 0.5$



$s = 0.9, N = 10$

From IBM to analytical model 2

Let $n_t(p, r)$ be the density of individuals with (p, r) at time t

p : allocation rate of eggs as parasitic

r : rejection rate of alien eggs

Reproductive output from own nest

$$s((1-p)N + (1-r)N_{para}) \times (1-p)N$$

Reproductive output from other nests

$$cpN \int (1-r')s((1-p')N + (1-r')(N_{para} + 1)) \frac{n_t(p', r')}{\int n_t(p, r) dp dr} dp' dr'$$

$$N_{para} : \text{Poisson with mean } \lambda = N \frac{\int p n_t(p, r) dp dr}{\int n_t(p, r) dp dr}$$

Analytical model 2

Assume p and r is asexually inherited and derive i -state distribution of p and r .

If $s(x) = s^x$, expanding expectation $E[*]$ gives

$$n_{t+1}(p, r) = s_H n_t(p, r) + (1-p)N s^{(1-p)N} e^{\lambda(s^{1-r}-1)} n_t(p, r) + cpN \int (1-r')s^{1-r'+(1-p')N} e^{\lambda(s^{1-r'}-1)} \frac{n_t(p', r')}{\int n_t(p, r) dp dr} dp' dr' n_t(p, r)$$

Adaptive dynamics of p and r

Assume monomorphic resident (p_0, r_0) and mutant (p_1, r_1) populations.

$$n_t(p, r) = n_0 \delta(p - p_0) \delta(r - r_0) + n_1 \delta(p - p_1) \delta(r - r_1)$$

Fitness of the mutant

$$F_{p_0, r_0}(p_1, r_1) = \lim_{p_1, r_1 \rightarrow 0} \frac{n'_1}{n_1} = s_H + (1-p_1)N s^{(1-p_1)N} e^{\lambda(s^{1-r_1}-1)} + c(1-r_0)p_1 N s^{1-r_0+(1-p_0)N}$$

Invasion fitness of the mutant

$$S_{p_0, r_0}(p_1, r_1) = F_{p_0, r_0}(p_1, r_1) - F_{p_0, r_0}(p_0, r_0) = \dots$$

Evolutionary trajectory of p and r

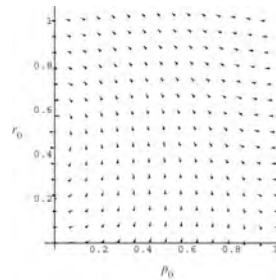
Local fitness gradient for r is non-negative

$$\left. \frac{\partial S}{\partial r_1} \right|_{p_1=p_0, r_1=r_0} \approx -p_0(1-p_0) \log s \geq 0$$

Direction of evolutionary trajectory

$$\frac{dp_0}{dt} = k_p \left. \frac{\partial S}{\partial p_1} \right|_{p_1=p_0, r_1=r_0}$$

$$\frac{dr_0}{dt} = k_r \left. \frac{\partial S}{\partial r_1} \right|_{p_1=p_0, r_1=r_0}$$



Results

We have qualitatively different two consequences:

- 1) Low parasitism, high rejection, variable eggs
- 2) High parasitism, high rejection, and nearly monomorphic eggs

The mutation rate of egg appearance is the key to determine the fate of the evolutionary dynamics. The threshold for the mutation rate to be explored

The weaver might owe its variable eggs to the high mutation rate

Comparative study on physiological mechanisms of egg shell production would be challenging in the *Ploceus* weavers

