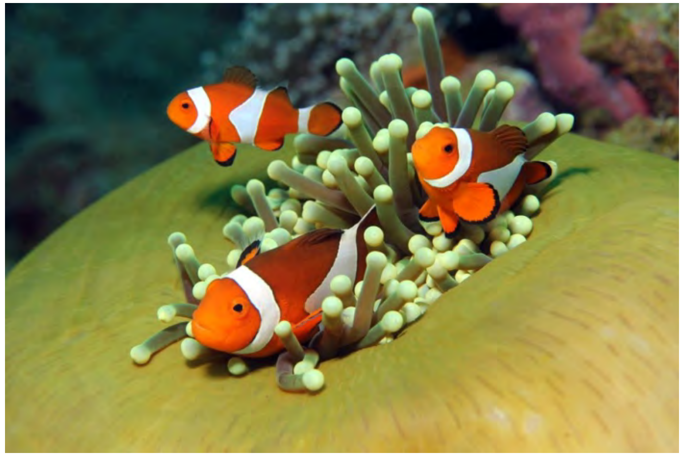
# Coevolution of mutualists

1) Evolution of mutualistic interactions

2) A mutualistic arms race?

3) Mutualism stability and the evolution of sanctions

4) Example exam questions



https://news.mit.edu/2016/species-relationships-jointly-beneficial-competitive-environments-0824

# 1) Evolution of mutualistic interactions

**Mutualism:**

Individuals of two species interact with the result that both benefit.

Contrast with “symbiosis”, which is any long-term intimate relationship between members of two species, whether mutualistic, parasitic, or commensal, etc.

**Coevolution (strictly):**

Reciprocal evolutionary change of interacting species

# 1) Evolution of mutualistic interactions

## Examples of mutualisms

*Symbiotic mutualisms:*

- micorrhizal associations between plants and fungi
- corals and photosynthetic dinoflagellates
- lichens (algae and fungi)

*Visitor mutualisms:*

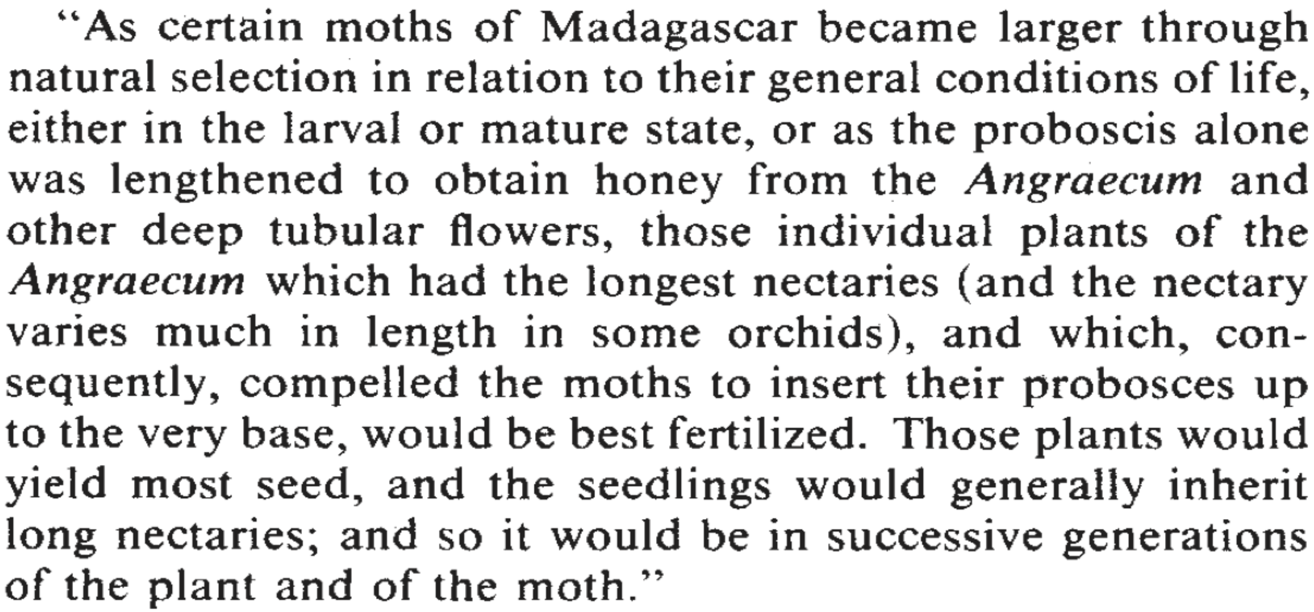
- plant-pollinator
- plants and frugivores
- cleaner fish and clients

For at least some systems, the extent to which the associations are truly mutualistic varies with environment.

# 2) Darwin’s arms race hypothesis

## Coevolution of flower length and pollinator tongue length

The orchid, *Angraecum sesquipedale*



> “As certain moths of Madagascar became larger through natural selection in relation to their general conditions of life, either in the larval or mature state, or as the proboscis alone was lengthened to obtain honey from the *Angraecum* and other deep tubular flowers, those individual plants of the *Angraecum* which had the longest nectaries (and the nectary varies much in length in some orchids), and which, consequently, compelled the moths to insert their probosces up to the very base, would be best fertilized. Those plants would yield most seed, and the seedlings would generally inherit long nectaries; and so it would be in successive generations of the plant and of the moth.”

Darwin (1859)
*On the Origin of Species*

http://www.pbase.com/bjramsay/image/90924215

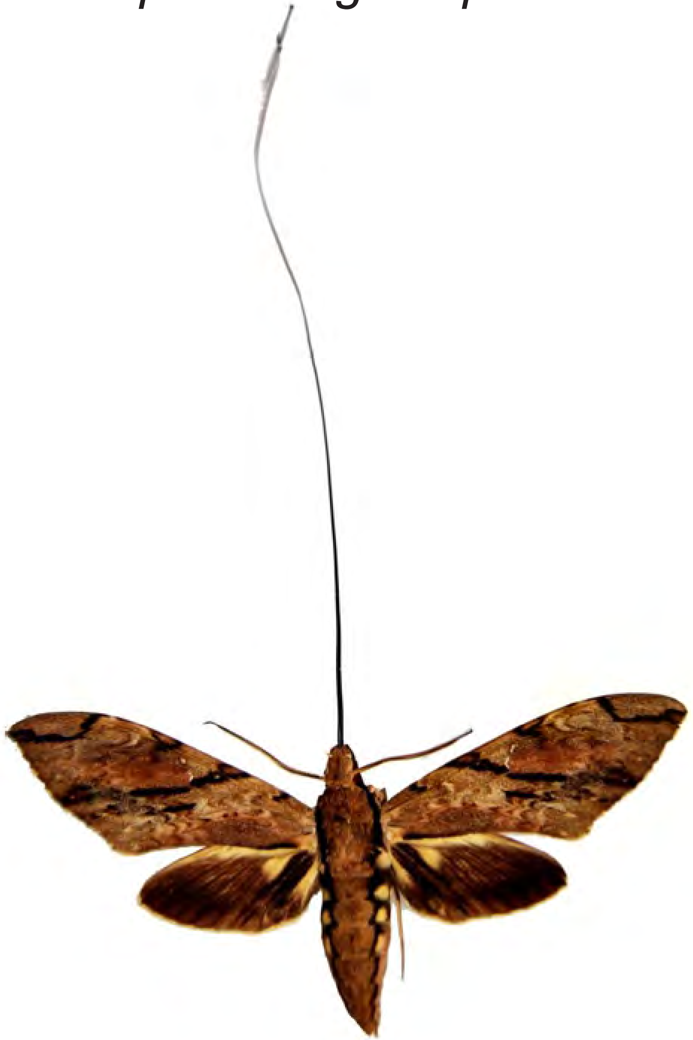
# 2) Darwin’s arms race hypothesis

## The predicted long-tongued pollinator was later found

The orchid, *Angraecum sesquipedale*

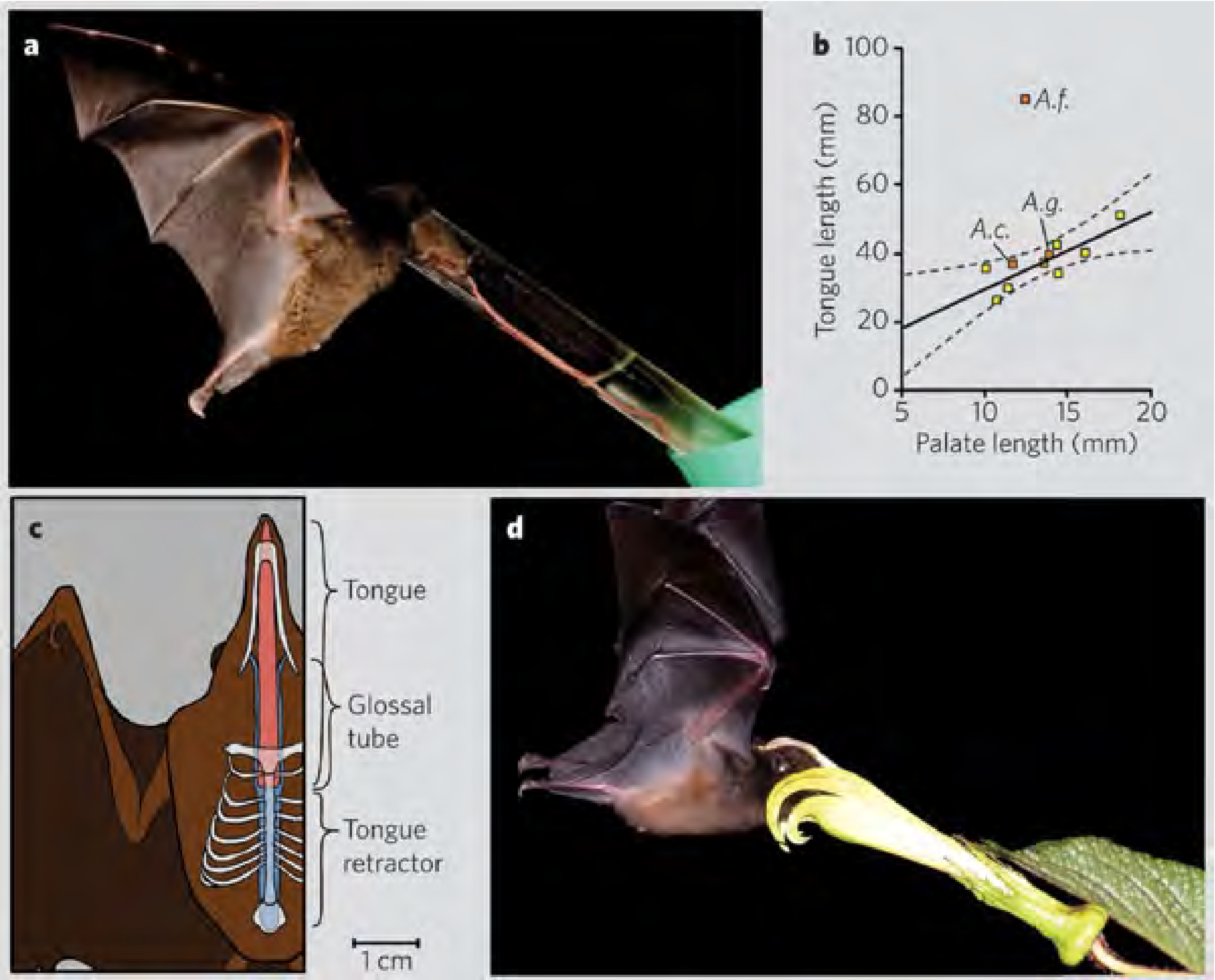
http://www.pbase.com/bjramsay/image/90924215

*Xanthopan morganii praedicta*



http://www.flickr.com/photos/kqedquest/3256354461/

# 2) Darwin’s arms race hypothesis



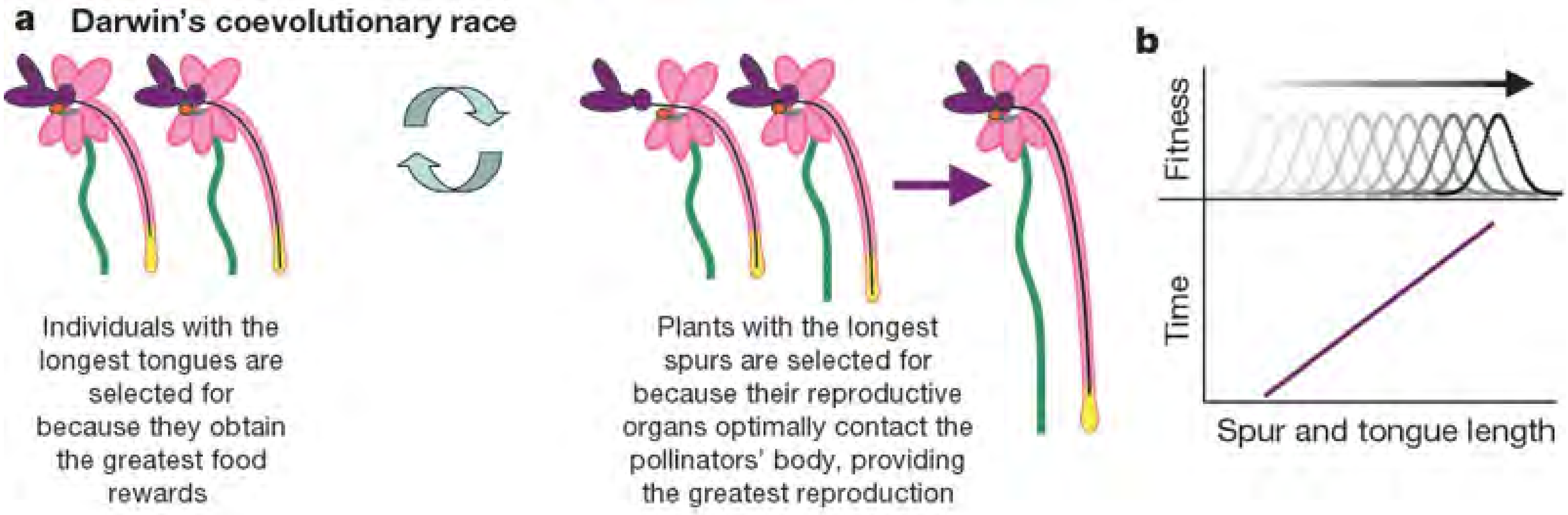
A recently-described nectar bat *Anoura fistulata,* discovered in the cloud forests of the Andes of Ecuador, can extend its tongue twice as far as those of related bats and is the sole pollinator of a plant with corolla tubes of matching length.

Muchhala (2006)

**a**, *Anoura fistulata* feeding from a test tube filled with sugared water; its tongue (pink) can extend to 150% of body length. **b**, Maximum tongue extension and palate length for 11 species of glossophagine nectar bat. *Anoura fistulata* is an outlier. **c**, Ventral view, showing tongue (pink), glossal tube and tongue retractor muscle (blue).

# 2) Darwin's arms race hypothesis

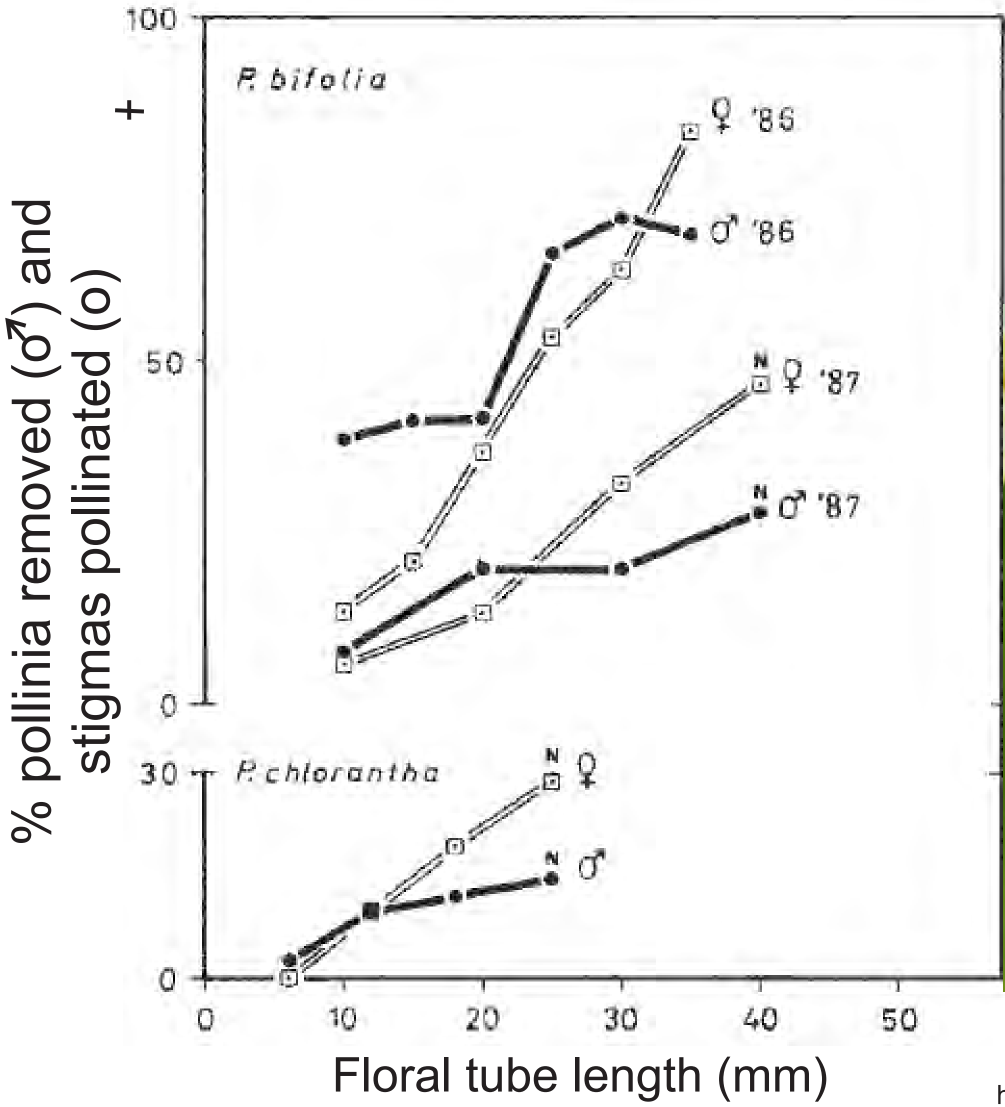
According to this hypothesis, directional natural selection alternates between plant and pollinator, causing a continual and gradual elongation of the pollinator's tongue and the flower's spur



Whittall & Hodges (2007) Nature

# 2) Darwin’s arms race hypothesis

## Experimental test: shortening of spur length reduces pollination



Experimental shortening of floral tubes has a strong negative effect on male (pollinia removal, black bars) and female (stigma pollen receipt, open bars) components of fitness in *P. biflora* (top) and *P. chlorantha* (bottom).

*Platanthera bifolia*

http://commons.wikimedia.org/wiki/Template:Potd/2008-08

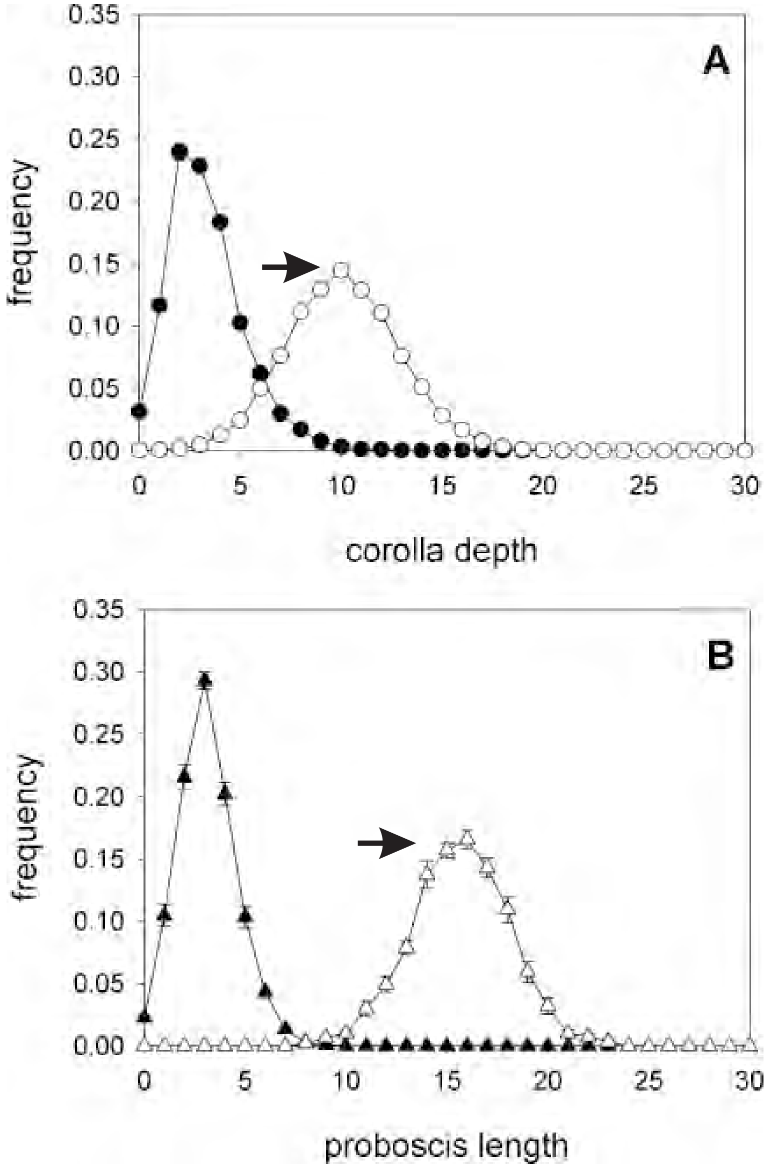
*Sphinx ligustri*

http://outdoors.webshots.com/photo/2441357260026021334gtQzHq

Nilsson (1988) Nature

# 2) Darwin’s arms race hypothesis

## Alternative hypothesis (also invokes coevolution)



Rodríguez-Gironés and Llandres (2008) Plos One

### Reduced pollen waste

Consider two plant and two pollinator species.

Competition for nectar between shorter- and longer-tongued pollinators can favor diverge in corolla tube depth, because this increases the proportion of pollen grains that lands on flowers of the right species.

Further divergence in tongue length can then be favored, which might lead to further divergence in corolla-tube depth between the two plant species ensues.

Endpoint is a steady state rather than a continual increase in tongue length and corolla tube depth.

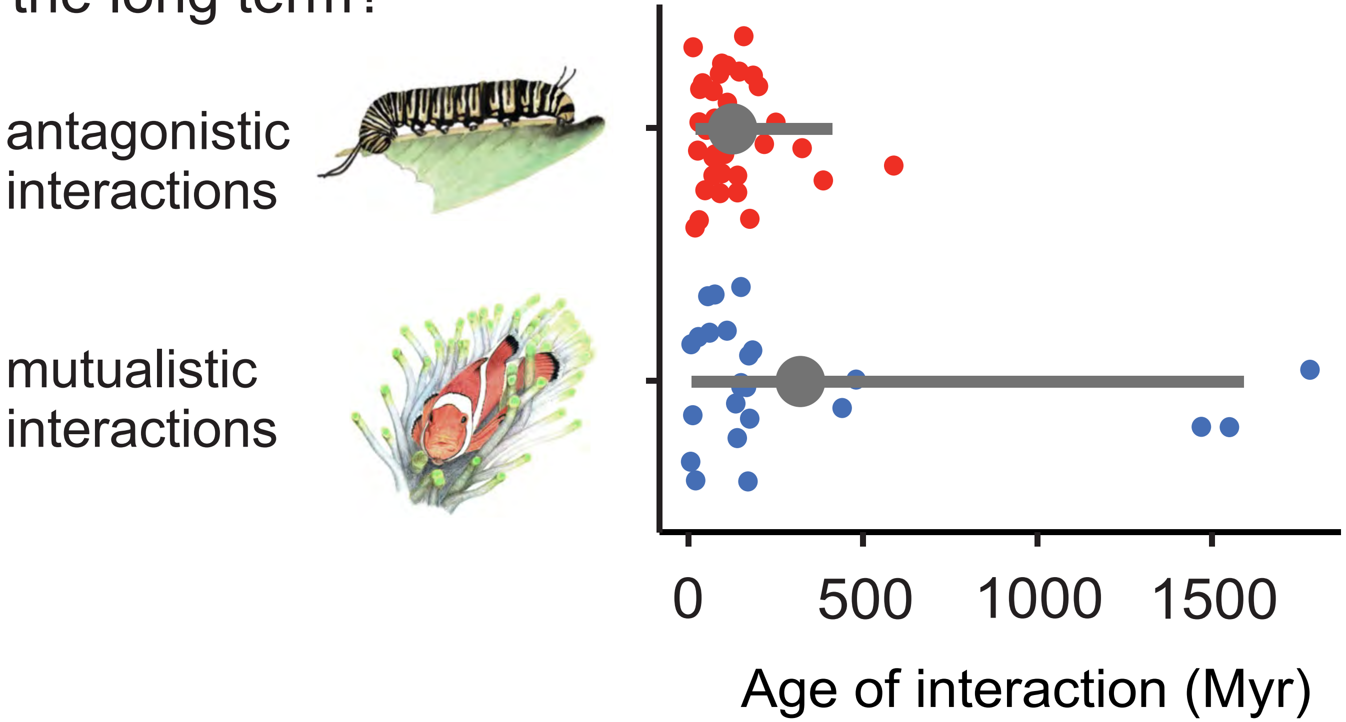
# 3) Mutualism stability and the evolution of sanctions

## Mutualism is mutual exploitation. How does it persist?

Mutualists are hardly “altruistic”. There is a potential for conflicts of interest between species involved in a mutualism.

Selection could ultimately result in one party over-exploiting the other, changing the mutualism to a host-parasite interaction or predator-prey interaction.

What keeps a mutualism stable over the long term?



Zeng & Wiens (2021) *Proc Roy Soc Lond B*

# 3) Mutualism stability and the evolution of sanctions

## The evolution of “sanctions”

A prevalent hypothesis is that stable mutualisms frequently involve the evolution of “sanctions”, traits that prevent the evolution of overexploitation.

Sanctions: the preferential supply of resources (or the curtailing of resources) to partners based on their mutualistic performance.

Sanctions may evolve in response to mutual exploitation, or they may evolve in response to other factors. Their evolution has been little studied.

https://commons.wikimedia.org/wiki/File:Hummingbird_hawkmoth_a.jpg

# 3) Mutualism stability and the evolution of sanctions

## Example: Yucca & yucca moth mutualism

*Yucca* species are completely dependent on the yucca moth *Tegiticula* for pollination. The moths eat developing seeds in the fruits.

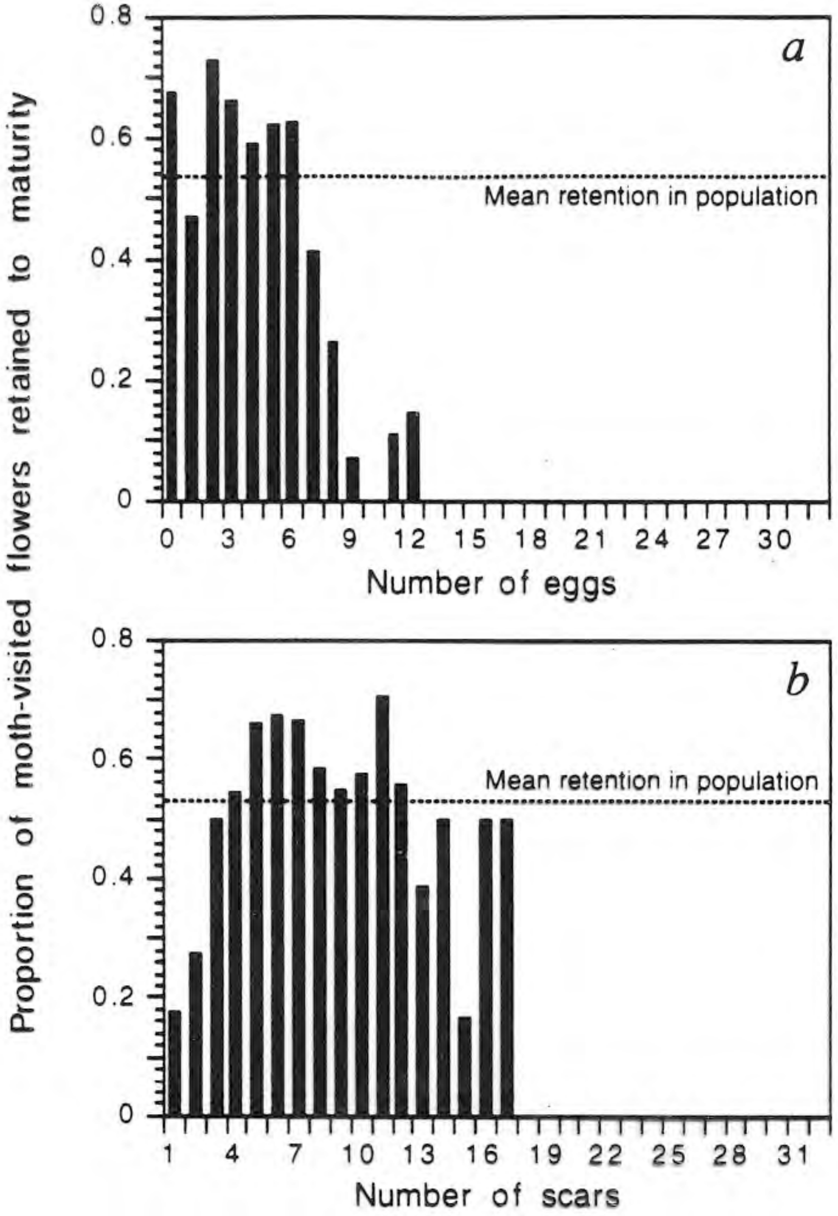
The female moth emerges, gathers pollen from the anthers of the yucca (specialized mouthparts). When ready to lay eggs she flies to a yucca flower, make an incision into an ovary (piercing ovipositor), lays an egg, then pollinates the stigma, ensuring development of the ovaries. Repeats several times within a flower.

The moth larvae feed on the developing seeds. Only a few seeds are so destroyed within a flower. At maturity, the larvae leave the seed capsule, drop to the ground, and pupate.

http://www.cals.ncsu.edu/course/ent525/close/Ostendorff http://www.opsu.edu/UnivSchools/ScienceMathNurs/PlantsGrassh/plants/pasturefiles/pasture30.html

# 3) Mutualism stability and the evolution of sanctions

## Flowers with many eggs/scars are abcissed



This is thought to represent a plant “sanction”

Graph shows proportion of retained flowers for each *Tegeticula* egg and scar number category. Dashed lines indicate grand mean retention in the entire sample.

Pellmyr and Huth (1994) *Nature*

# 3) Mutualism stability and the evolution of sanctions

## The evolution of non-mutualistic yucca moths

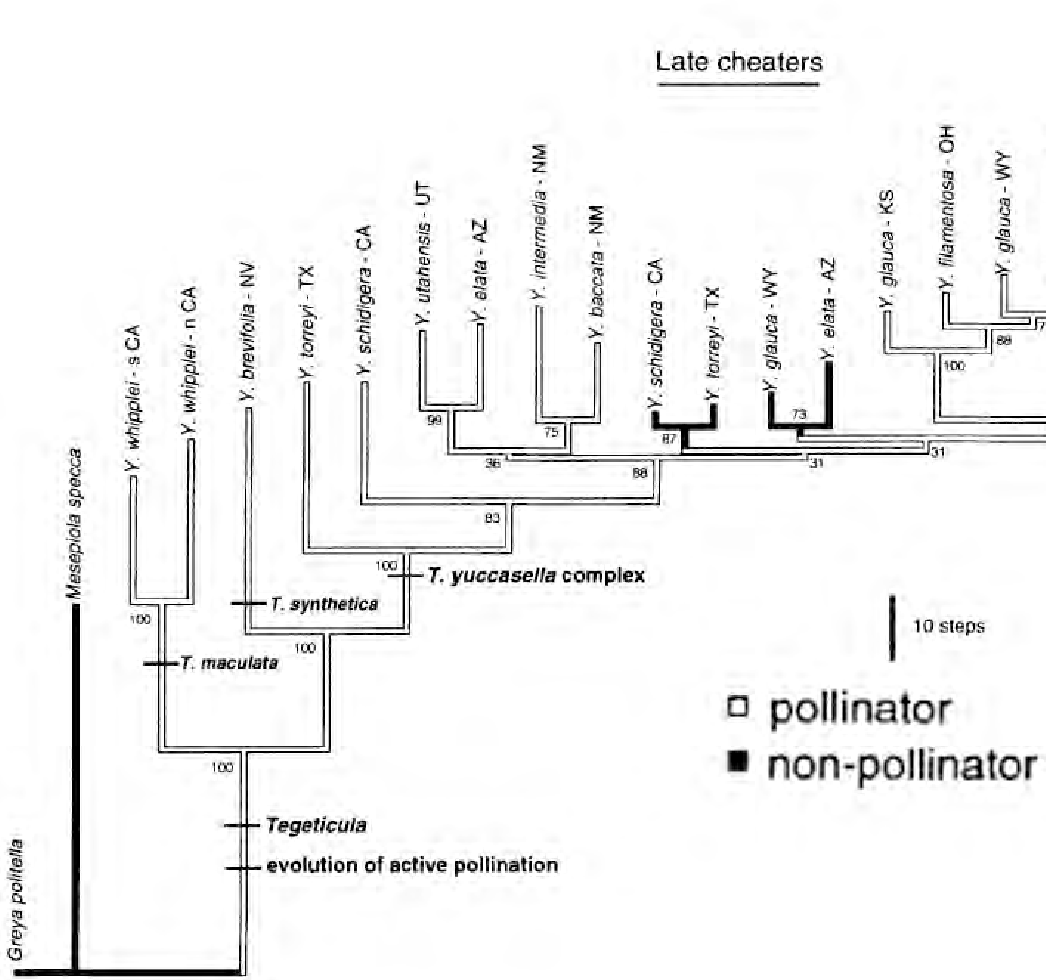


FIG. 1 Phylogenetic relationships among pollinating and cheating yucca moths as estimated from a 2.1-kb mitochondrial DNA sequence. *Greya* and *Mesepiola* were chosen as outgroups based on morphological and molecular data[27]. All *Tegeticula* species are labelled by *Yucca* host and US state. Members of the *T. yuccasella* complex were selected as pairs of coexisting pollinators and cheaters for each taxon; for *Yucca glauca*, two pollinators were included because they coexisted with different cheater taxa. For *Y. baccata* and *Y. utahensis*, known 'late cheaters' were not available for DNA analysis.

Pellmyr, Leebens-Mack and Huth (1996) *Nature*

# 3) Mutualism stability and the evolution of sanctions

## Timing of egg-laying by “cheaters”

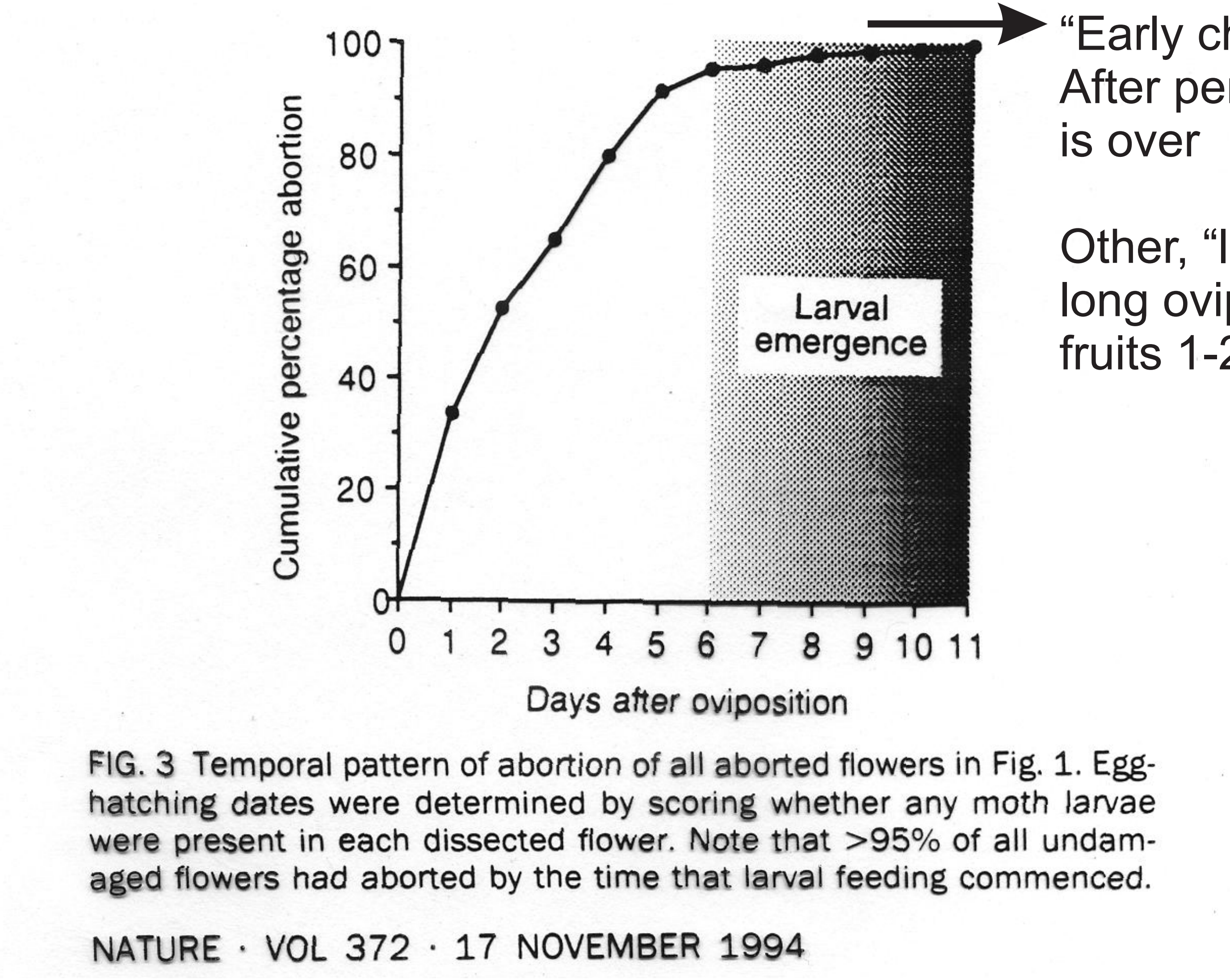


FIG. 3 Temporal pattern of abortion of all aborted flowers in Fig. 1. Egg-hatching dates were determined by scoring whether any moth larvae were present in each dissected flower. Note that >95% of all undamaged flowers had aborted by the time that larval feeding commenced.

NATURE · VOL 372 · 17 NOVEMBER 1994

“Early cheaters”:
After period of abcission
is over

Other, “late cheater” species have very long ovipositors and cut into full-sized fruits 1-2 weeks later.

Pellmyr, Leebens-Mack and Huth (1996) Nature

http://www.uoregon.edu/~udovic/yucca_photos.html

# 3) Mutualism stability and the evolution of sanctions

## “Cheaters” cause high seed destruction

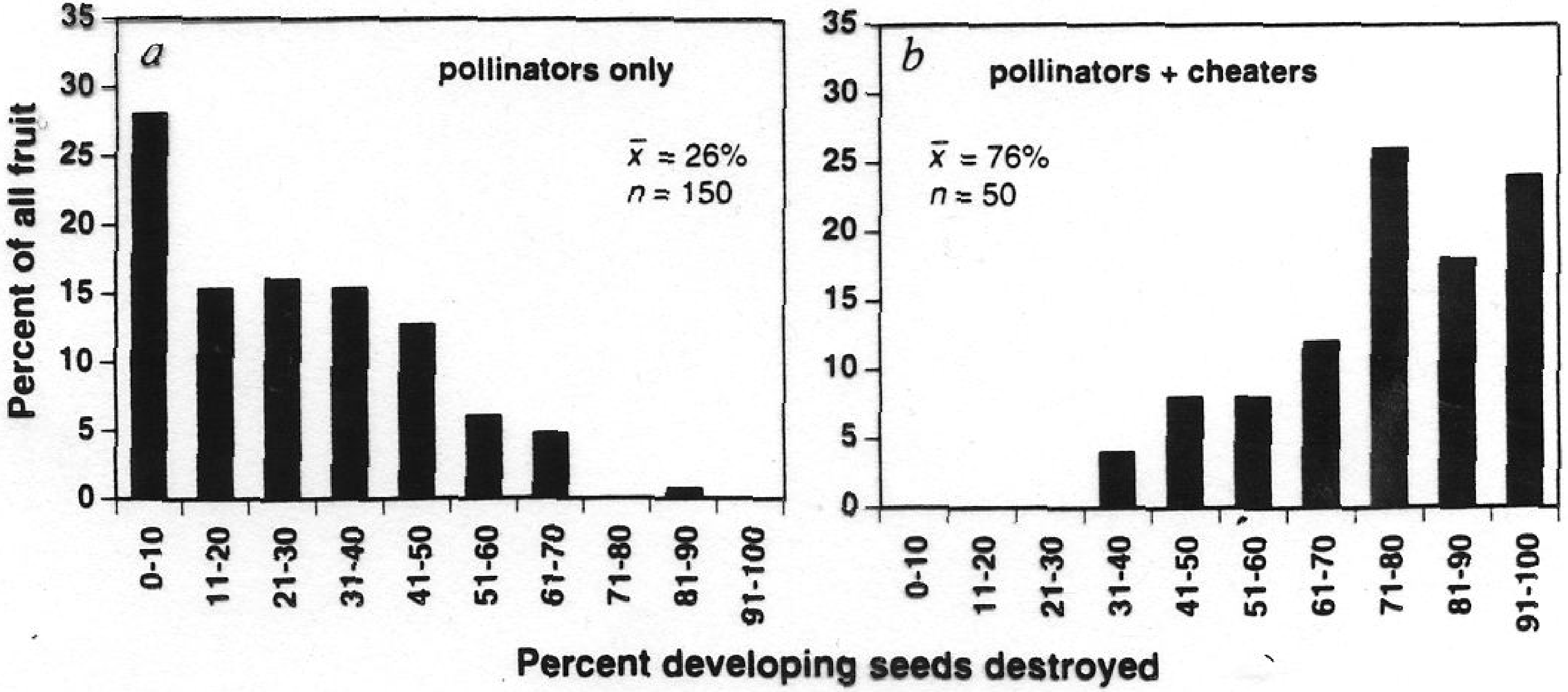
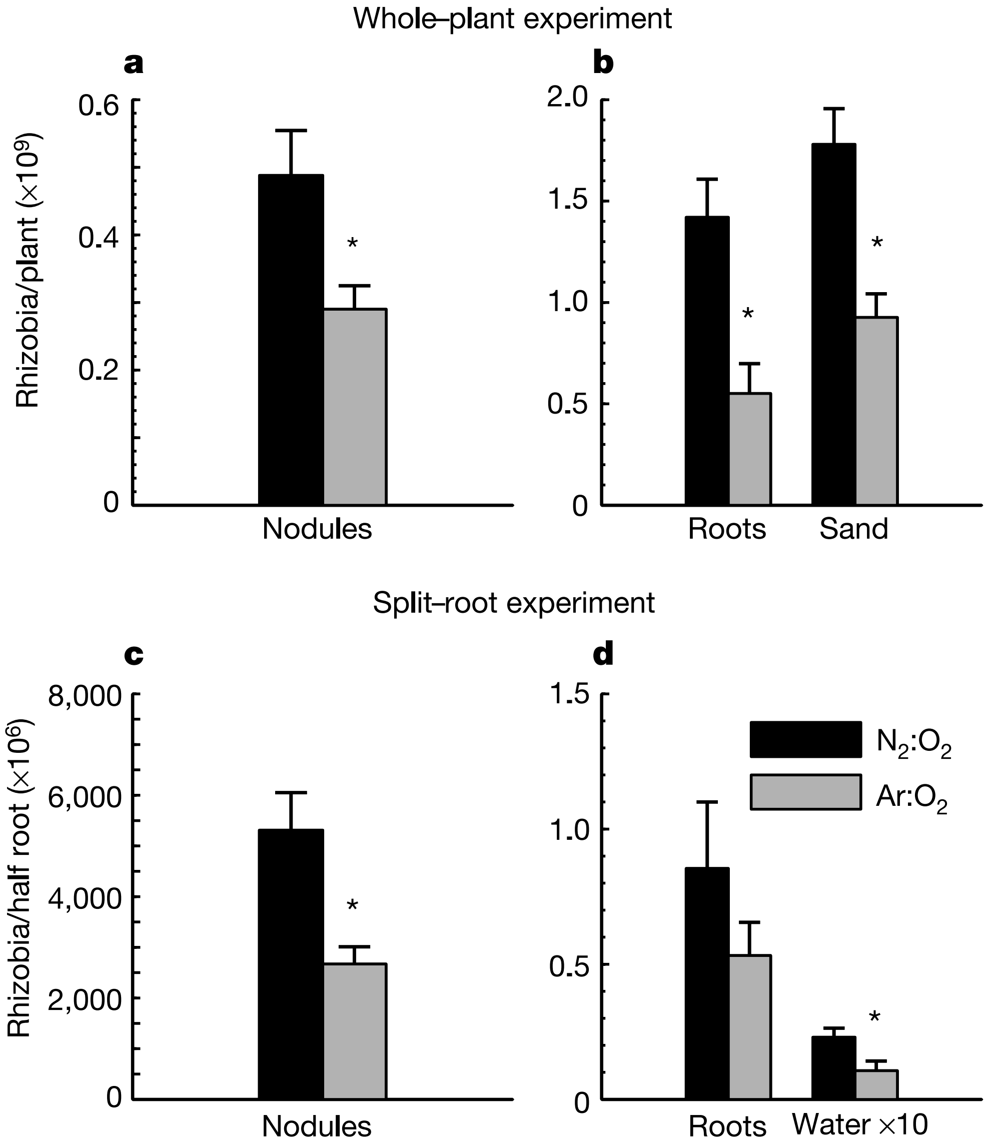


FIG. 2 Levels of seed destruction in populations of *Yucca filamentosa*, *a*, without and *b*, with cheaters. Fruits (25) were collected at random after larvae had exited from each of 8 populations in Ohio and Tennessee, and the proportion of developing seeds destroyed by yucca moth larvae was determined by seed counts.

Pellmyr, Leebens-Mack and Huth (1996) Nature

# 3) Mutualism stability and the evolution of sanctions

## Test of the presence of “sanctions” in legume-rhizobium mutualism



Kiers et al (2003) Science

**Rhizobia bacteria fix $N_2$** within the root nodules of their host legume plants (soybean). $N_2$ fixation supplies nitrogen needed for plant growth and photosynthesis. But $N_2$ fixation (at rates that greatly exceed the nitrogen needs of rhizobia) is energetically costly to the bacteria.

Rhizobia strains that fix little or no $N_2$ after they form root nodules on legumes are common in some soils. Why haven’t these “cheats” completely displaced cooperators?

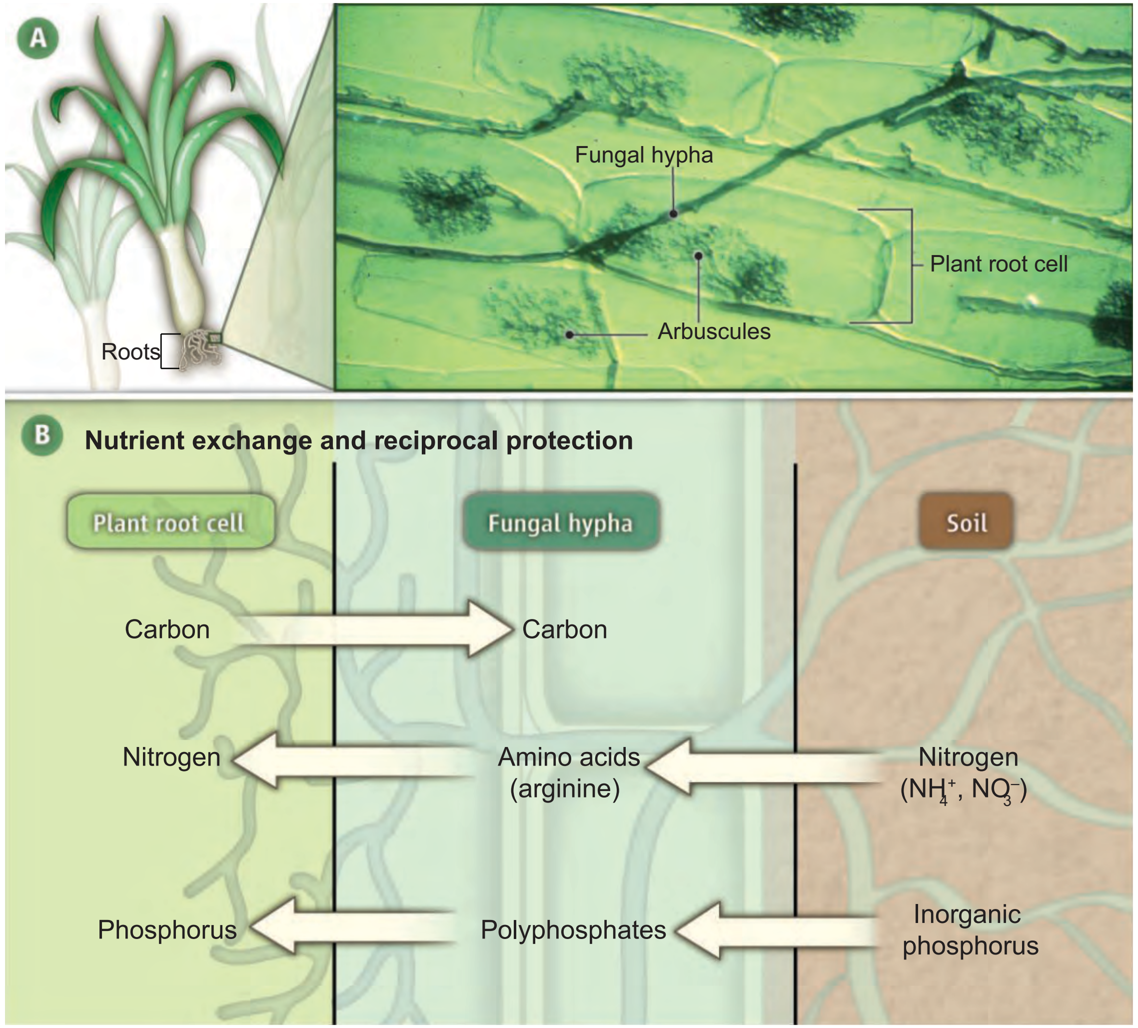
Rhizobia experimentally forced to “cheat” by replacing air ($N_2$:$O_2$, 80:20) with a gas mixture (Ar:$O_2$, 80:20) containing only traces (1% of normal) of $N_2$. As predicted by the sanctions hypothesis, preventing $N_2$ fixation led to a significant decrease in their fitness, as though plant is sanctioning.

(They estimate that even a reduction to 1% of normal $N_2$ fixation rate would not limit rhizobial growth).

# 3) Mutualism stability and the evolution of sanctions

## Tests of the presence of “sanctions” in plant - arbuscular mycorrhizal fungus mutualism

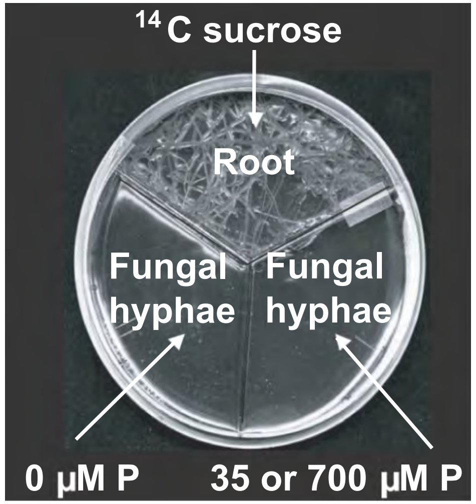
Arbuscular mycorrhizal fungi provide their host plants with mineral nutrients and other benefits such as protection against biotic (pathogens and herbivores) and abiotic (e.g., drought) stresses

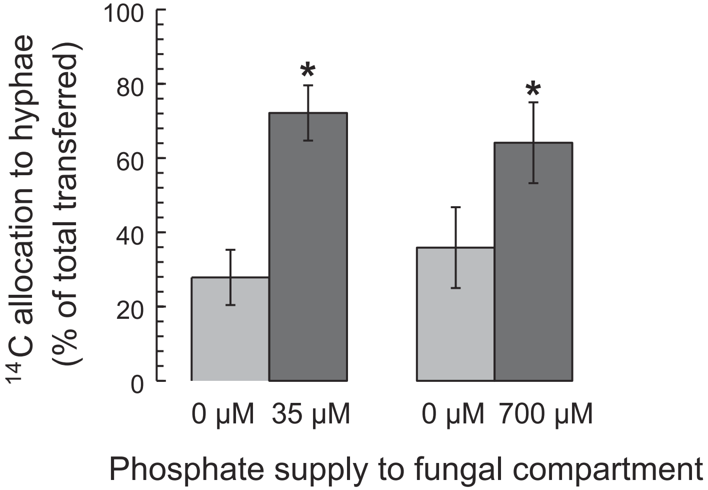


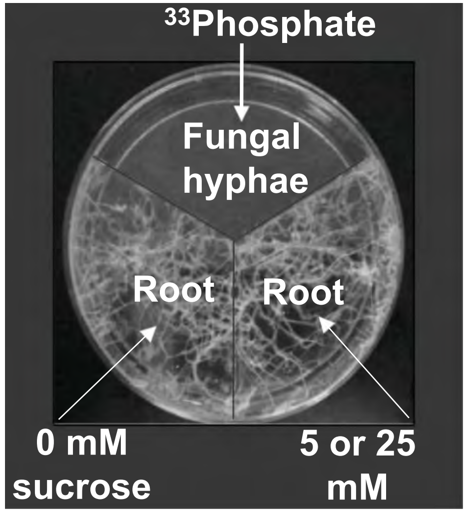
Selosse & Rousset (2011) Nature

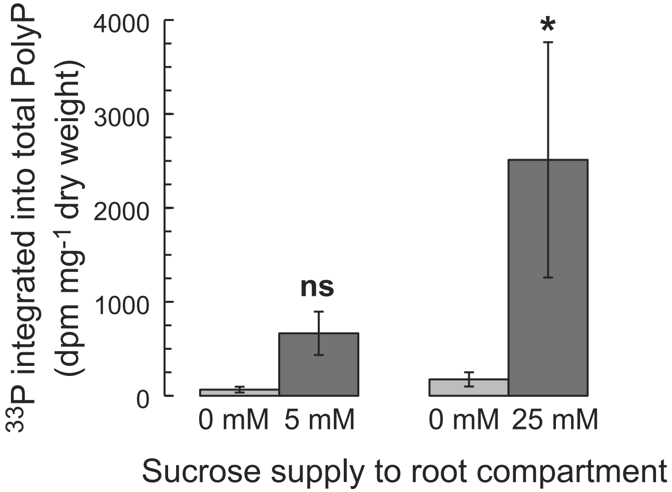
# 3) Mutualism stability and the evolution of sanctions

## Tests of the presence of “sanctions” in plant - arbuscular mycorrhizal fungus mutualism









Experimenters inoculated a single root *(Medicago,* a legume) with two different fungi, which were allowed to grow into separate environmental compartments. Then, they enforced each fungus to be cooperative (or not) by adding some (or no) phosphorus to its own compartment. The more cooperative fungus received more carbon from root cells.

They manipulated plant cooperation by exposing roots to variable amounts of sucrose as a carbon source (which Glomeromycetes only use after plants hydrolyze it to glucose). The fungi made more phosphorus available to the roots that offered more carbon.

Thus, both partners “choose” more rewarding symbionts, and control cooperation based on bidirectional exchange of nutrients.

Kiers et al. (2011) Nature

# 3) Mutualism stability and the evolution of sanctions

## Sanctions in cleaner wrasse - client fish mutualism?

ANIMAL BEHAVIOUR, 2002, 63, 547–555
doi:10.1006/anbe.2001.1937, available online at http://www.idealibrary.com on

### Asymmetric cheating opportunities and partner control in a cleaner fish mutualism

REDOUAN BSHARY* & ALEXANDRA S. GRUTTER†
*Max-Planck-Institut für Verhaltensphysiologie, Seewiesen, Germany
†Department of Zoology and Entomology, University of Queensland

*(Received 12 September 2000; initial acceptance 14 December 2000; final acceptance 2 October 2001; MS. number: 6680R)*

How can cooperation persist if, for one partner, cheating is more profitable than cooperation in each round, while the other partner has no option to cheat? Our laboratory experiments suggest that such a situation exists between the cleaner fish *Labroides dimidiatus* and its nonpredatory client reef fish species, which actively seek cleaners to have their ectoparasites removed. Clients *Ctenochaetus striatus* regularly jolted in response to cleaner mouth contact, and these jolts were not linked to the removal of parasites. In addition, cleaners did not search for parasites but fed on mucus when exposed to anaesthetized clients, which could not control the cleaners' behaviour. Field data showed that clients often terminated an interaction immediately after a jolt. Client species with access to only one cleaning station, owing to their small territories or home ranges, terminated interactions mainly by chasing cleaners while clients with access to two or more cleaning stations mainly swam away. Thus, the chasing of cleaners appeared to be a form of punishment, imposing costs on the cleaner at the client's (momentary) expense. Chasing yields future benefits, as jolts were on average less frequent during interactions between cleaners and individuals that had terminated their previous interaction by aggressive chasing.

# 4) Example exam questions

Provide two alternative explanations (hypotheses) for the presence of flowers having long nectar spurs that are pollinated by animals with long tongues.

One hypothesis for the maintenance of mutualisms over the long term is that “sanctions” have evolved that prevent the evolution of overexploitation. Define sanction in the context of a two-species mutualisms.

Provide an example of a mutualism that appears to have evolved sanctions Describe the proposed sanction and explain how it is thought to prevent the evolution of overexploitation.