Coevolution of parasites and hosts

1) Evolution of host-parasite interactions

2) Evolution of virulence

3) Trade-offs in host defense

4) Brood parasitism - an arms race?

5) End of arms race?

6) Example exam questions

1) Evolution of host-parasite interactions

Parasitism:
Individuals of one species live on or in members of another species, which are not killed immediately.

One party (parasite) gains at the expense of the other (host).

Coevolution (strictly):

Reciprocal evolutionary change of interacting species

1) Evolution of host-parasite interactions

- immune systems and pathogens
- chemical and physical defenses against phytophagous insects (e.g., *Heliconius* caterpillars on *Passiflora* vines)
- brood parasitism (e.g., cuckoos and hosts)
- kleptoparasitism (e.g., frigate birds)
- interspecific “slavery” (e.g., ants)

1) Evolution of host-parasite interactions

Interspecific slavery in ants

Colony foundation by *Epimyrma* queens follows the typical pattern seen in many temporary social parasites and obligatory slave makers, and involves the forceful usurpation of a host colony. ...

E. kraussei queens approach host colonies in an aggressive manner. Once the parasite penetrates the host nest, she kills the host queen and is adopted by the host workers. The queens of *E. ravouxi* use a more 'conciliatory' approach initially, grooming and stroking host workers, but, once inside the nest, the parasite mounts the host queen from behind and kills her by seizing her around the neck with her sabre-shaped mandibles.

E. stumperi queens crouch down, freeze and seem to feign death during their initial encounters with host workers, but subsequently begin to mount workers from behind and to groom them, perhaps acquiring chemical recognition cues in the process. However, once inside the nest, the parasite queen systematically eliminates the host queens by mounting them, rolling them over and grasping their necks in her mandibles until they succumb.

- *Lewis, et al, eds. 2002. The behavioural ecology of parasites. CABI*.

Photo *of E. ravouxi* by Olivier Delattre
http://the-scorpion-and-the-frog.blogspot.ca/2012_10_01_archive.html

2) Evolution of virulence

Virulence: the severity of a parasite's harm to the host, usually measured as the magnitude of the effect on host survival or reproductive success.

The conventional wisdom once was that parasites should inevitably evolve so as to reduced their virulence to their hosts.

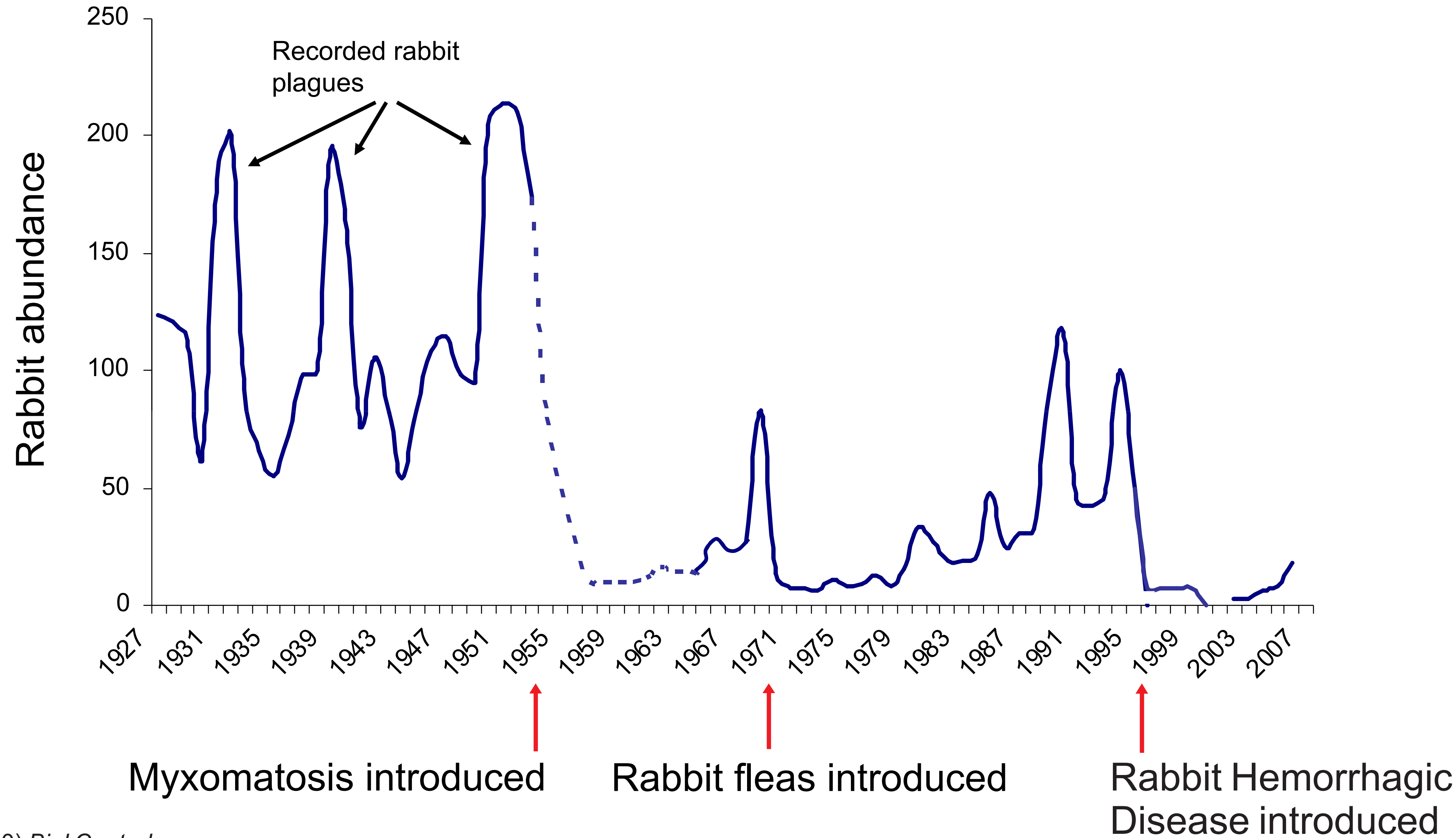
This was based on observations that:

- some mutualistic associations have evolved from once-pathogenic interactions (lichens? mycorrhizal fungi?).

- highly virulent parasites kill their hosts, and thereby themselves.

2) Evolution of virulence

Rabbit abundance in northeast South Australia accompanying rapid evolution of lower virulence by viruses (and of resistance by rabbits)



Saunders et al (2010) *Biol Control*

2) Evolution of virulence

Example: evolution of *Myxoma* virulence

TABLE 4. THE VIRULENCE OF STRAINS OF MYXOMA VIRUS RECOVERED FROM THE FIELD IN AUSTRALIA BETWEEN 1951 AND 1981, EXPRESSED AS PERCENTAGES

virulence grade	I	II	III	IV	V	
case fatality rate (%)	>99	95–99	70–95	50–70	<50	number of
mean survival time/day	<13	14–16	17–28	29–50	—	samples
1950–51†	100‖					1
1952–55†	13.3	20.0	53.3	13.3	0	60
1955–58†	0.7	5.3	54.6	24.1	15.5	432
1959–63‡	1.7	11.1	60.6	21.8	4.7	449
1964–66‡	0.7	0.3	63.7	34.0	1.3	306
1967–69‡	0	0	62.4	35.8	1.7	229
1970–74‡	0.6	4.6	74.1	20.7	0	174
1975–81§	1.9	3.3	67.0	27.8	0	212

† Data from Marshall & Fenner (1960).
‡ Data from Edmonds *et al*. (1975).
§ Data from J. W. Edmonds and R. C. H. Shepherd (personal communication, 1982).
‖ Although only one strain was tested, the very high mortality rates in the initial outbreaks justify this extrapolation.

2) Evolution of virulence

An alternative perspective is that selection should favor genotypes whose level of virulence maximizes their rate of increase.

Maximizing rate of increase involves evolution of high transmission rates to new hosts.

Genotypes that increase transmission are not necessarily those genotypes with the lowest virulence. An increased transmission rate might come from rapid multiplication of parasite in infected hosts, which might increase virulence.

The evolution of virulence is likely to depend on a balance between the advantages of high virulence (increased multiplication of parasite in infected host, increasing transmission) and disadvantages of high virulence (increased host mortality, decreasing transmission).

Consequently, selection might often favor an intermediate virulence.

2) Evolution of virulence

Evolution of *Myxoma* virulence

TABLE 1. Comparison of the virulence of field strains of myxoma virus in Great Britain, Australia, and France (from Ross, 1982), contrasting initial frequencies with those several years after introduction.

	VIRULENCE GRADE (AS PERCENTAGE OCCURRENCE)					
	I	II	IIIA	IIIB	IV	V
GREAT BRITAIN						
1953	100	—	—	—	—	—
1962–1967	3.0	15.1	48.4	22.7	10.3	0.7
1968–1970	0	0	78.0	22.0	0	0
1971–1973	0	3.3	36.7	56.7	3.3	0
1974–1976	1.3	23.3	55.0	11.8	8.6	0
1977–1980	0	30.4	56.5	8.7	4.3	0
AUSTRALIA						
1950–1951	100	—	—	—	—	—
1958–1959	0	25.0	29.0	27.0	14.0	5.0
1963–1964	0	0.3	26.0	34.0	31.3	8.3
FRANCE						
1953	100	—	—	—	—	—
1962	11.0	19.3	34.6	20.8	13.5	0.8
1968	2.0	4.1	14.4	20.7	58.8	4.3

2) Evolution of virulence

Experimental evolution of virulence

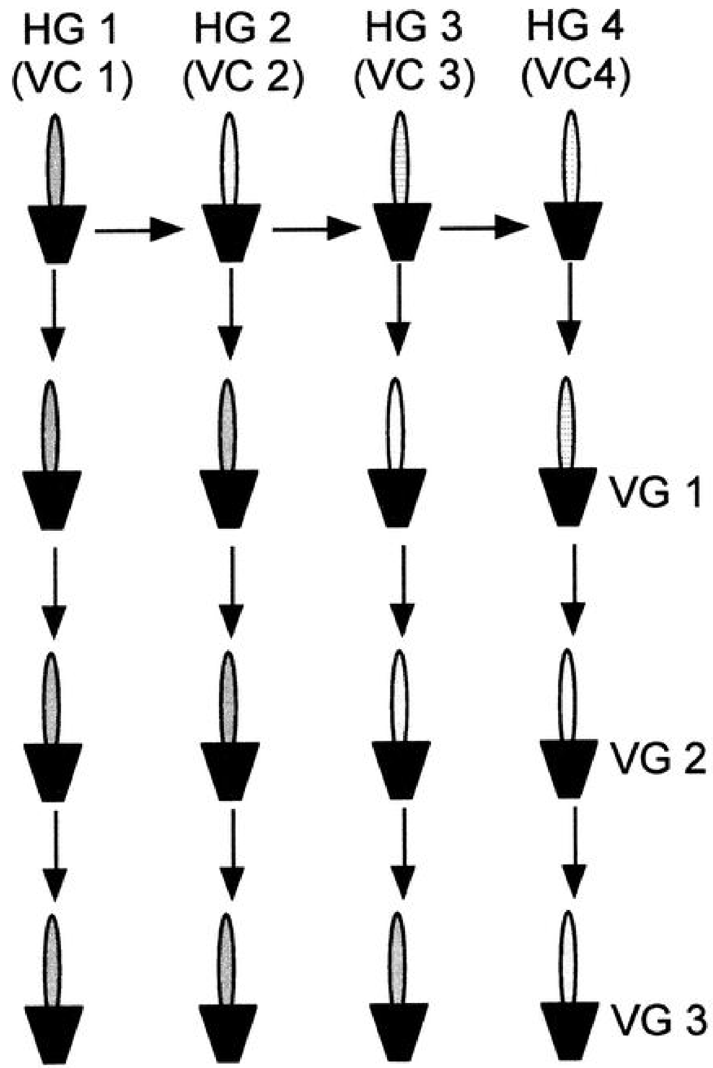
Parasite: barley stripe mosaic virus

Host: barley (*Hordeum vulgare*)

http://www.albertabarley.com/barley/barley/images/BarleyCommission-stock4.JPG

horizontal transmission treatment
(4 barley generations)

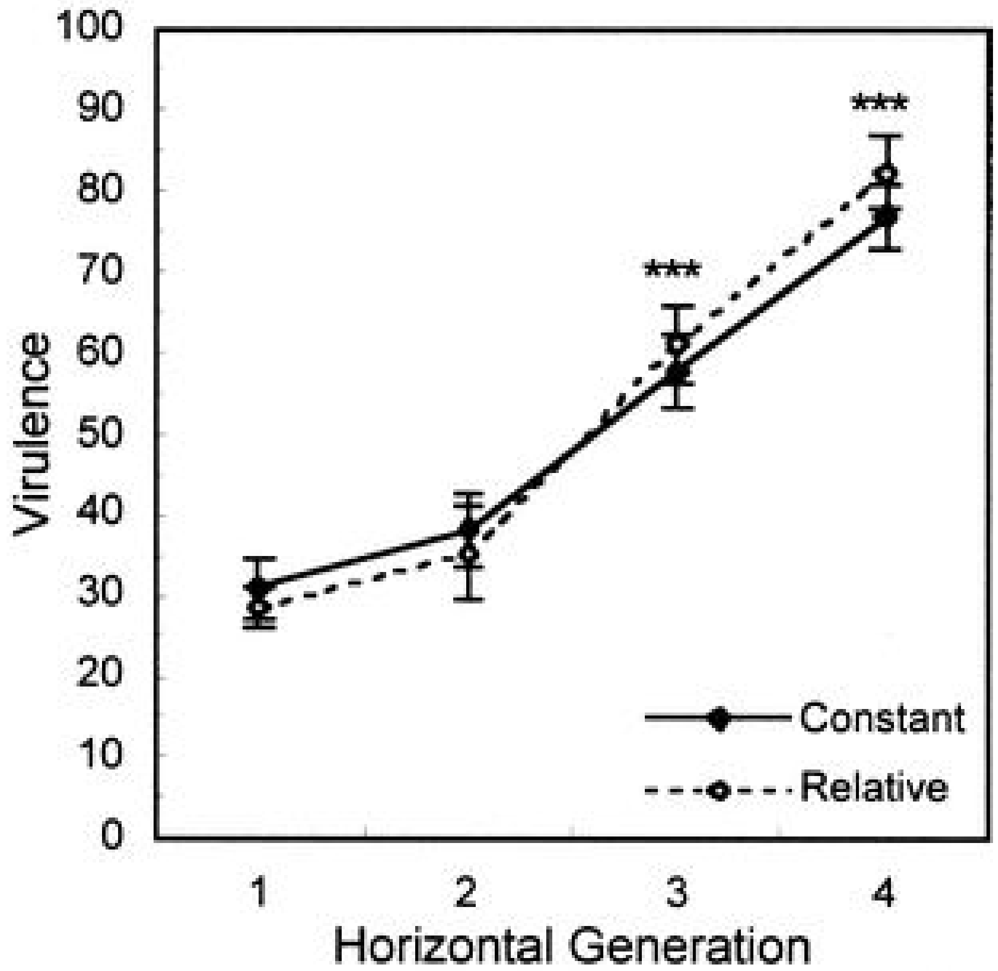
vertical transmission treatment
(4 barley generations, transmission by seeds)



Stewart et at. (2005)

2) Evolution of virulence

horizontal transmission treatment(4 barley generations)



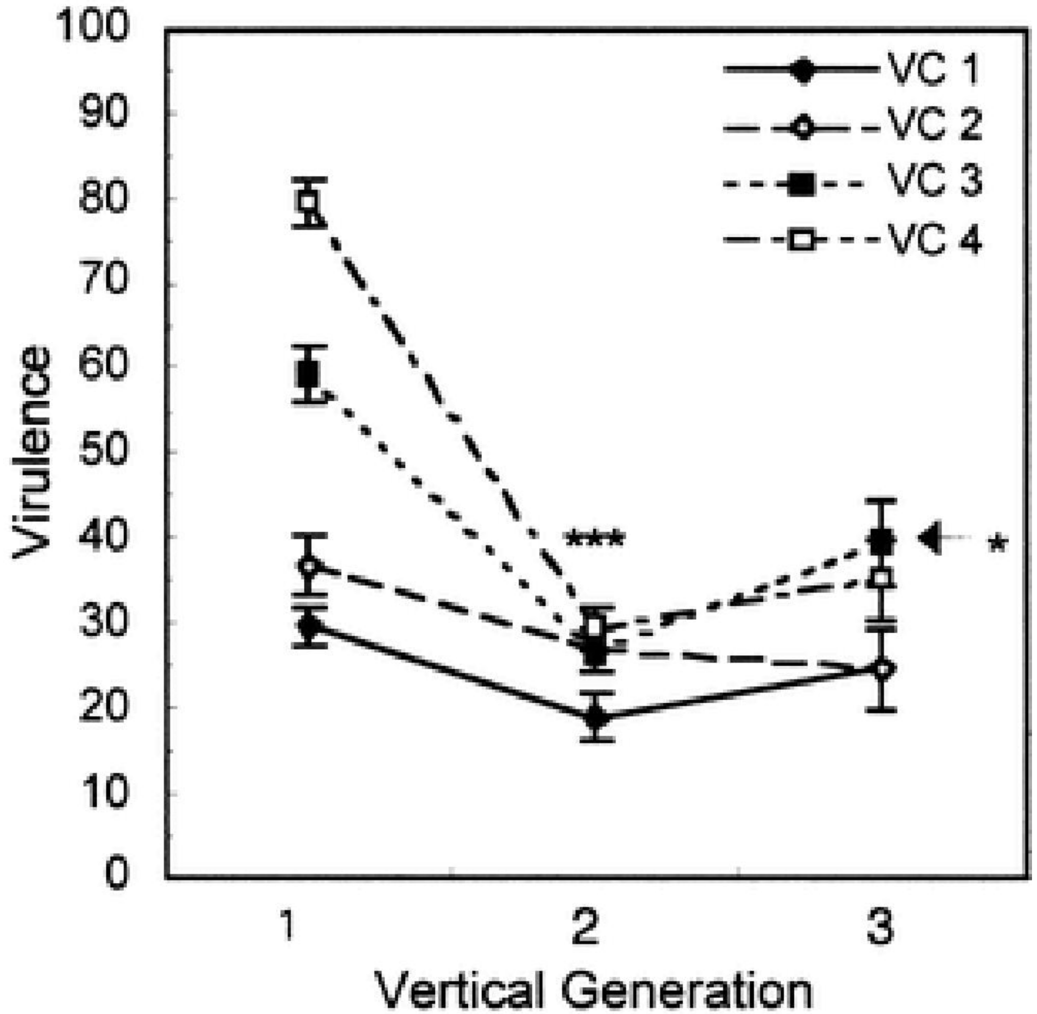
“virulence” measured by number of viable seeds produced by infected plant

1 – (viable seeds of infected plants) / (viable seeds of control plants) x 100%

Stewart et at. (2005)

2) Evolution of virulence

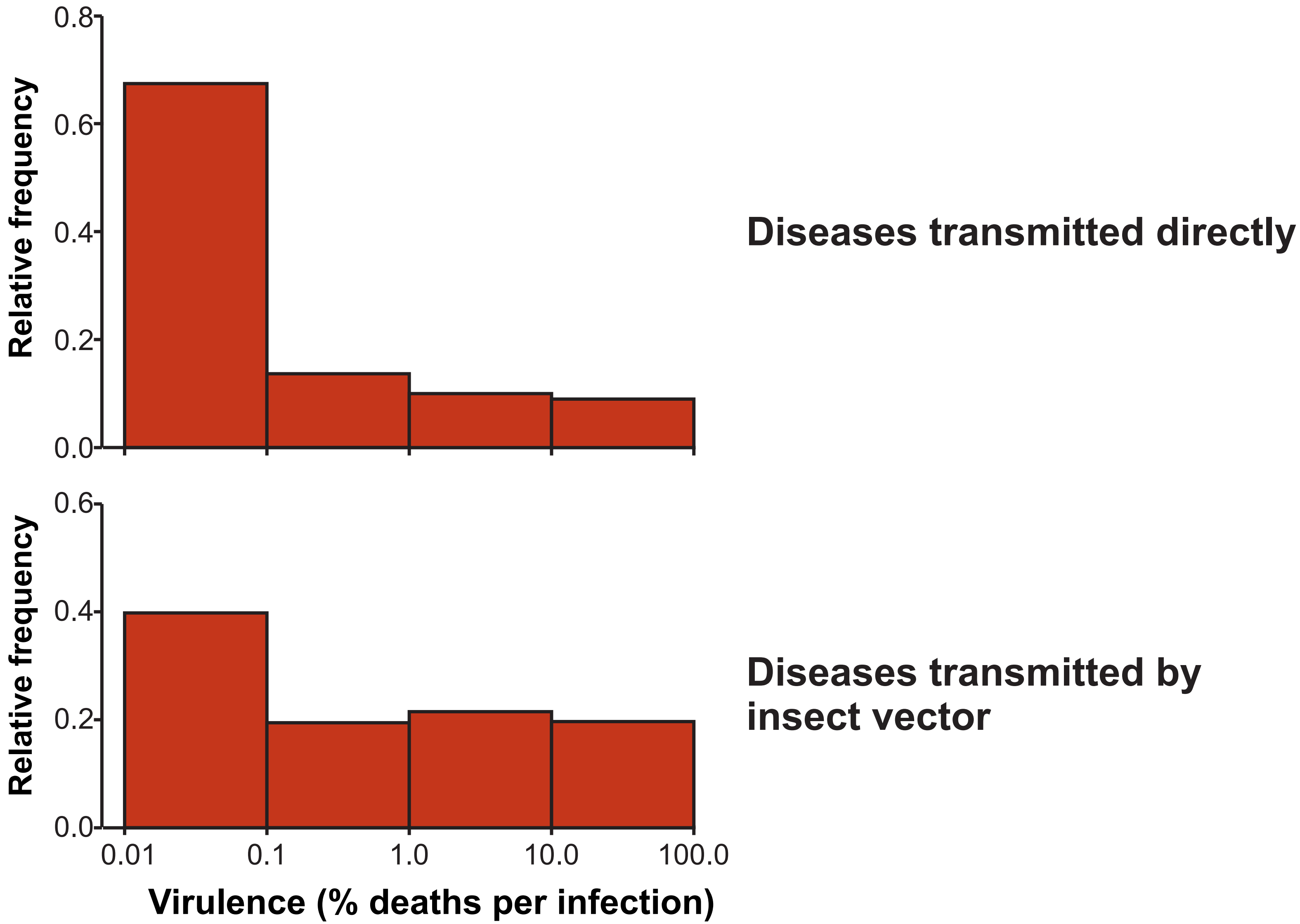
vertical transmission treatment



Stewart et at. (2005)

2) Evolution of virulence

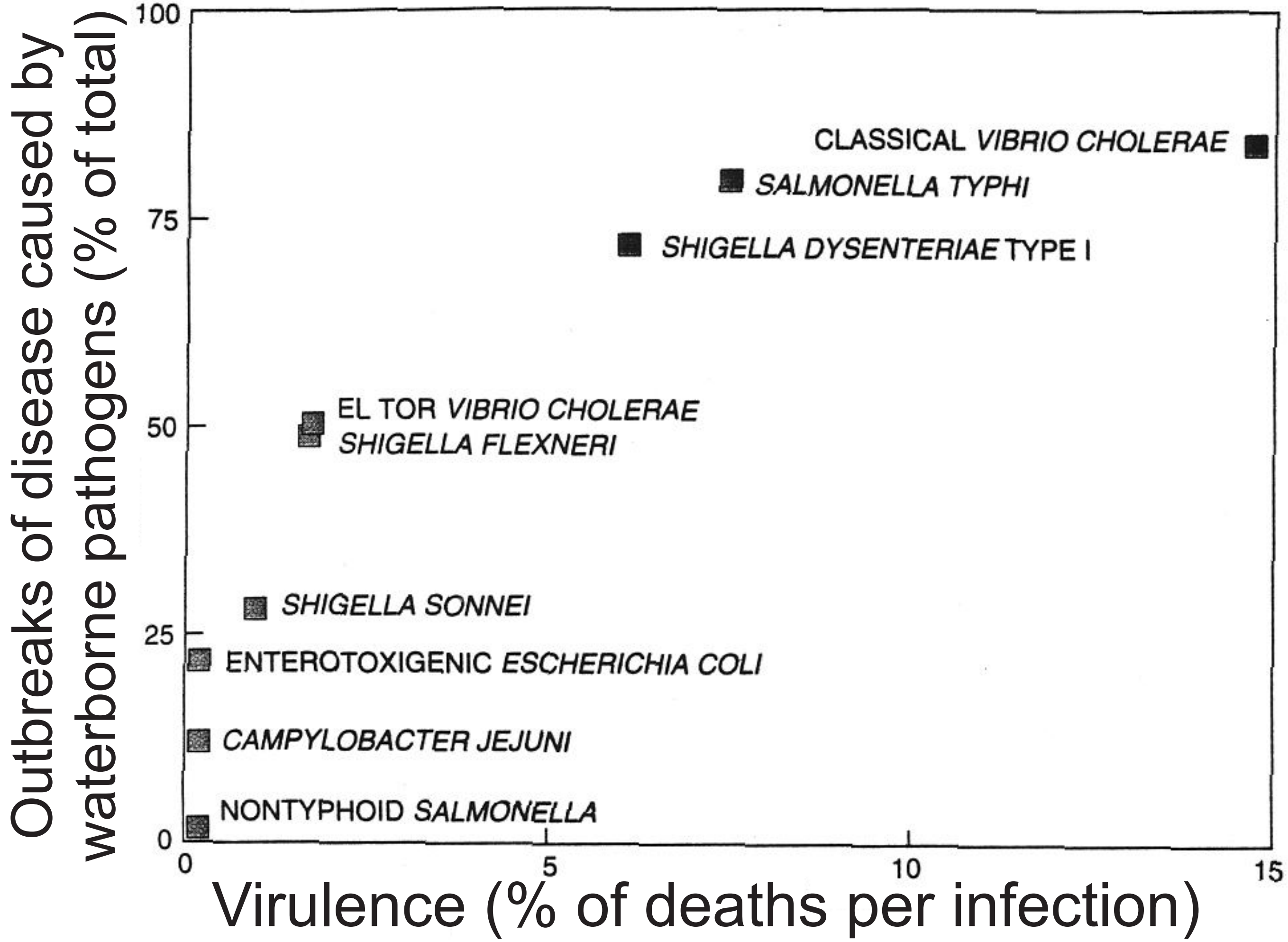
Virulence and mode of transmission of human diseases



Ewald (1993)

2) Evolution of virulence

Waterborne human diseases are deadly



PATHOGENS that are most frequently transported by water systems, such as classical *Vibrio cholerae*, are more virulent than those that are not, such as nontyphoid *Salmonella*. A waterway contaminated by wash or sewage can serve as a cultural vector, a transporter of pathogens that is created by human behavior.

Ewald (1993)

3) Trade-offs in host defense

Coevolution between wild parsnip and the parsnip webworm

Cost of defense in wild parsnip

Negative genetic correlations between leaf secondary compounds (furanocoumarins) and indices of flower size

TABLE 8. Significant genetic correlations between seed or leaf furanocoumarins and fitness characters and between fitness characters in greenhouse plants.

	r	SE
BERl × number of secondary rays	−0.632	0.309
BERl × number of primary rays	−0.675	0.297
XANl × number of secondary rays	−0.790	0.340
XANl × number of primary rays	−0.643	0.295
SPHl × number of secondary rays	−0.688	0.267
pBERs × number of secondary rays	−1.528	0.689
pISOs × number of secondary rays	−0.888	0.408
Number of primary rays × number of secondary rays	0.809	0.183

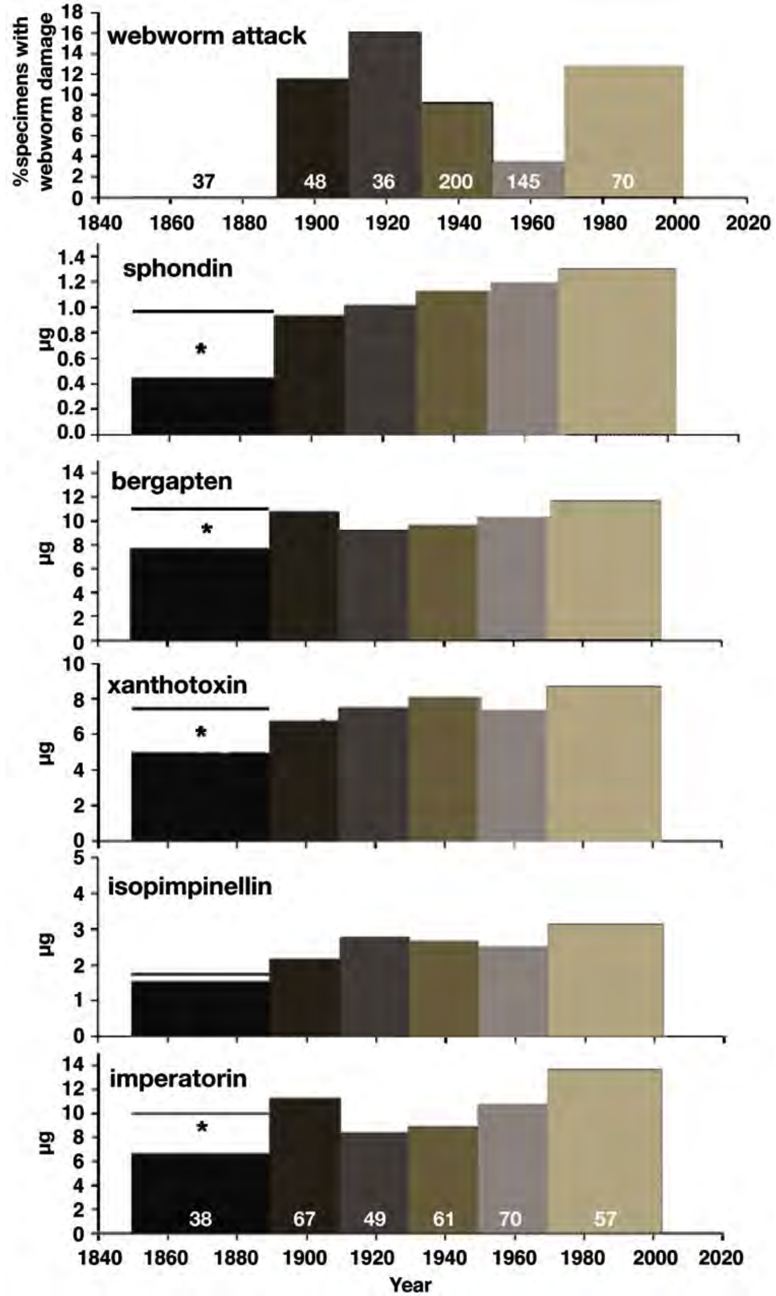
http://www.ontariowildflower.com/lakeedge.htm

Berenbaum et al (1986)

3) Trade-offs in host defense

Coevolution between wild parsnip and the parsnip webworm

Wild parsnip was introduced to North America before the parsnip webworm. In the 1800's, concentrations of furanocoumarins in parsnip seeds in herbarium specimens were lower than that in Old World plants (indicated by horizontal bars). Furanocoumarin concentrations rose after webworm damage began to appear (1900's).



http://mothphotographersgroup.msstate.edu/larva.php?plate=01.0&sort=h

Zangerl & Berenbaum 2005

4) Brood parasitism - an arms race?

Coevolution between European cuckoos and hosts

reed warbler

cuckoo chick

reed warbler nest

http://fleetpond.wordpress.com/2009/05/

4) Brood parasitism - an arms race?

Adaptation:
Nest parasitism by European cuckoos

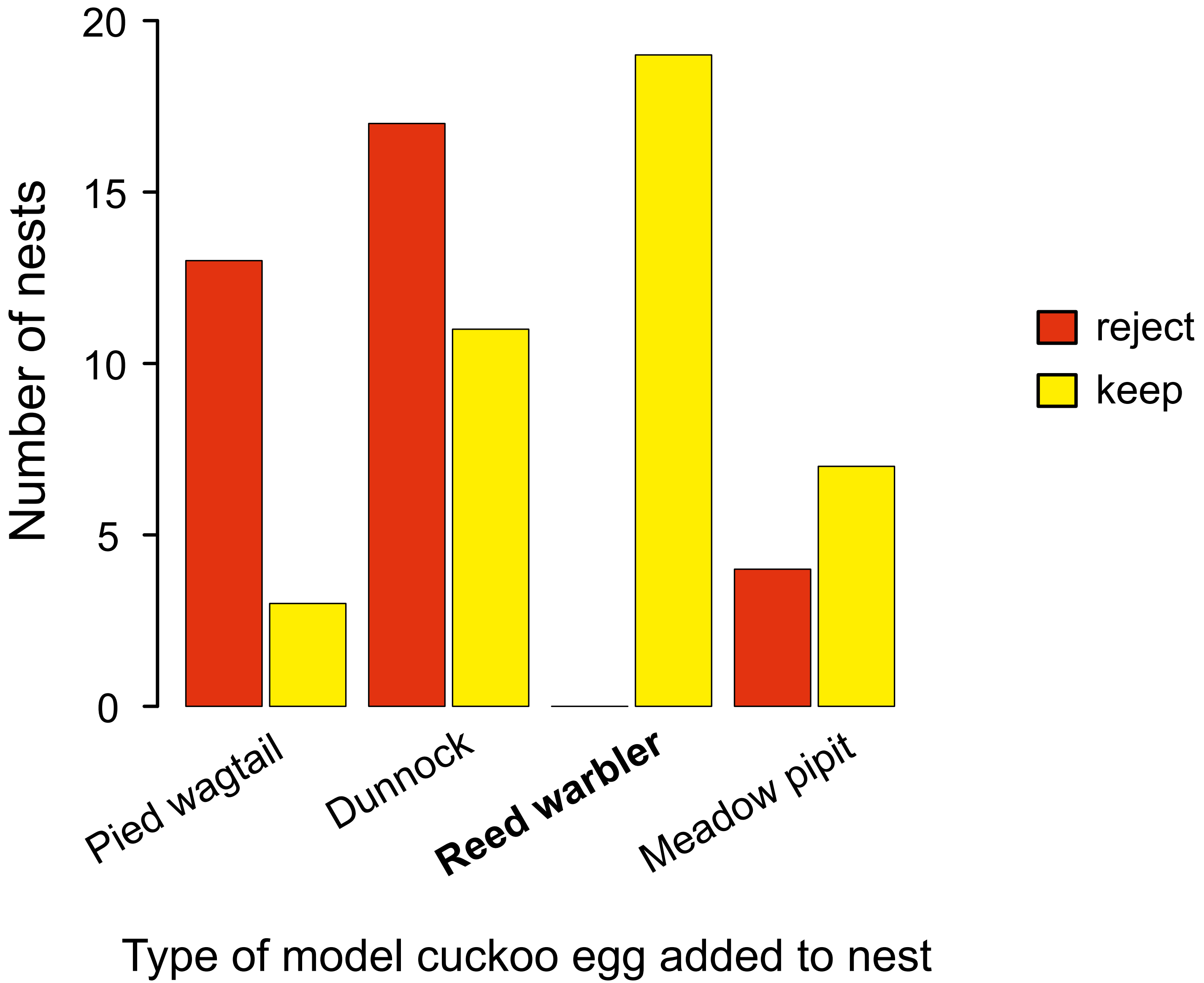
Newly-hatched cuckoo chick ejecting host eggs and chicks

Hosts frequently parasitized by common cuckoo in the UK are reed warbler, meadow pipit, pied wagtail, and dunnock.

4) Brood parasitism - an arms race?

Counteradaptation:
Host species have evolved rejection of eggs unlike their own

Frequency of rejection by **reed warblers** of rubber model cuckoo eggs placed in their nests



Brooke & Davies (1988)

4) Brood parasitism - an arms race?

Counteradaptation:
Host species have evolved rejection of eggs unlike their own

		Britain cuckoos present	**Iceland** cuckoos absent
Meadow pipit	Reject	**28**	**5**
	Keep	**30**	**22**
Pied/white wagtail	Reject	**27**	**5**
	Keep	**11**	**23**

Host populations in Iceland, where cuckoos are absent, are less likely to reject eggs unlike their own than in Britain, where cuckoos are present.

Davies & Brooke (1989)

4) Brood parasitism - an arms race?

Counter-counter adaptation:
Cuckoos have evolved egg mimicry (or not, in case of dunnock)

Brooke & Davies (1988)

4) Brood parasitism - an arms race?

Counter-counter adaptation:
Cuckoos have evolved egg mimicry (or not, in case of dunnock)

Reed warbler

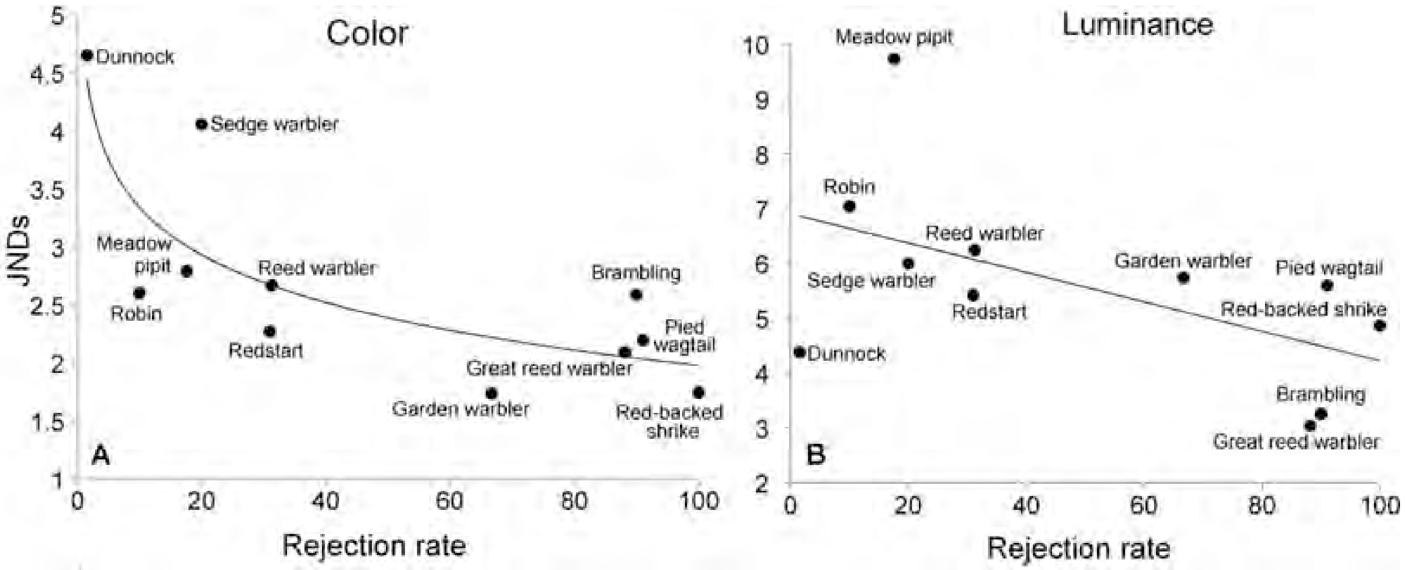
http://www.britannica.com/EBchecked/topic-art/128222/21/Coevolution-of-one-species-with-many-species

Meadow pipit

Dunnock

4) Brood parasitism - an arms race?

Counter-counter adaptation:
Cuckoos have evolved egg mimicry (or not, in case of dunnock)



Host rejection rate of nonmimetic eggs and mean “just noticeable differences” (JND - a composite metric) between cuckoo and host eggs in background color and background luminance. Data from continental Europe. Closer mimicry is associated with higher rejection rates of eggs unlike the hosts’ own.

Stoddard & Stevens (2011) Evolution

4) Brood parasitism - an arms race?

Counter-counter adaptation:
Cuckoos have evolved hawk-like 'chuckle' call

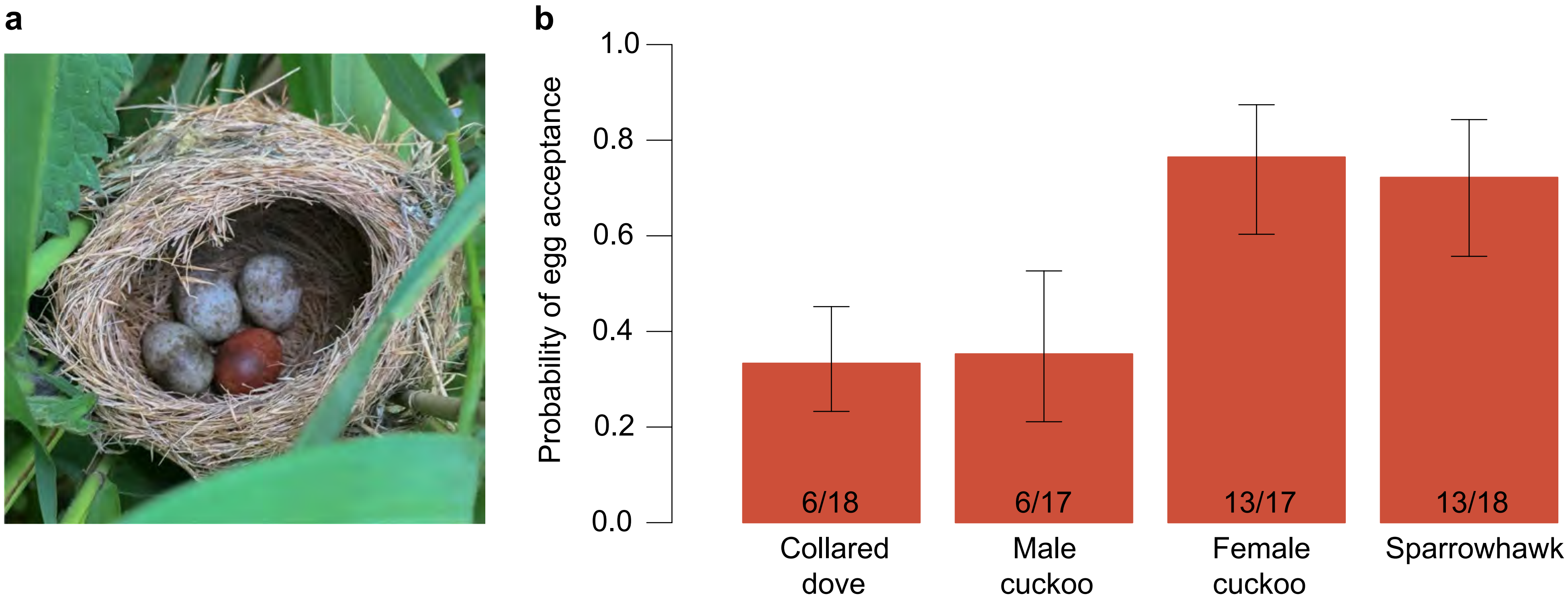


Fig. 2 | Reed warblers were more likely to accept a foreign egg after playback of female cuckoo or hawk calls than after the calls of a male cuckoo or dove. **a**, A reed warbler clutch with one egg painted brown to simulate parasitism. **b**, The probability of reed warblers accepting a foreign egg one day after the experiment was greater after exposure to female cuckoo or hawk calls compared with dove or male cuckoo calls (experiment 3 in Table 1; n = 70 nests; data are predicted means ± s.e.m.; the raw proportions of the nests in which foreign eggs were accepted are also shown at the base of each bar). Male cuckoo calls had no more effect than control dove calls (χ^2 = 0.015; P = 0.90), whereas female cuckoo calls reduced egg rejection as much as hawk calls (χ^2 = 0.083; P = 0.77).

York & Davies (2017) Nature Ecology & Evolution

4) Brood parasitism - an arms race?

Counter-counter adaptation:
Cuckoos have evolved egg mimicry (or not, in case of dunnock)

The paradox of the dunnock - why no egg rejection?

https://www.rspb.org.uk/birds-and-wildlife/bird-and-wildlife-guides/bird-a-z/d/dunnock/

4) Brood parasitism - an arms race?

Absence of chick recognition by hosts

Rate of food provisioning to cuckoo chicks compared to other chicks

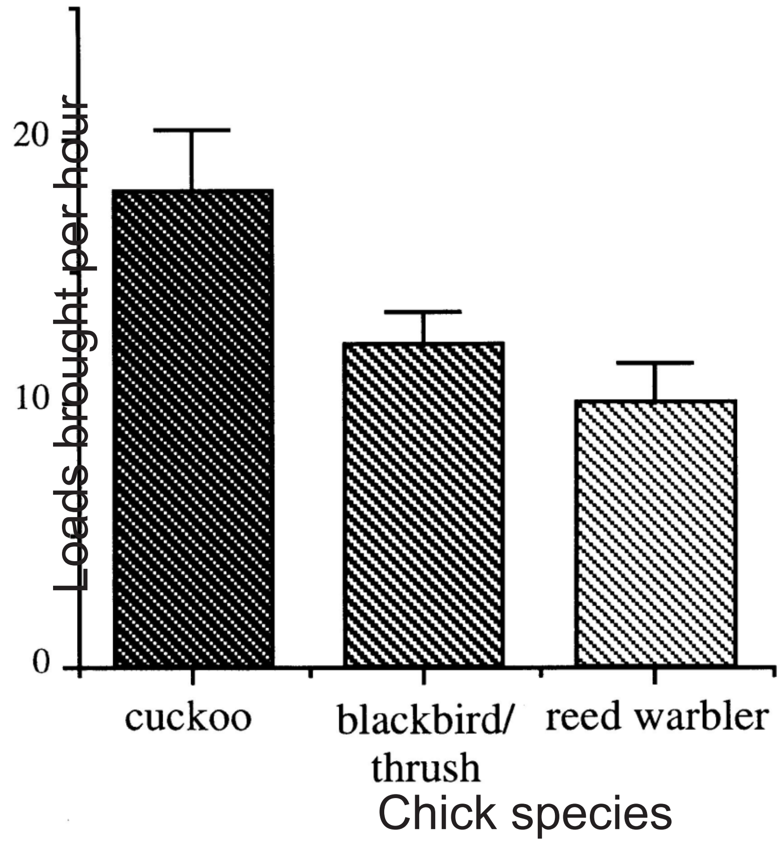
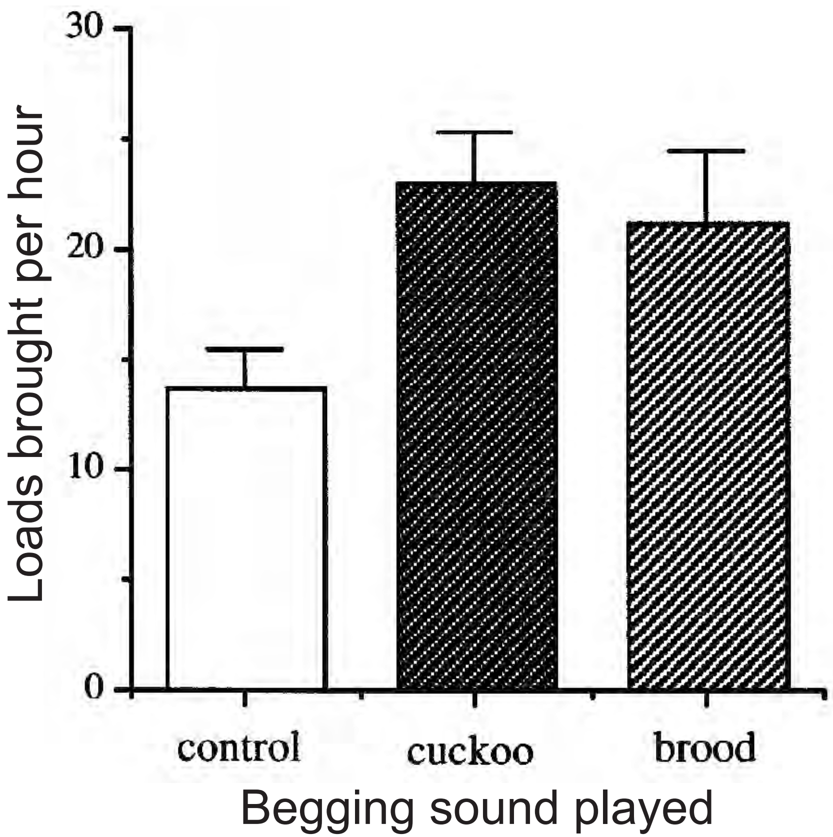


Figure 1. Number of food loads (mean ± 1 s.e.) brought per hour by pairs of reed warblers to single cuckoo chicks ($n=13$), single blackbird or song thrush chicks ($n=19$) the same mass as a cuckoo, and single reed warbler chicks ($n=12$).

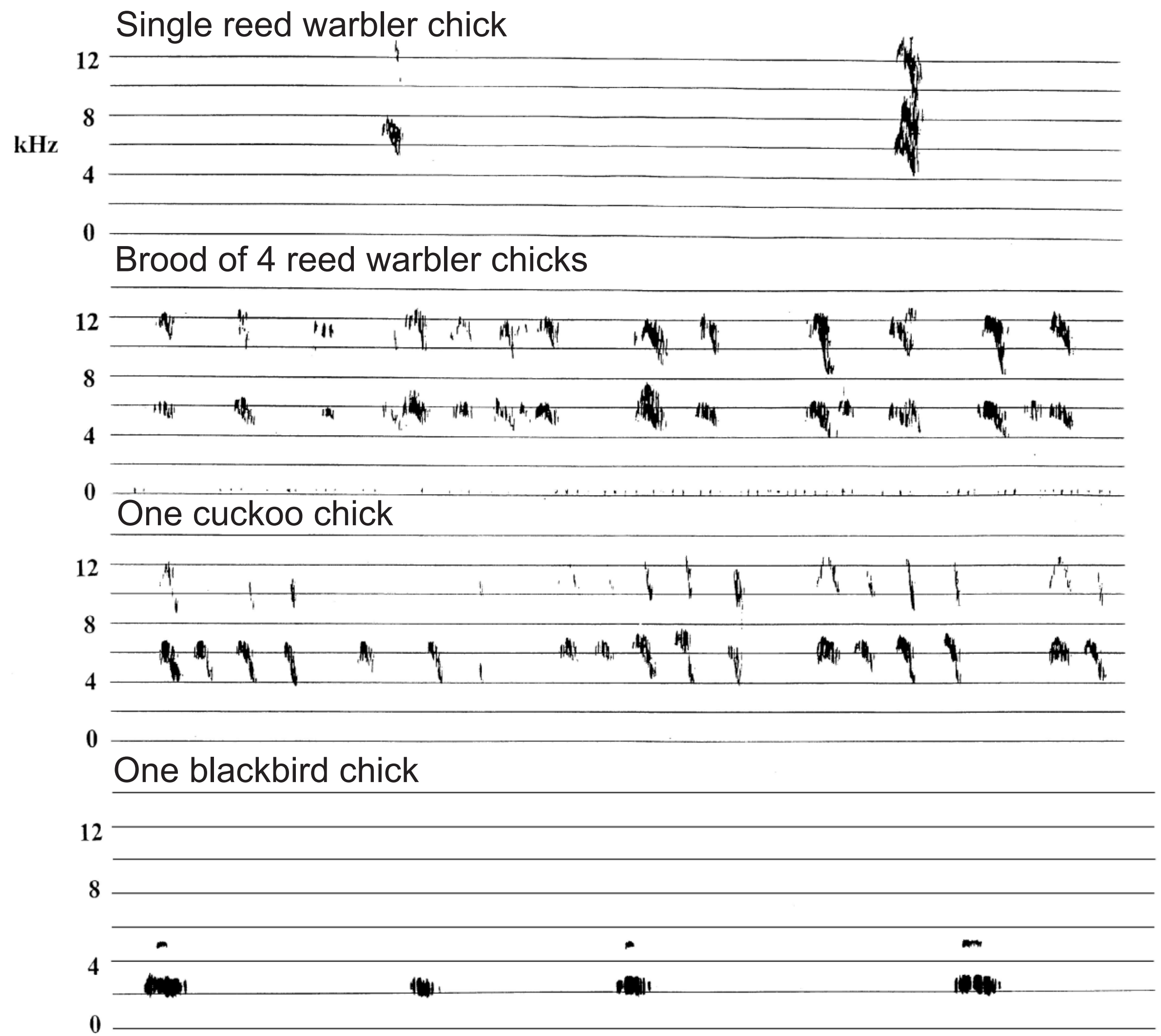
Davies et al. (1998)

4) Brood parasitism - an arms race?

Cuckoo chicks have evolved begging call like that of host (reed warbler)



Provisioning rate by reed warbler parents (mean ± 1SE) to single blackbird (n=6) or song thrush (n=3) chicks tested with no sound, sound of cuckoo chick begging, or sound of a brood of four reed warblers.

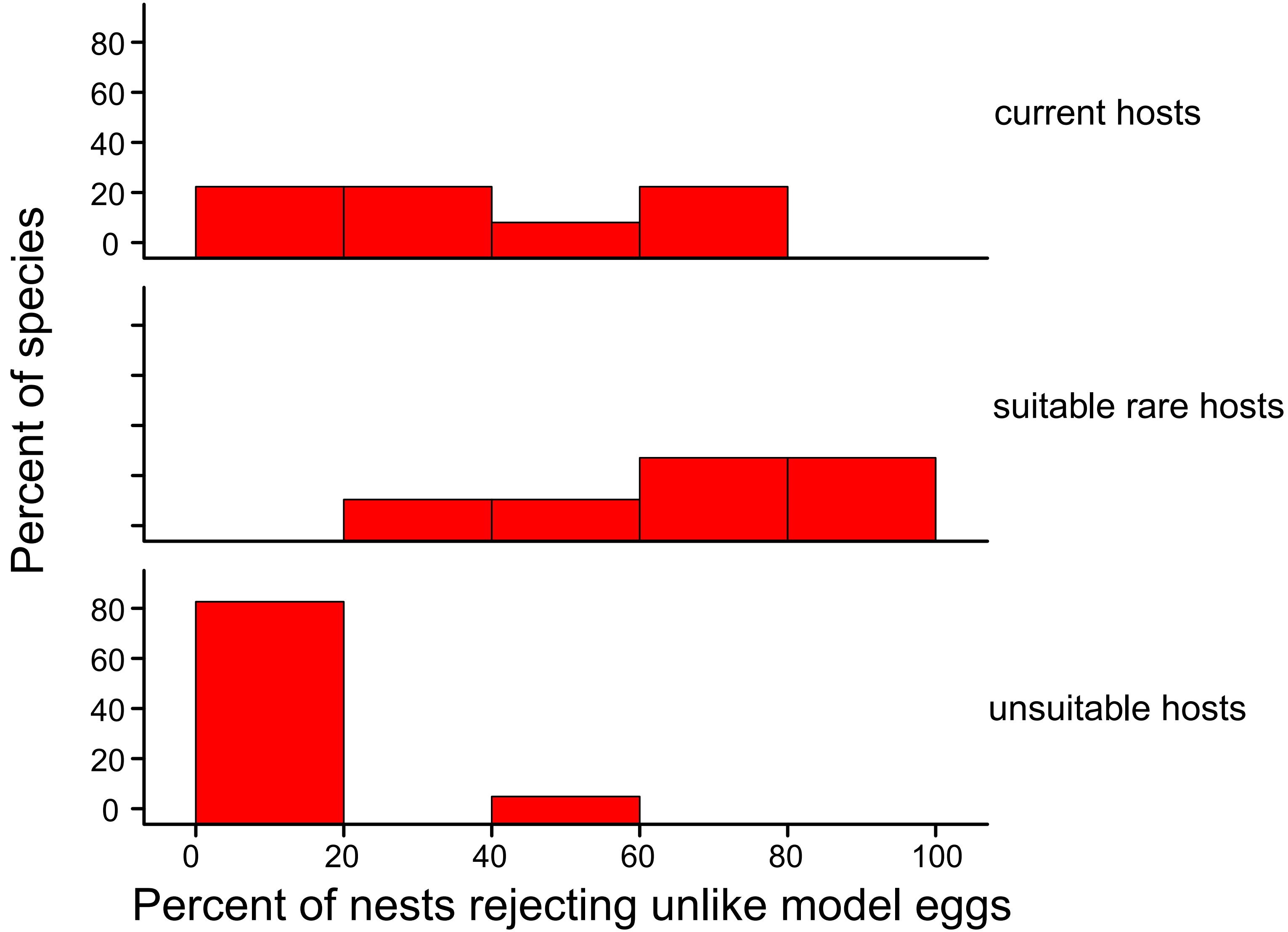


Sonograms of begging calls (recorded 60 min after feeding to satiation)

Davies et al. (1998)

5) End of arms race?

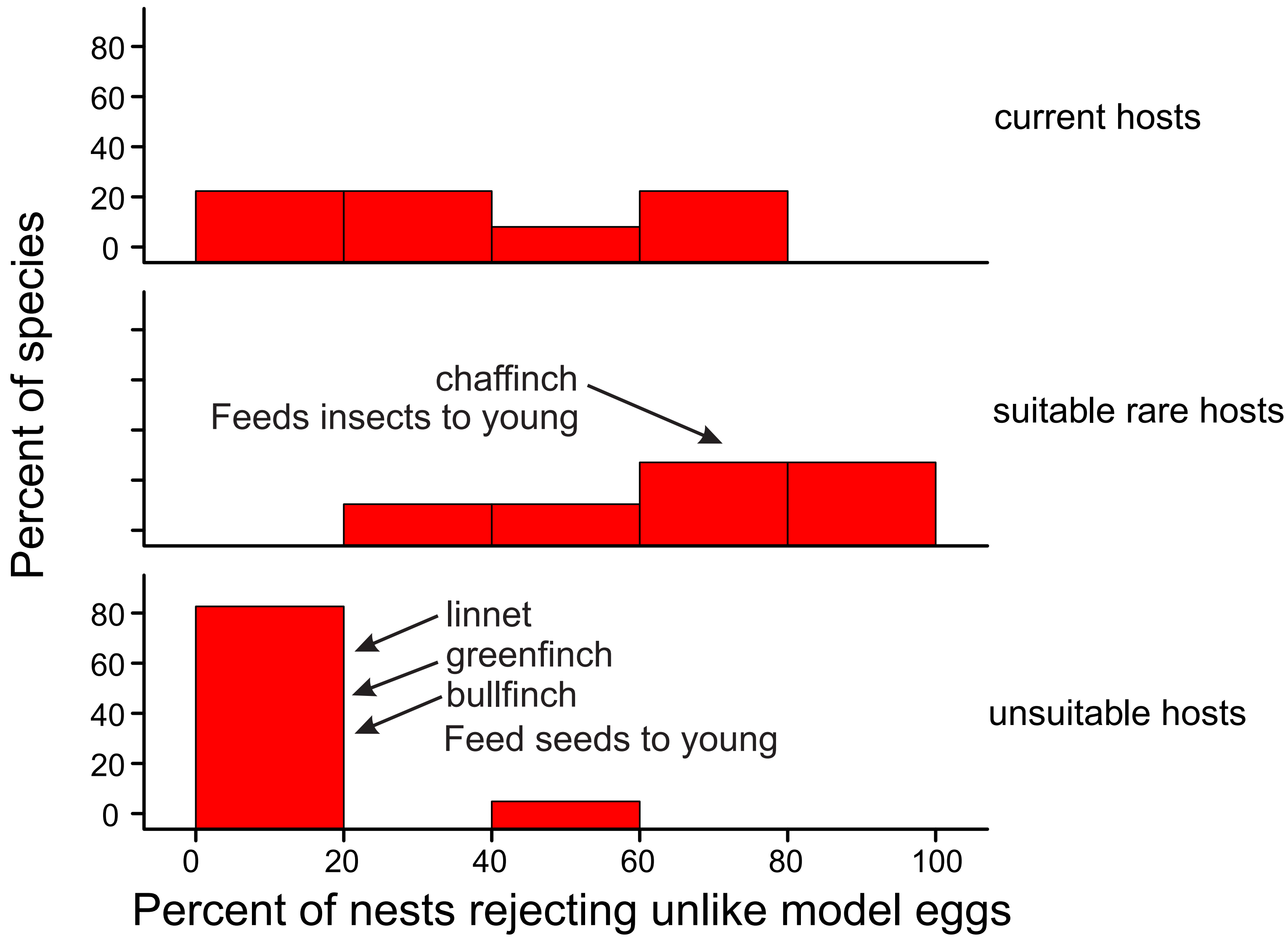
Some non-host species have evolved high egg rejection rates



Davies & Brooke (1989)

5) End of arms race?

Some non-host species have evolved high egg rejection rates



Davies & Brooke (1989)

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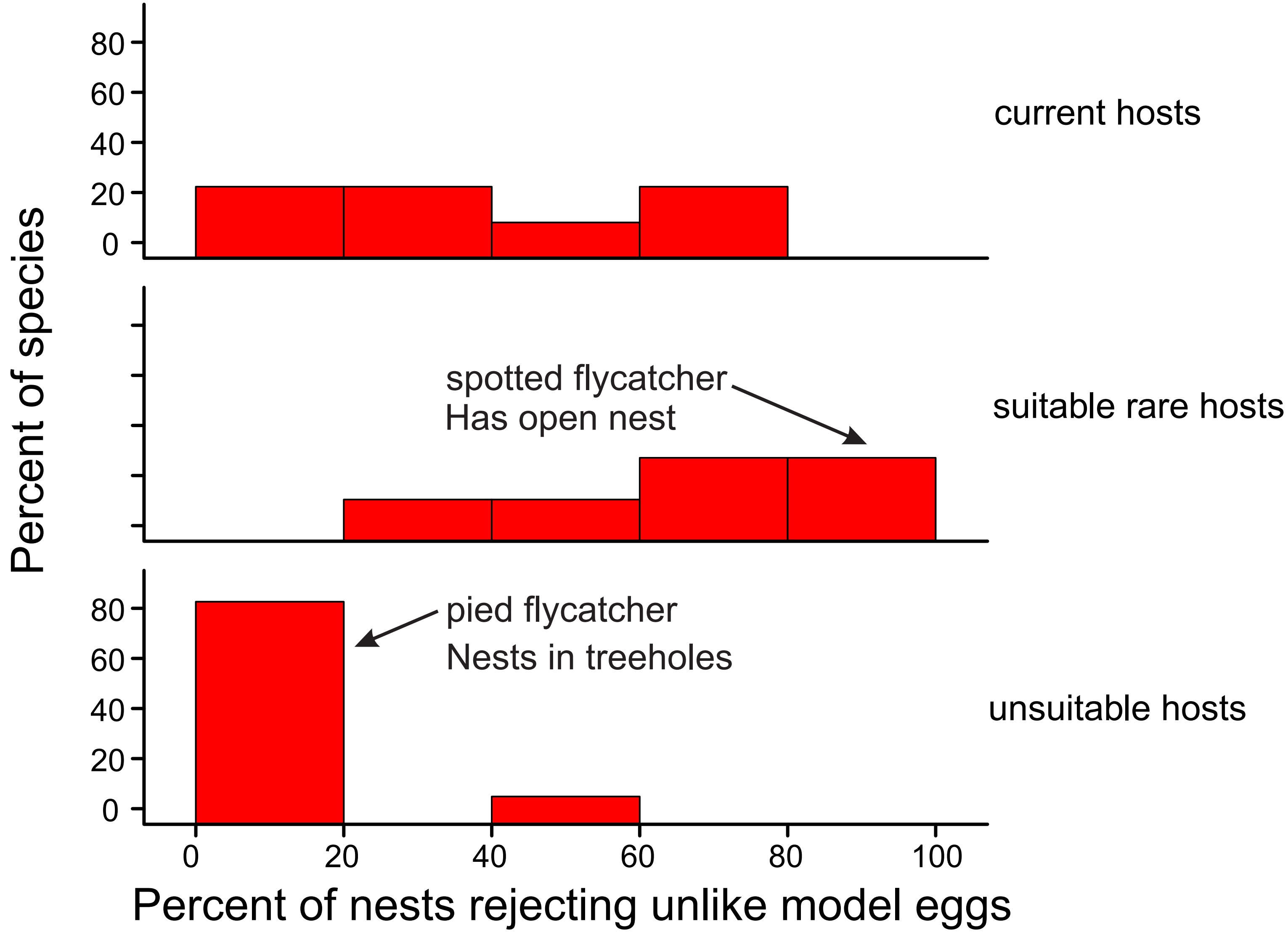

Davies & Brooke (1989)

6) Example exam questions

Why are some parasites more virulent than others? Present a study design for testing alternative hypotheses.

Consider a coevolutionary interaction between a disease and its host. Under what circumstances might we expect natural selection to favor a low virulence of the disease? Under what circumstances might we expect natural selection to favor a high virulence of the disease? Explain.

Is the coevolution between cuckoo brood parasites and their avian hosts best described as an arms race or as steady-state coevolution (in the language of Abrams)? Explain your reasoning.

Is the coevolution between wild parsnip and the parsnip webworm best described as an arms race or as steady-state coevolution (in the language of Abrams)? Explain your reasoning.

Suggest a hypothesis for why waterborne human pathogens are often highly virulent. Explain the basis for your hypothesis, and suggest an experimental test.