

# Change to structure of Exam 3

- Equations you do not need to memorize will now be included as an Appendix
- Equations will no longer be included within the question in which they are used

**What does this mean for you?**

➔ You need to be able to recognize which equation you should use for each type of question

# Mutualism



# Types of interactions between species

<b>Interaction</b>	<b>Effect on Species 1</b>	<b>Effect on Species 2</b>
<b>Competition</b>	-	-
<b>Antagonism</b>	-	+
<b>Mutualism</b>	+	+

# Mutualisms are pervasive

## Important types of mutualisms:

- **Pollination mutualisms**
- **Dispersal mutualisms**
- **Protection mutualisms**
- **Nutrient acquisition mutualisms**

# Pollination mutualisms



*Angraecum arachnites*  
(Madagascan orchid)



**Hawkmoth**

- Plants get ovules fertilized
- Animals get pollen or nectar as food

# Pollination mutualisms





# Pollination mutualisms



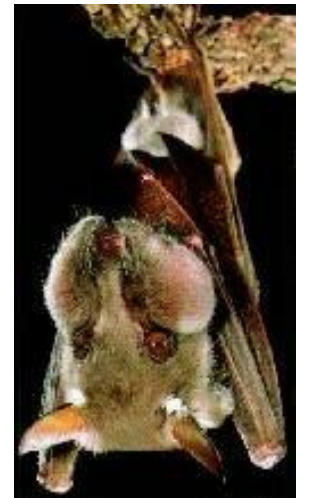
*Marcgravia evenia* has leaves that act like satellite dishes.

Photograph courtesy Corinna U. Koch

# Seed dispersal mutualisms

## *Epomophorous wahlbergi* Whalberg's Epauletted Fruit Bat

- Plant gets its seeds dispersed
- Animal gets food





# Seed dispersal mutualisms



*Virola surinamensis*  
(Wild nutmeg)



*ramphastos swainsonii*  
(Toucan)

# Protection mutualisms



*Acacia cornigera*  
(Swollen Thorn Acacia)

<https://www.youtube.com/watch?v=KiAEzfF2y0M>

- Plants provide ants with nectar and other resources
- Ants protect plants from herbivores



*Pseudomyrmex ferruginea*

# Protection mutualisms: *lycaenid* butterflies



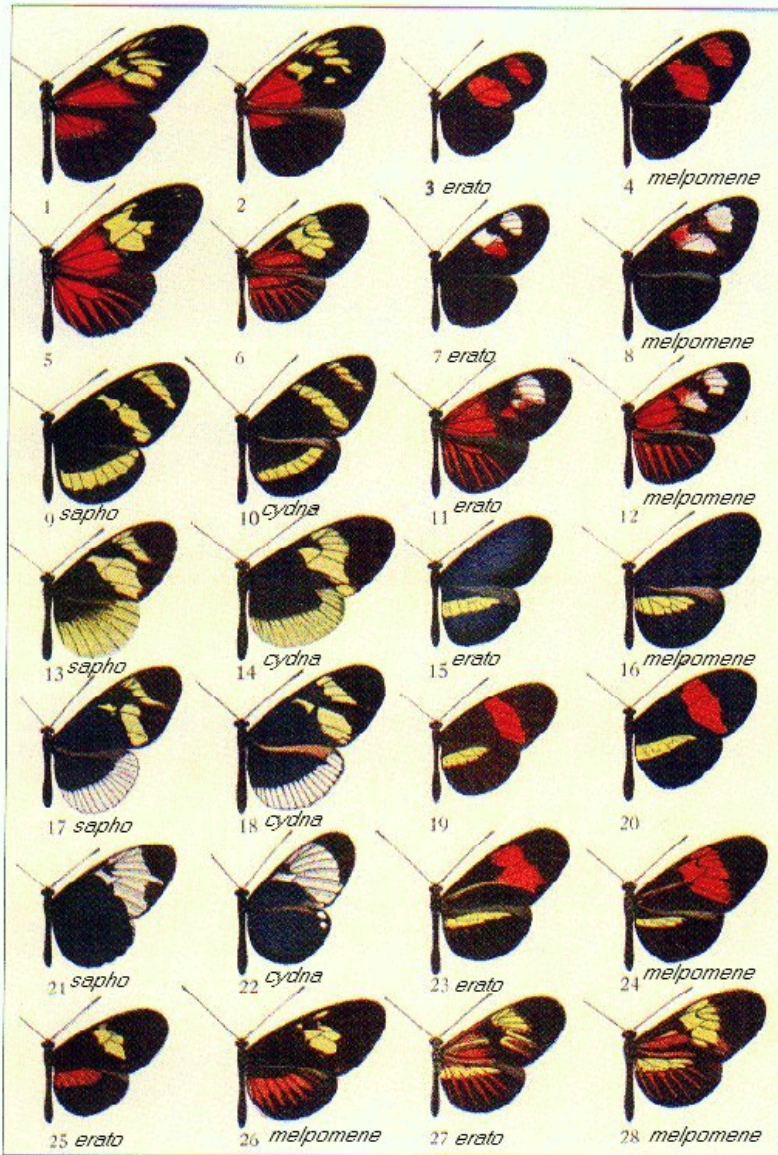
*Plebejus acmon*



- Butterfly larvae produce ‘honeydew’ that the ants eat
- The ants protect the larvae from predation



# Protection mutualisms: *Heliconius* butterflies



- Both species are distasteful to avian predators (*Mullerian mimicry*)
- Predators learn to avoid color patterns more rapidly when color patterns are prevalent
- Mimicry decreases the likelihood of predation for each species in this mutualism!
- Strong convergence of color pattern within populations

# Nutrient acquisition mutualisms

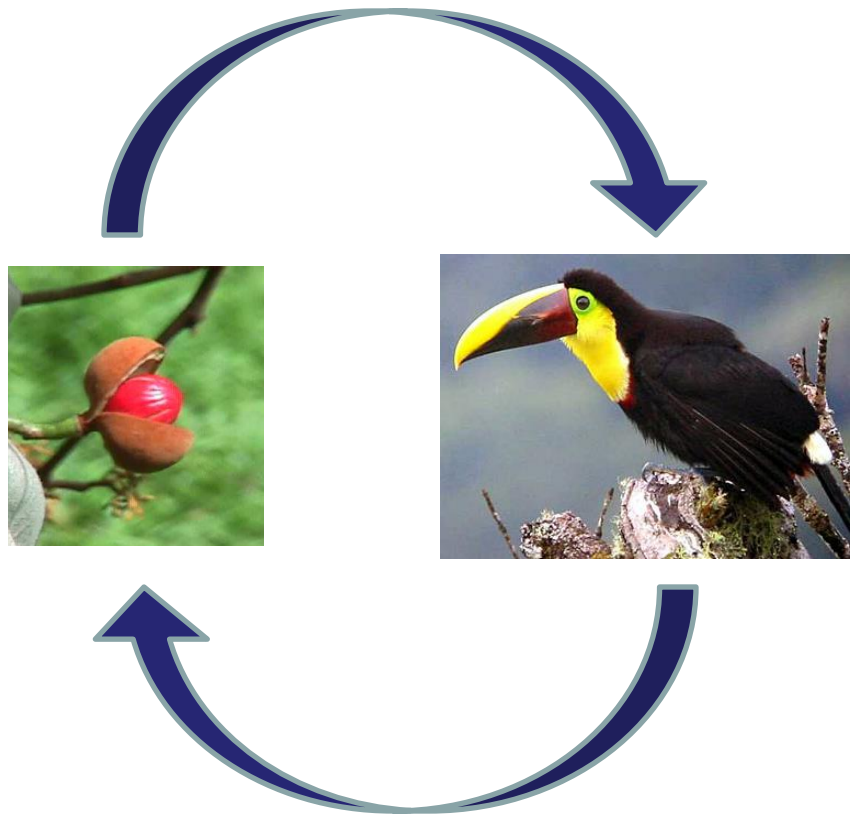


*Rhizobium* nodules  
(Bacteria)

- The plant (legumes) supplies energy to the bacteria from photosynthesis
- The bacteria ‘fix’ nitrogen for the plant (convert atmospheric  $N_2$  gas to ammonium ( $NH_4^+$ ) in the nodules
- Economically very important



# Do mutualisms regulate population sizes?



# Do mutualisms regulate population sizes?

## Assumptions

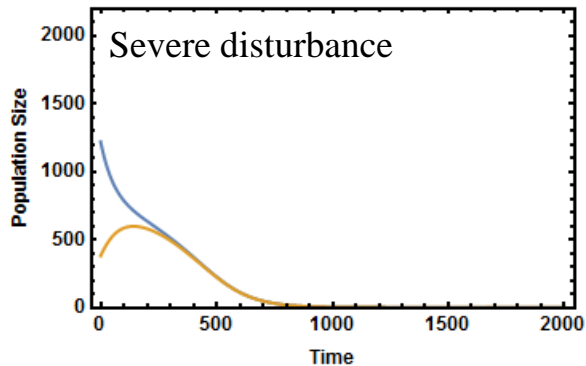
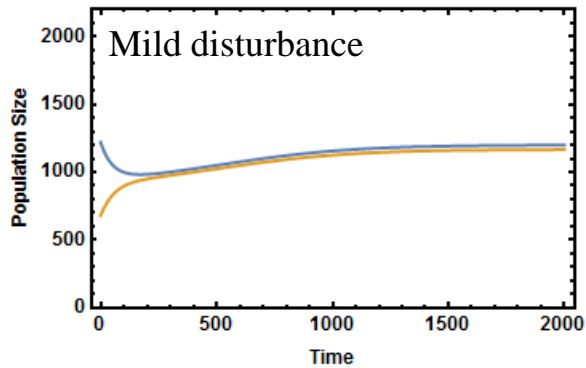
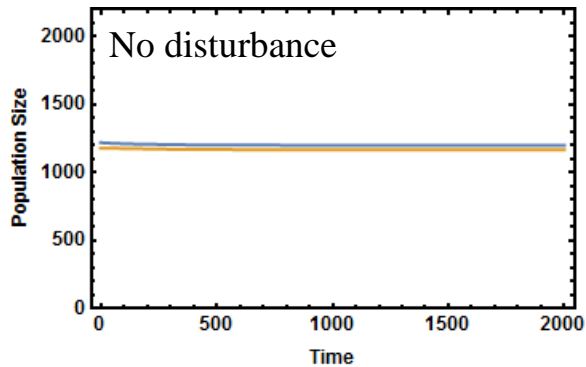
- Two mutualists with abundances X and Y
- Interactions increase growth rate
- Obligate interactions
- Density dependent growth

## Model

$$\frac{dX}{dt} = \alpha_X XY \left( 1 - \frac{X}{K_X} \right) - d_X X$$

$$\frac{dY}{dt} = \alpha_Y XY \left( 1 - \frac{Y}{K_Y} \right) - d_Y Y$$

# Do mutualisms regulate population sizes?



- **Mutualisms sustain viable populations**
- **Mutualisms can be sensitive to disturbance**
- **One extinction can lead to another**

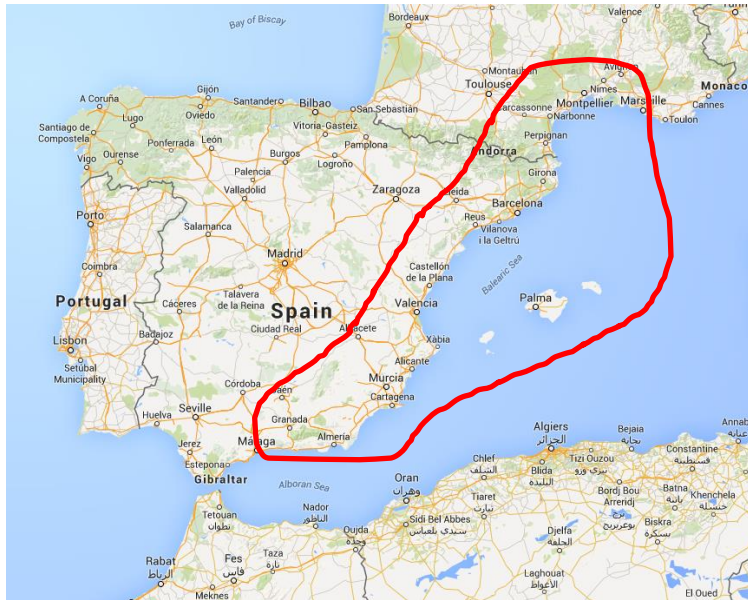
# Do mutualisms regulate population sizes?

## Long-term demographic consequences of a seed dispersal disruption

Anna Traveset<sup>1,\*</sup>, Juan P. González-Varo<sup>2</sup> and Alfredo Valido<sup>2</sup>

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<sup>2</sup>Integrative Ecology Group, Estación Biológica de Doñana (EBD-CSIC), C/Américo Vespucio s/n, La Cartuja, 41092 Sevilla, Spain



*Cneorum tricoccon*  
(Mediterranean Spurge Olive)



*Podarcis pityusensis*



*Podarcis lilfordi*



*Podarcis siculus*

Historically, this plant was dispersed by lizards in the genus *Podarcis*

# Do mutualisms regulate population sizes?



In some populations, lizards have gone extinct and been replaced by alien carnivores (some of which also disperse)



*Cneorum tricocon*



*Martes martes*



*Genetta genetta*



# Do mutualisms regulate population sizes?

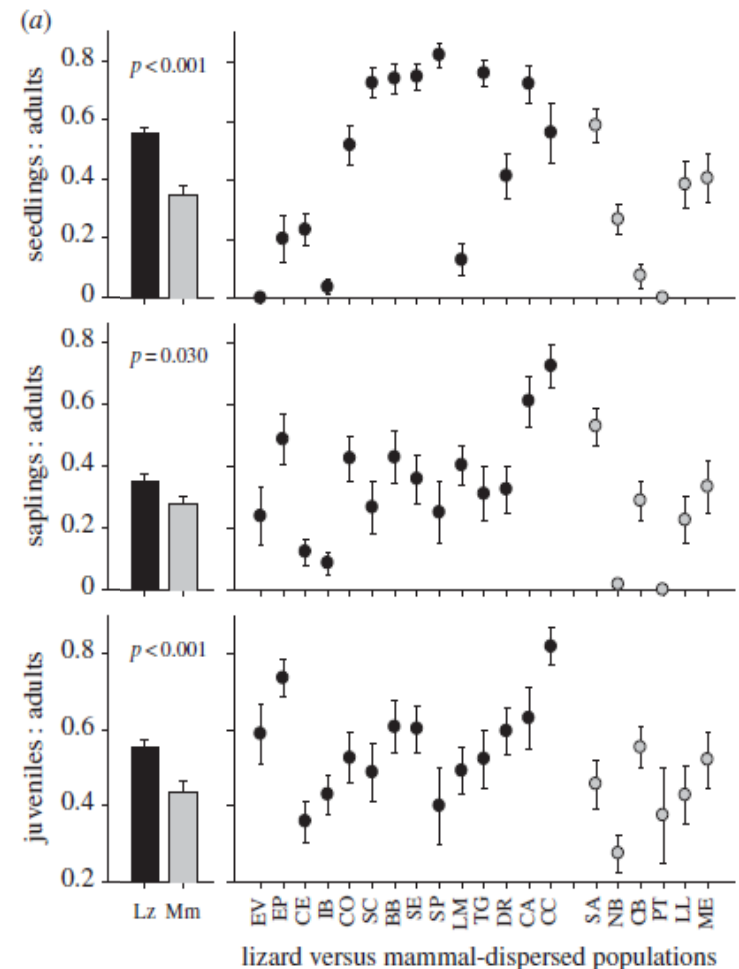
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- Studied populations with and without lizards
- Estimated components of population growth
- Growth rates lower in populations lacking lizards
- Suggests the mutualism promotes population growth

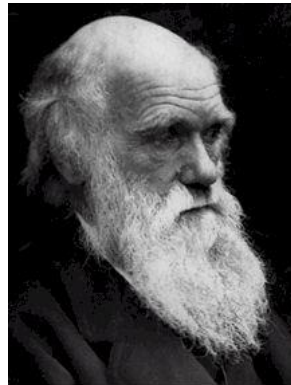


# The evolutionary origins of mutualism

**The fundamental mystery of mutualism is why one species has apparently evolved to help another...**

**“for such could not have been produced through natural selection”**

**– Charles Darwin**



**The answer, of course, is that each species “helps the other” only for the sake of benefits that it itself accrues.**

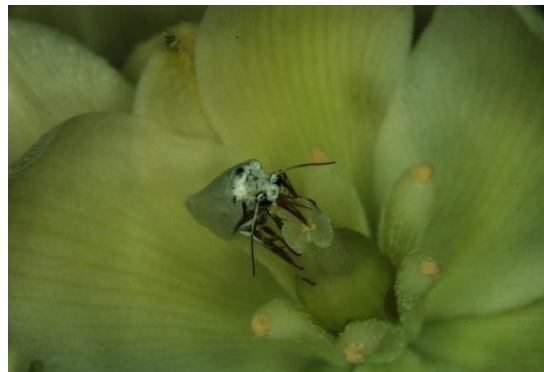
**Most mutualisms probably evolved from originally parasitic interactions**

# The evolutionary origins of mutualism



*Yucca*

- Moths lay eggs inside the flower capsule of the yucca
- Moth larvae eat some of the plants developing seeds
- So what does the plant get from this mutualism?



*Yucca moth*



# The evolutionary origins of mutualism



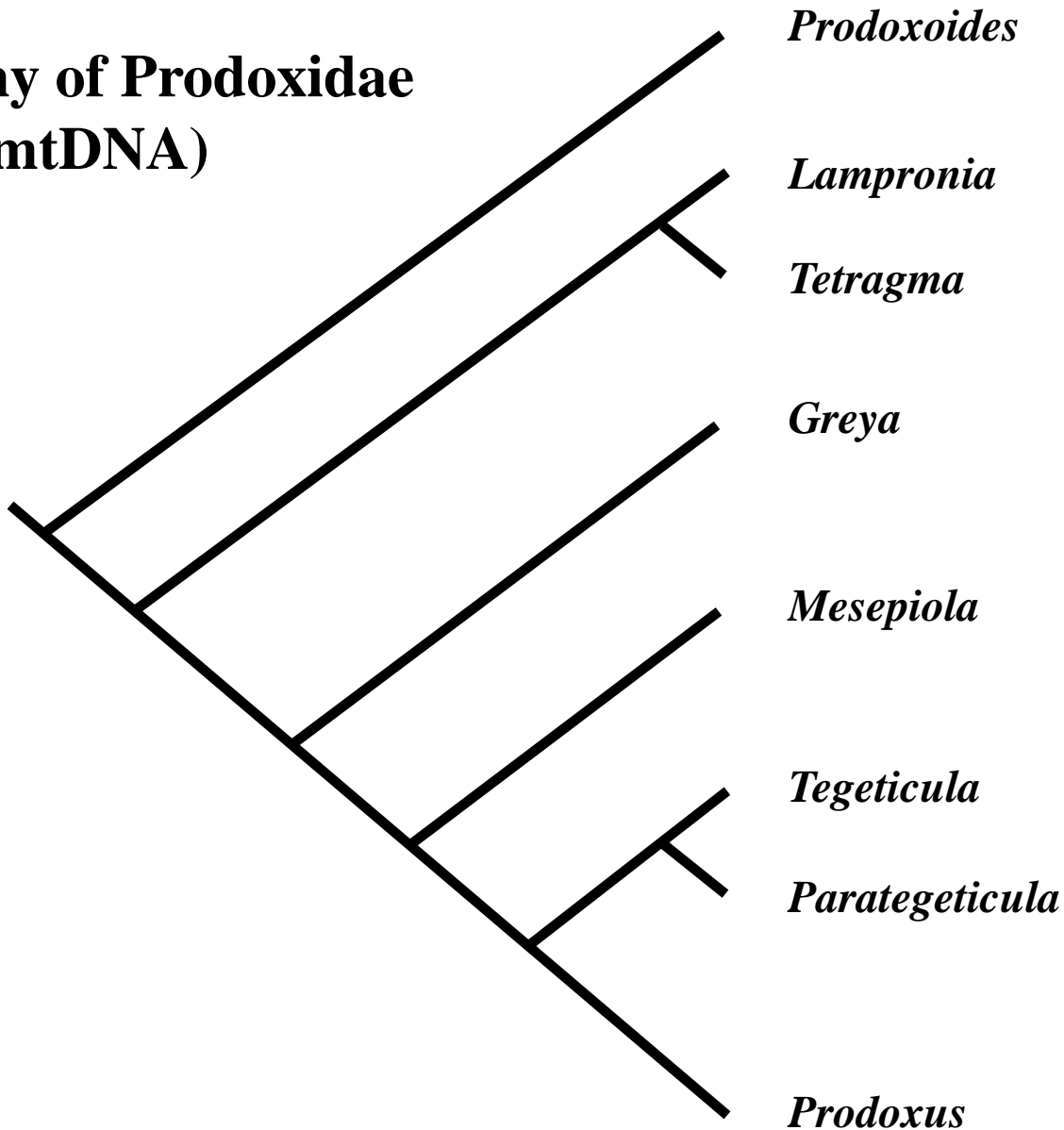
- **Moths pollinate the plant**
- **The plant has no other pollinators**



**So how might this mutualism have evolved?**

# The evolutionary origins of mutualism

## Phylogeny of Prodoxidae (mtDNA)



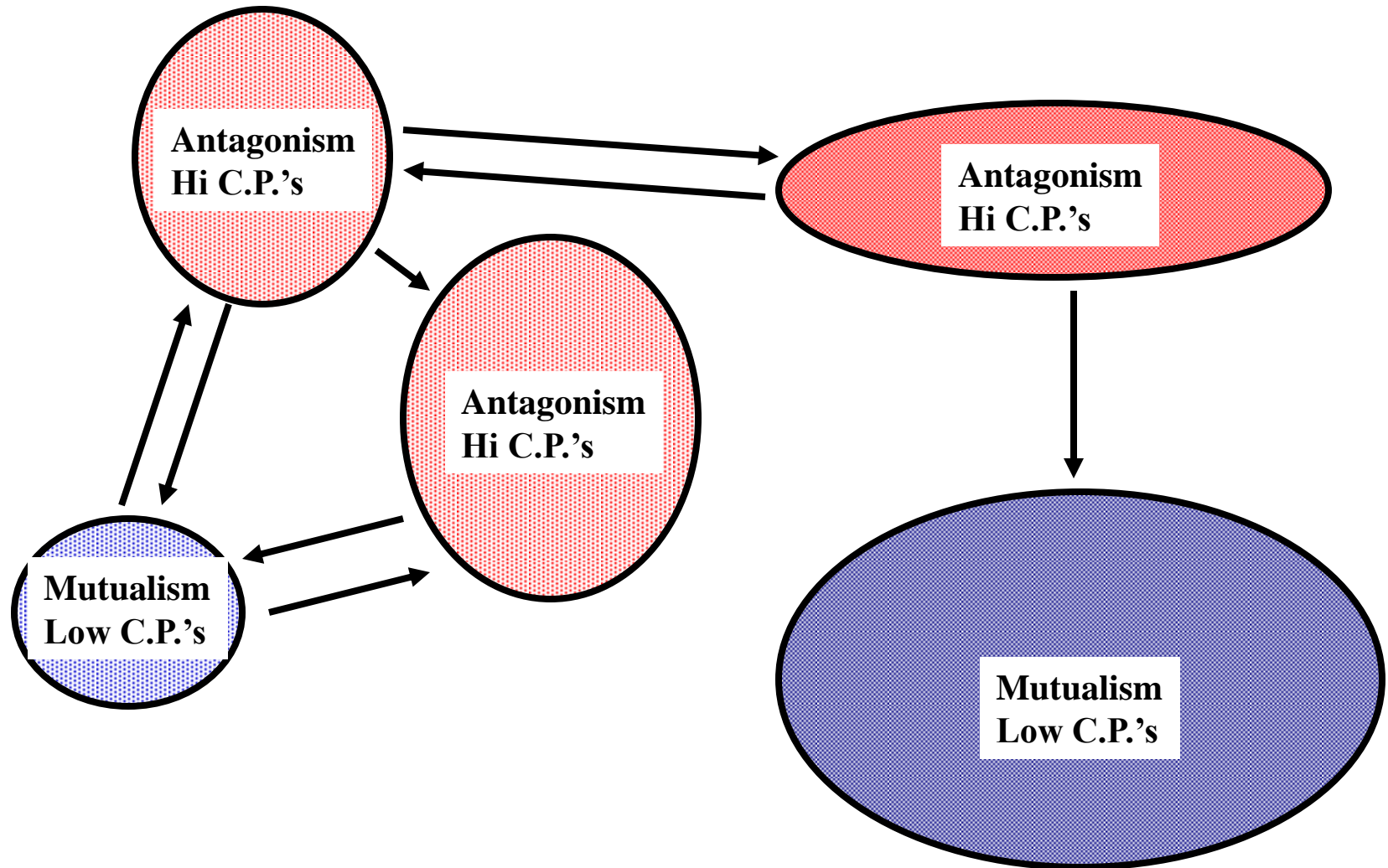


# *Greya politella* and *Lithophragma parviflorum*



- **Moth pollinates plant**
- **Larvae eat seeds**
- **Co-pollinators**

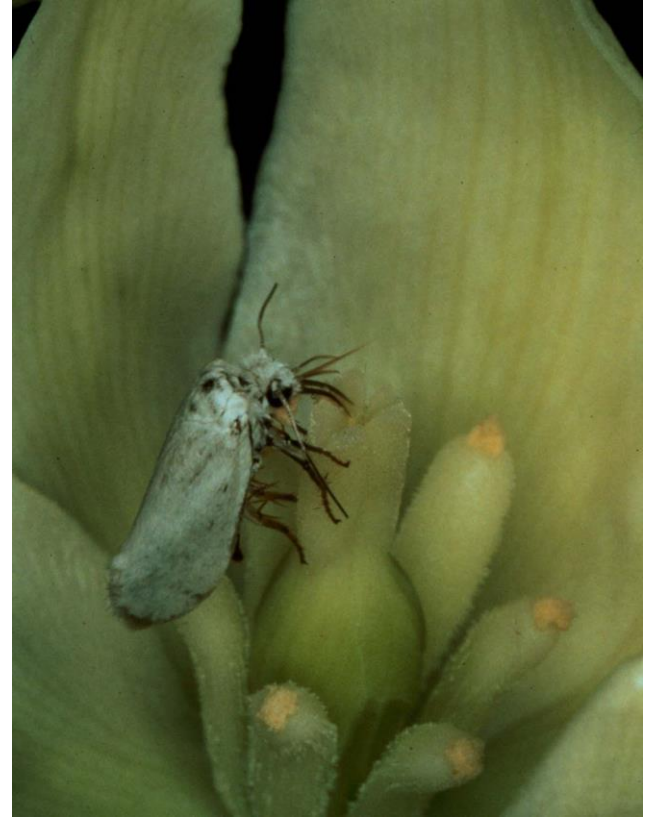
# The evolutionary origins of mutualism: Yuccas and Yucca moths



# The evolutionary origins of mutualism: Yuccas and Yucca moths



???



# The evolutionary origins of mutualism: Yuccas and Yucca moths

## Summary:

- Yuccas and Yucca moths form an *obligate* mutualism. Each species needs the other
- A group of closely related species, the *Greya* moths, can be either parasitic or mutualistic
- Yucca moths may have evolved under conditions of limited co-pollinator availability

# Practice Problem

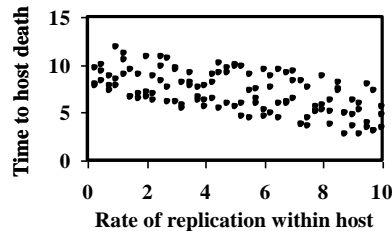
A team of scientists from the CDC has compiled data on a recently discovered infectious disease. This disease has been observed in 5 different geographic regions and has probably been present, although previously unreported, for the last 100 years. Some of the data collected by the CDC scientists is presented below:

Geographical region	% of outbreaks that are vector transmitted
1	33.6
2	1.2
3	38.2
4	35.5
5	42.6

A (10pts). In which geographic region do you expect the disease to be the least virulent? Why?

B (10pts). What is the trade-off theory for the evolution of virulence?

C (20pts). To test whether the trade-off theory for the evolution of virulence applied to this infectious disease, the CDC scientists infected rabbits with 20 different genetic strains of the disease (each strain was tested in 5 different rabbits). They then measured the rate of disease replication within the rabbits, and the time it took for the rabbit to succumb to the disease. A plot of their data is shown below:



Does this data support the trade-off hypothesis? Justify your response.



# But even established mutualisms can be invaded by 'cheaters'



- What if a mutant moth emerged that did not bother to pollinate the plant?
- The new mutant would receive the benefit from the plant, but not pay the cost of pollination.
- Would such a 'cheating' genotype be able to invade a cooperative population?

# A theoretical framework: the prisoners dilemma

- Two haploid species (e.g., moth and plant)

- Two genotypes in each species:

Species 1 (e.g., moth)

- Cheating genotype (A) (does not pollinate)
- Cooperative genotype (a) (pollinates)

Species 2 (e.g., plant)

- Cheating genotype (D) (kills moth larvae)
- Cooperative genotype (d) (does not kill moth larvae)

- If two cooperative genotypes meet (e.g.,  $a \leftrightarrow d$ ), each receives a benefit  $b$  and pays a cost,  $c$
- If a cooperative genotype meets a cheating genotype (e.g.,  $a \leftrightarrow D$ ) the cheater receives a benefit  $b$ , but the cooperator suffers a cost  $c$ .
- If two cheating genotypes (e.g.,  $A \leftrightarrow D$ ) meet neither receives a benefit or a cost

# This leads to the following fitness matrices

**Fitness matrix for Species 1 (Moth):**

		Species 2 genotype (Plant)	
		Cheat (D)	Cooperate (d)
Species 1 Genotype (Moth)	Cheat (A)	0	$b$
	Cooperate (a)	$-c$	$b-c$

**Fitness matrix for Species 2 (Plant):**

		Species 1 genotype (Moth)	
		Cheat (A)	Cooperate (a)
Species 2 Genotype (Plant)	Cheat (D)	0	$b$
	Cooperate (d)	$-c$	$b-c$

**Under these conditions, can a cheating genotype invade a cooperative population?**

# If individuals encounter one another at random:

## Species 1 (Moth) expected genotypic fitnesses:

$$\begin{array}{lll} \text{Cheater Fitness:} & W_A = p_D(0) + (1-p_D)(b) & = b(1-p_D) \\ \text{Cooperator Fitness:} & W_a = p_D(-c) + (1-p_D)(b-c) & = b(1-p_D) - c \end{array}$$

Where  $p_D$  is the frequency of the cheating allele in species 2 (Plant)

## Species 2 (Plant) expected genotypic fitnesses:

$$\begin{array}{lll} \text{Cheater Fitness:} & W_D = p_A(0) + (1-p_A)(b) & = b(1-p_A) \\ \text{Cooperator Fitness:} & W_d = p_A(-c) + (1-p_A)(b-c) & = b(1-p_A) - c \end{array}$$

Where  $p_A$  is the frequency of the cheating allele in species 1 (Moth)

**Which strategy evolves?**

Since we do observe mutualisms, however, something must prevent cheating from evolving???



# **What factors can prevent the evolution of cheating?**

**1. Repeated encounters – Provides an opportunity to retaliate against non-cooperators**

**2. Spatial structure – The same individuals are likely to interact time and time again**

**3. Partner choice – Individuals can choose who they are going to interact with and so punish genotypes or individuals that ‘cheat’**

# What mechanisms regulate cheating yucca moths?

## The selective abortion hypothesis:

- Some moth genotypes will ‘cheat’ by laying too many eggs
- In order to stabilize this mutualism, the plant must possess a mechanism whereby moth genotypes that ‘cheat’ are penalized
- Selective abortion of seed capsules with high numbers of larvae could be such a mechanism

# A test of the selective abortion hypothesis

## Pellmyr and Huth (1994):

- Both aborted and retained fruit was collected from 10 naturally pollinated yucca inflorescences

- Fruit was dissected and the number of moth oviposition scars\* and larvae were determined

\* Not all oviposition attempts are successful, but female moths are no less likely to pollinate even when oviposition is unsuccessful, so scars are a good measure of pollination



*Yucca filamentosa*

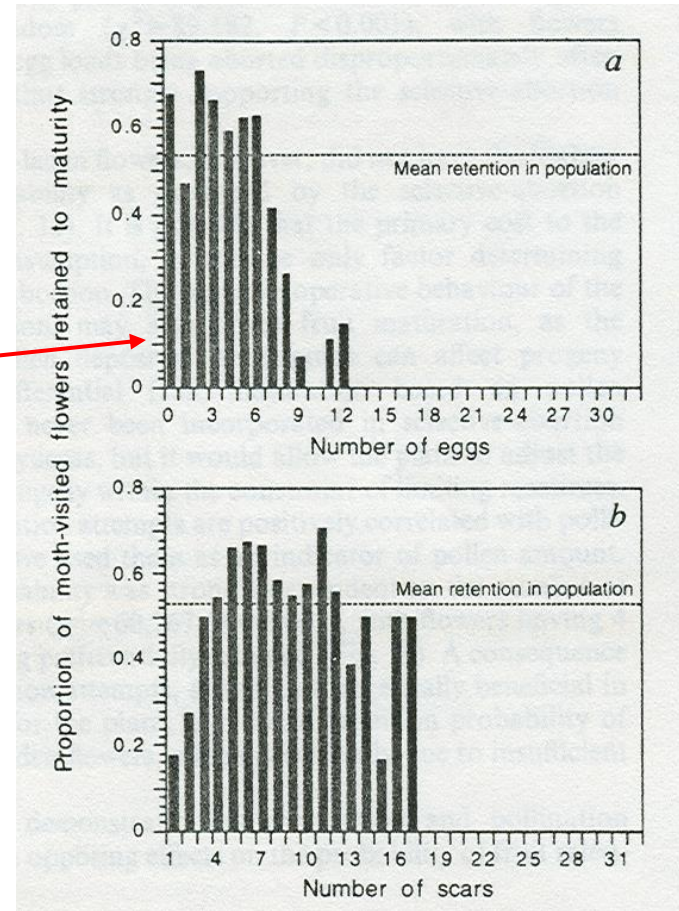


**Fruit**

# Results I

## Pellmyr and Huth (1994):

- The greater the number of eggs per fruit, the lower the probability a fruit was retained

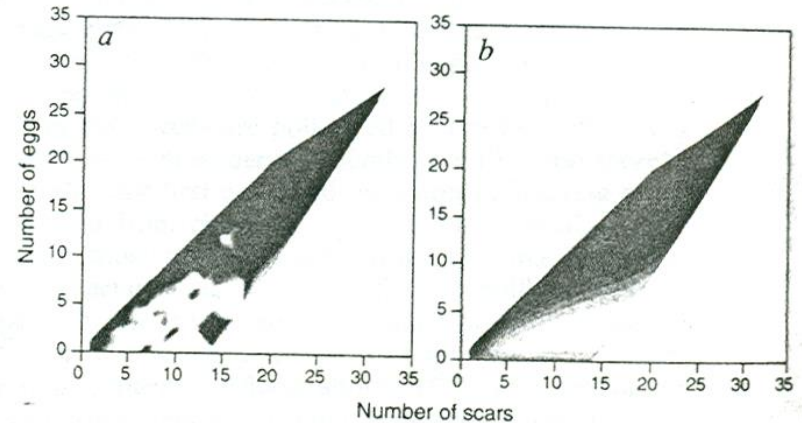




# Results II

## Pellmyr and Huth (1994):

- The greater the ratio of eggs (cost) to scars (benefit) the less likely a fruit is to be retained.
- The greater the ratio of scars (benefit) to eggs (cost), the more likely a fruit is to be retained.
- Together, this evidence seems to support the selective abortion hypothesis



**Black region – Low probability of flower retention**

**White region – High probability of flower retention**

# Summary of mutualisms

- **Mutualisms comprise a wide array of types of interactions and taxonomic groups.**
- **Mutualisms regulate population sizes**
- **Most mutualisms probably evolved from initially parasitic interactions**
- **Mutualisms are susceptible to invasion by ‘cheaters’**

# Practice Problem

You have observed that a butterfly species, *Papilio falsificada*, is regularly associated with the plant, *Prunus fauxviflorum*. Based on your observations, it is clear that the butterfly can, in principle, pollinate the plant and that the plant generally offers a nectar reward to the butterfly. Consequently, you have hypothesized that this interaction is a mutualism. To test this hypothesis, you collected information on plant fitness (seed set) for 22 individual plants visited by the butterfly vs. 22 individual plants that were not. In addition, you measured the fitness (# of surviving offspring) of 48 butterfly individuals that visited the plant vs. 48 butterfly individuals that did not. Your data are shown below as summary statistics:

<b>Visited by butterfly?</b>	<b>Sample mean of plant seed set</b>	<b>Sample variance of plant seed set</b>	<b>Visited plant?</b>	<b>Sample mean of butterfly fitness</b>	<b>Sample variance of butterfly fitness</b>
Yes	56.2	6.6	Yes	16.6	4.6
No	22.7	3.5	No	6.5	3.2

Does your data support your hypothesis that this interaction is a mutualism? Justify your response statistically.