

# 11

Sexual selection has produced many of the most striking traits in animals, such as the antlers of this bull elk.



# Sex

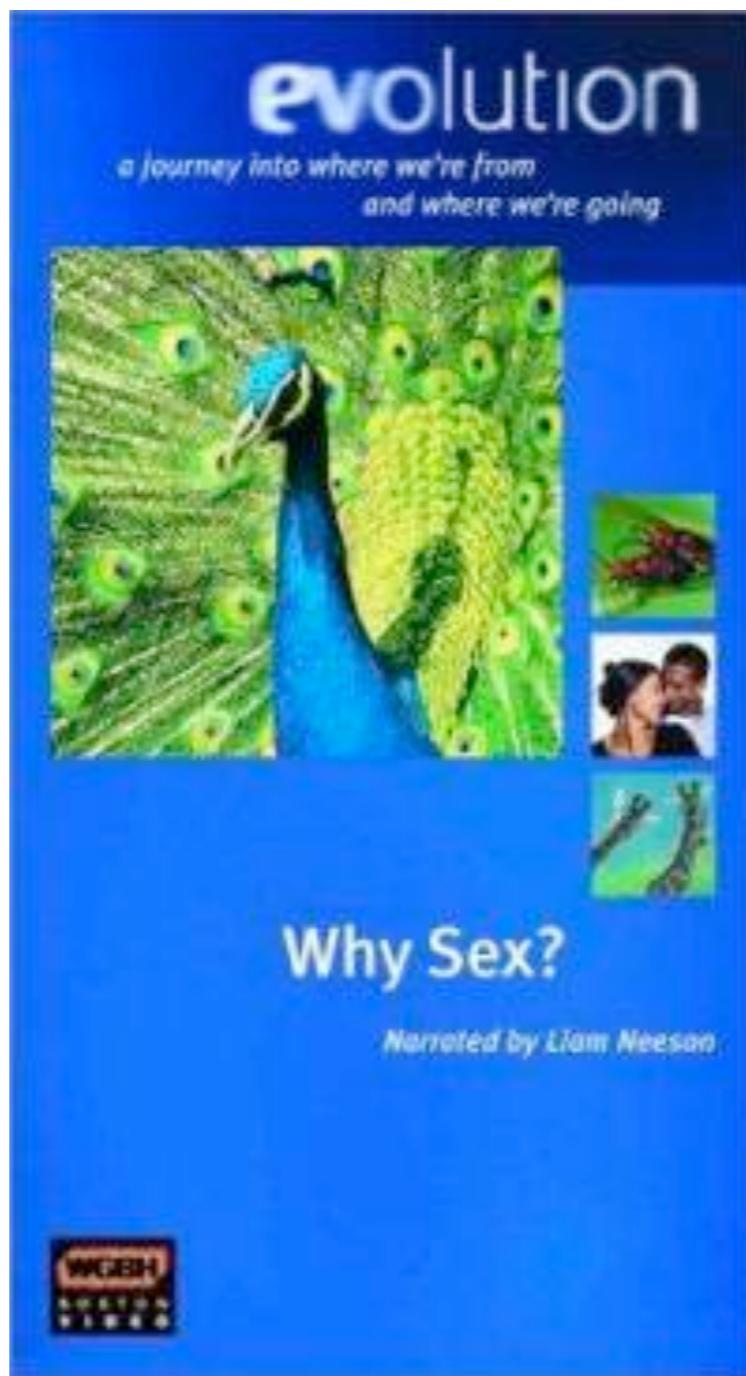
## Causes and Consequences

### Learning Objectives

- Define sex and identify possible mechanisms for the evolution of sex.
- Identify the genetic consequences of sexual and asexual reproduction.
- Explain the Red Queen effect.
- Explain why asexual organisms evolved alternatives to sex.
- Identify the different investments made in sexual reproduction by males and females.
- Explain how differential investment can result in conflicting selection pressure in males and females.
- Analyze how the different reproductive strategies of males and females lead to sexual selection.
- Explain why sexual dimorphism is an outcome of sexual selection.
- Identify the direct and indirect benefits of male choice.
- Apply Fisher's runaway model to a preexisting sensory bias for red.
- Compare and contrast the good genes and arbitrary choice models of sexual selection.
- Compare and contrast social monogamy with polygyny and polyandry.
- Analyze how competing interests of males and females in sexual reproduction may influence selection.

# tarea

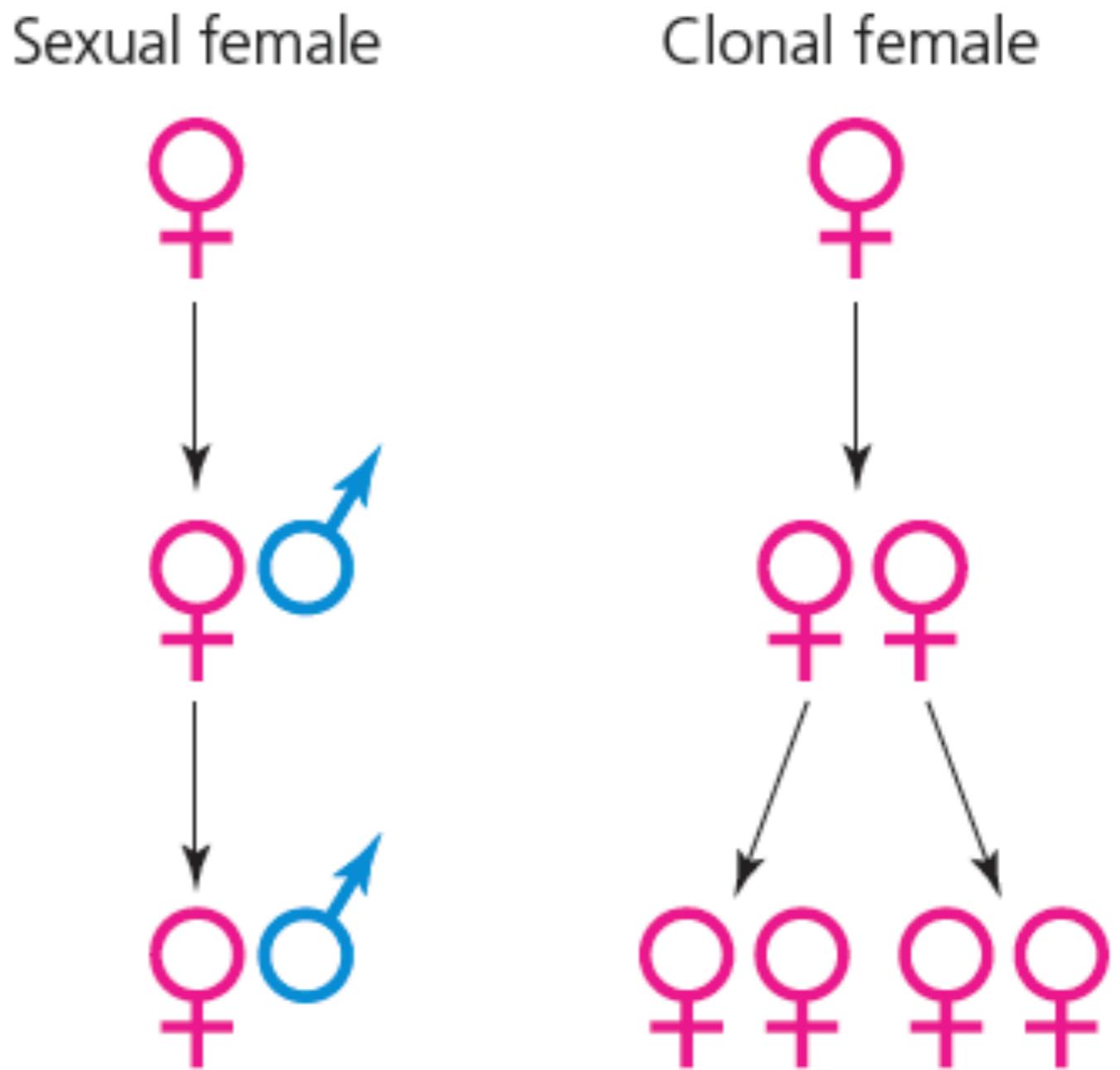
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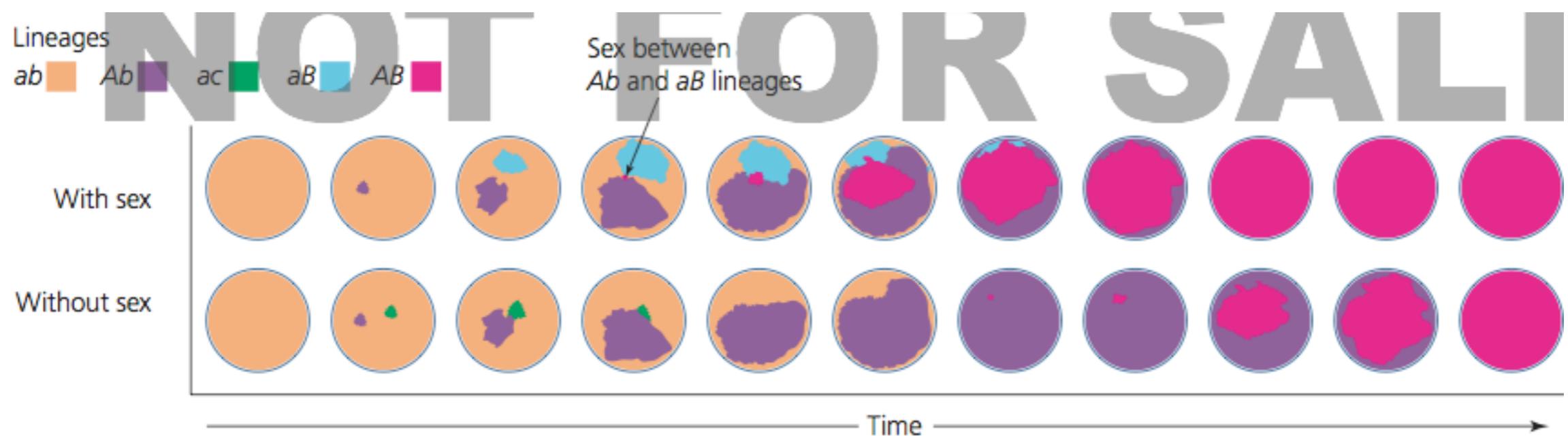
<https://youtu.be/JakdRczkmNo>

# costos de la reproducción sexual

**Twofold cost of sex:** Asexual lineages multiply faster than sexual lineages because all progeny are capable of producing offspring. In sexual lineages, half of the offspring are males who cannot themselves produce offspring. This effectively halves the rate of replication of sexual species.



# ventaja de la reproducción sexual: combinación rápida de mutaciones beneficiosas



**Figure 11.4** One hypothesis for why sex persists is based on its ability to produce new genotypes. This figure shows a sexual population (top) and an asexual one (bottom). Each population starts out with a single allele, *a*, for one genetic locus, and a single allele, *b*, for another locus. Over time, a mutation changes *a* to a new allele, *A*, in a single individual. This mutation is beneficial, and so descendants with *A* become more common (purple). Meanwhile, another individual

acquires a beneficial mutation to *b*, producing the allele *B* (light blue). In a sexual population, *aB* and *Ab* individuals can mate and produce offspring with the *AB* genotype (red), which has even higher fitness. In an asexual population, on the other hand, it takes longer for the *AB* genotype to evolve because both genes have to mutate in the same lineage.

# cuando las mutaciones “neutrales” adquieren importancia

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## The Loom

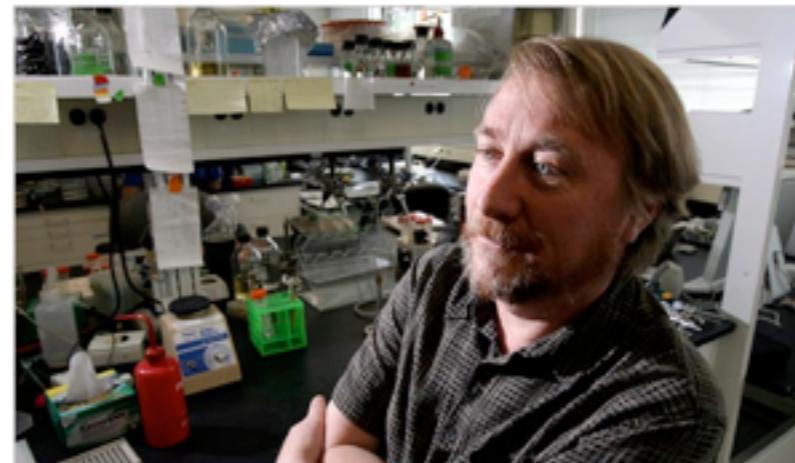
« The Slow, Slow Road to De-Discovery

Irish cannibals and Neanderthal sex: Just how big is our species? »

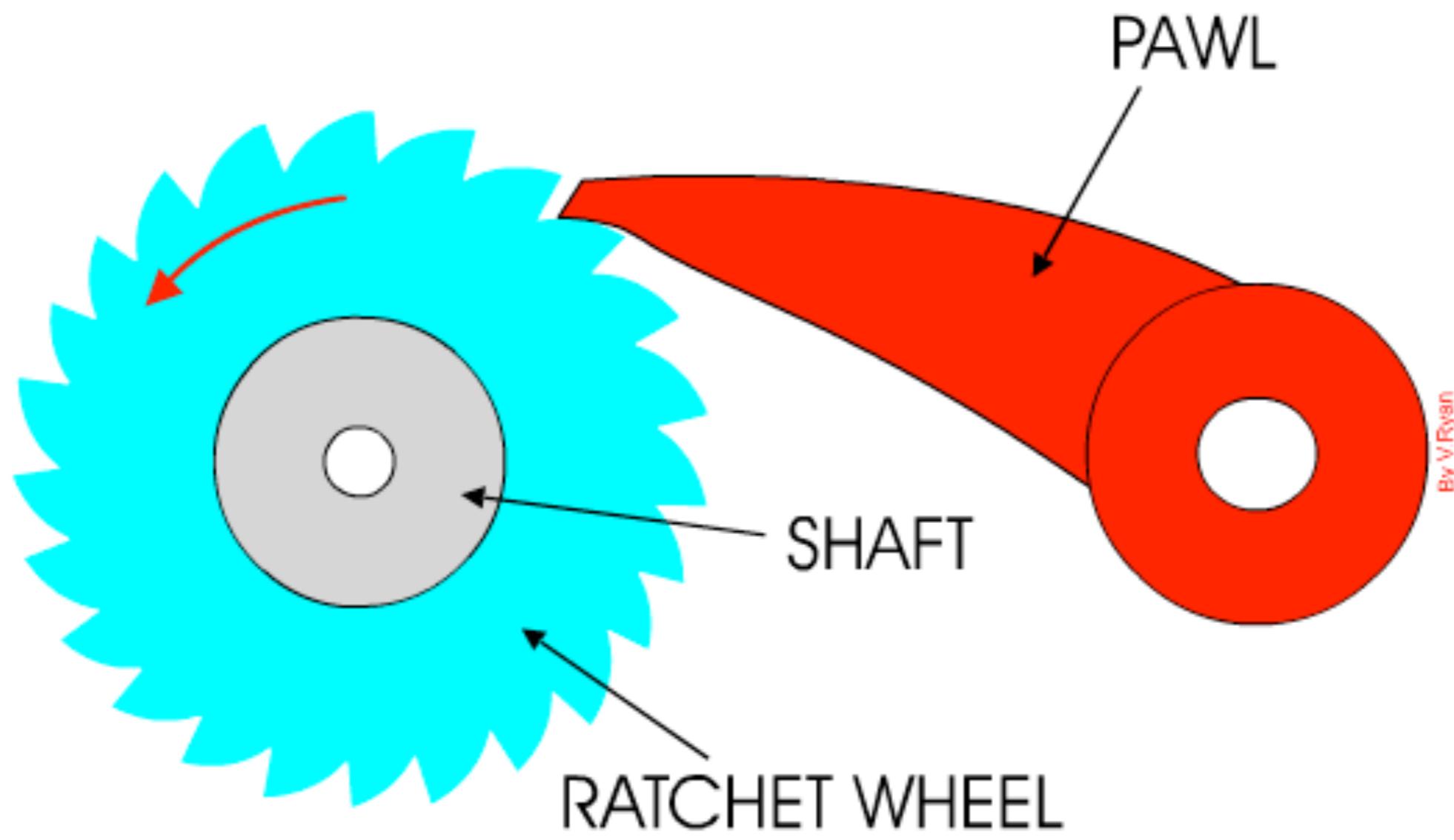
### The Birth of the New, The Rewiring of the Old

By Carl Zimmer | September 19, 2012 1:00 pm

In 1988, Richard Lenski, an evolutionary biologist now at Michigan State University, launched the longest running experiment on natural selection. It started with a single microbe—*E. coli*—which Lenski used to seed twelve genetically identical lines of bacteria. He placed each line in a separate flask, which he provisioned with a scant supply of glucose. The bacteria ate up the sugar in a few hours. The next day, he took a droplet of microbial broth from each flask and let it tumble into a new one, complete with a fresh supply of food. The bacteria boomed again, then starved again, and then were transferred again to a new home. Lenski and his colleagues have repeated this procedure every day for the past 24 years, rearing over 55,000 generations of bacteria.



<http://bit.ly/Qmi4O0>



<http://www.technologystudent.com/cams/ratch1.htm>

# THE EVOLUTIONARY ADVANTAGE OF RECOMBINATION<sup>1</sup>

JOSEPH FELSENSTEIN

*Department of Genetics SK-50, University of Washington, Seattle, Washington 98195*

Manuscript received October 3, 1973

Revised copy received March 25, 1974

## ABSTRACT

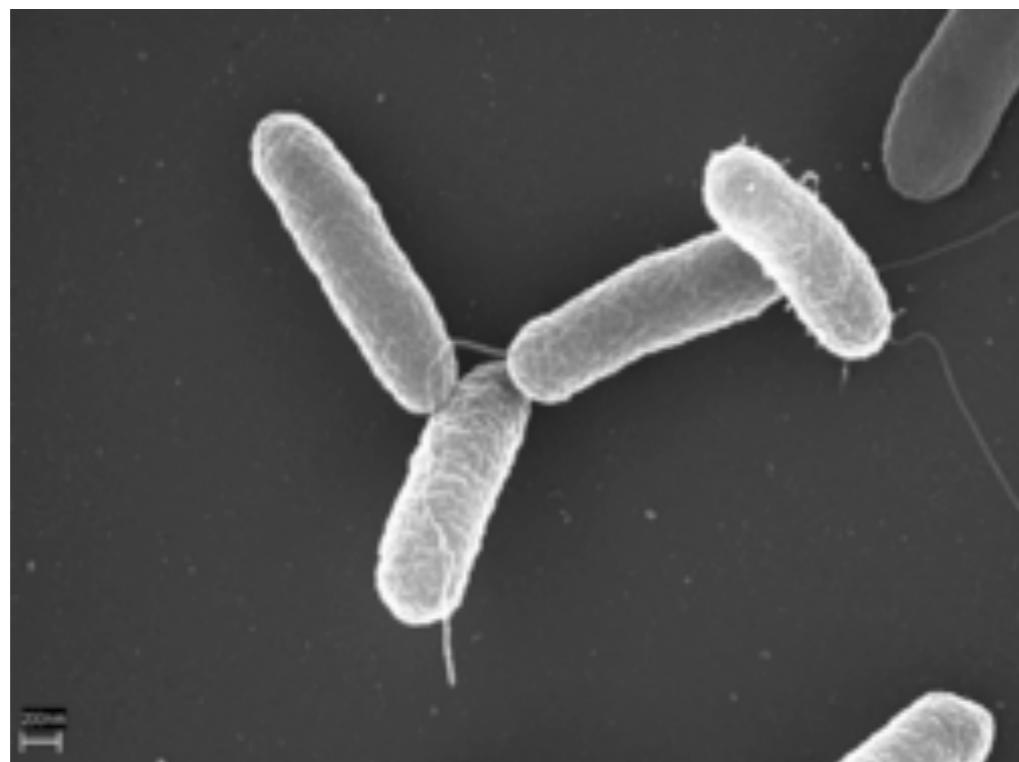
The controversy over the evolutionary advantage of recombination initially discovered by FISHER and by MULLER is reviewed. Those authors whose models had finite-population effects found an advantage of recombination, and those whose models had infinite populations found none. The advantage of recombination is that it breaks down random linkage disequilibrium generated by genetic drift. HILL and ROBERTSON found that the average effect of this randomly-generated linkage disequilibrium was to cause linked loci to interfere with each other's response to selection, even where there was no gene interaction between the loci. This effect is shown to be identical to the original argument of FISHER and MULLER. It also predicts the "ratchet mechanism" discovered by MULLER, who pointed out that deleterious mutants would more readily increase in a population without recombination. Computer simulations of substitution of favorable mutants and of the long-term increase of deleterious mutants verified the essential correctness of the original FISHER-MULLER argument and the reality of the MULLER ratchet mechanism. It is argued that these constitute an intrinsic advantage of recombination capable of accounting for its persistence in the face of selection for tighter linkage between interacting polymorphisms, and possibly capable of accounting for its origin.

# evidencia experimental de “Muller’s ratchet” en organismo asexual

Table 1. Generation time for the five mutants found

wt	mut9	mut4	mut20	mut5	mut3
23.2 ± 0.7	25.0 ± 1.1	25.1 ± 1.0	27.0 ± 1.3	46.5 ± 1.1	47.5 ± 3.5

The generation time (in min) for each slow grower represents the average of at least six measurements. Values are mean ± the standard deviation within a 95% confidence limit. wt, Wild type.



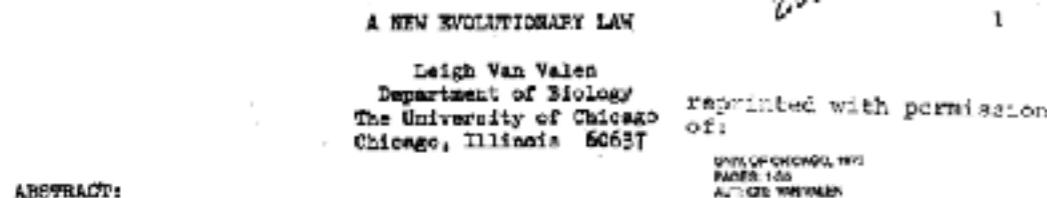
*Salmonella typhimurium*

## Muller’s ratchet decreases fitness of a DNA-based microbe

DAN I. ANDERSSON\* AND DIARMAID HUGHEST†

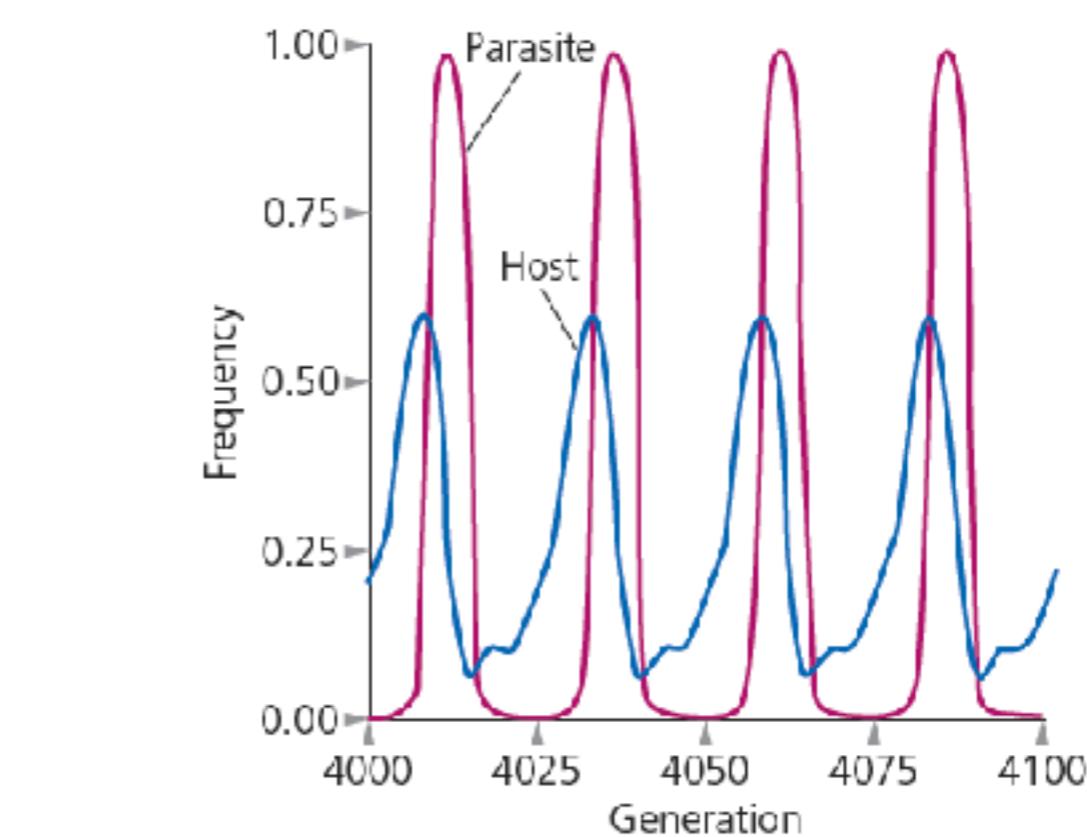
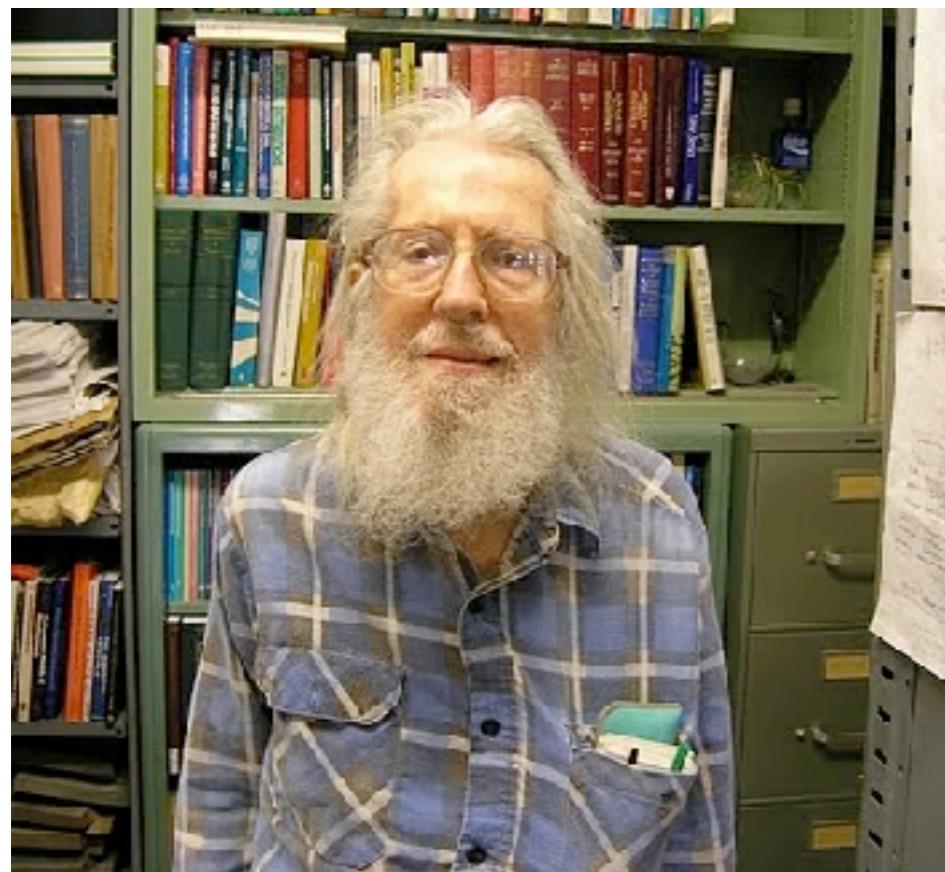
*Proc. Natl. Acad. Sci. USA*  
Vol. 93, pp. 906–907, January 1996

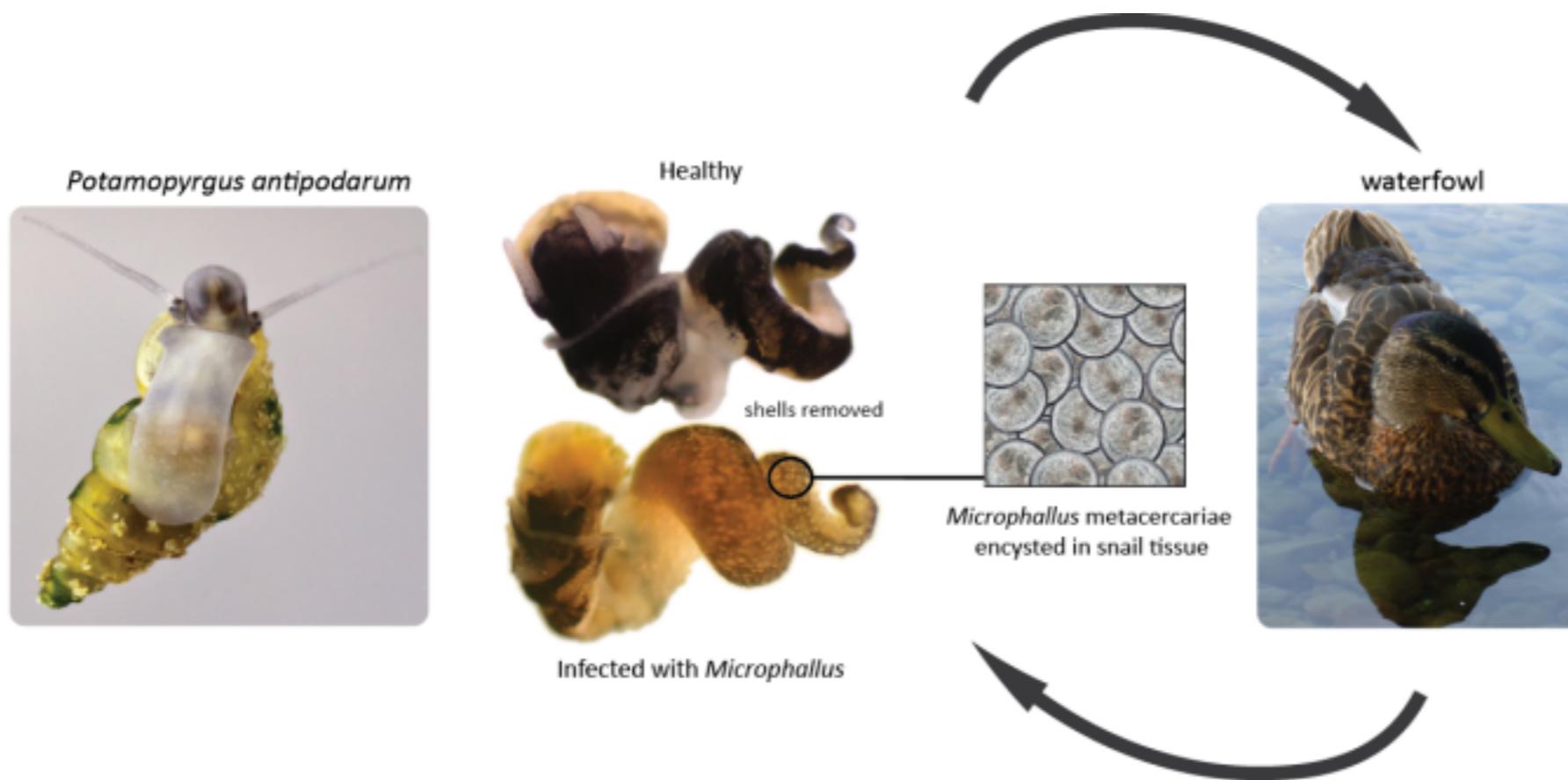
# Leigh van Valen y la Hipótesis de la Reina Roja



## ABSTRACT:

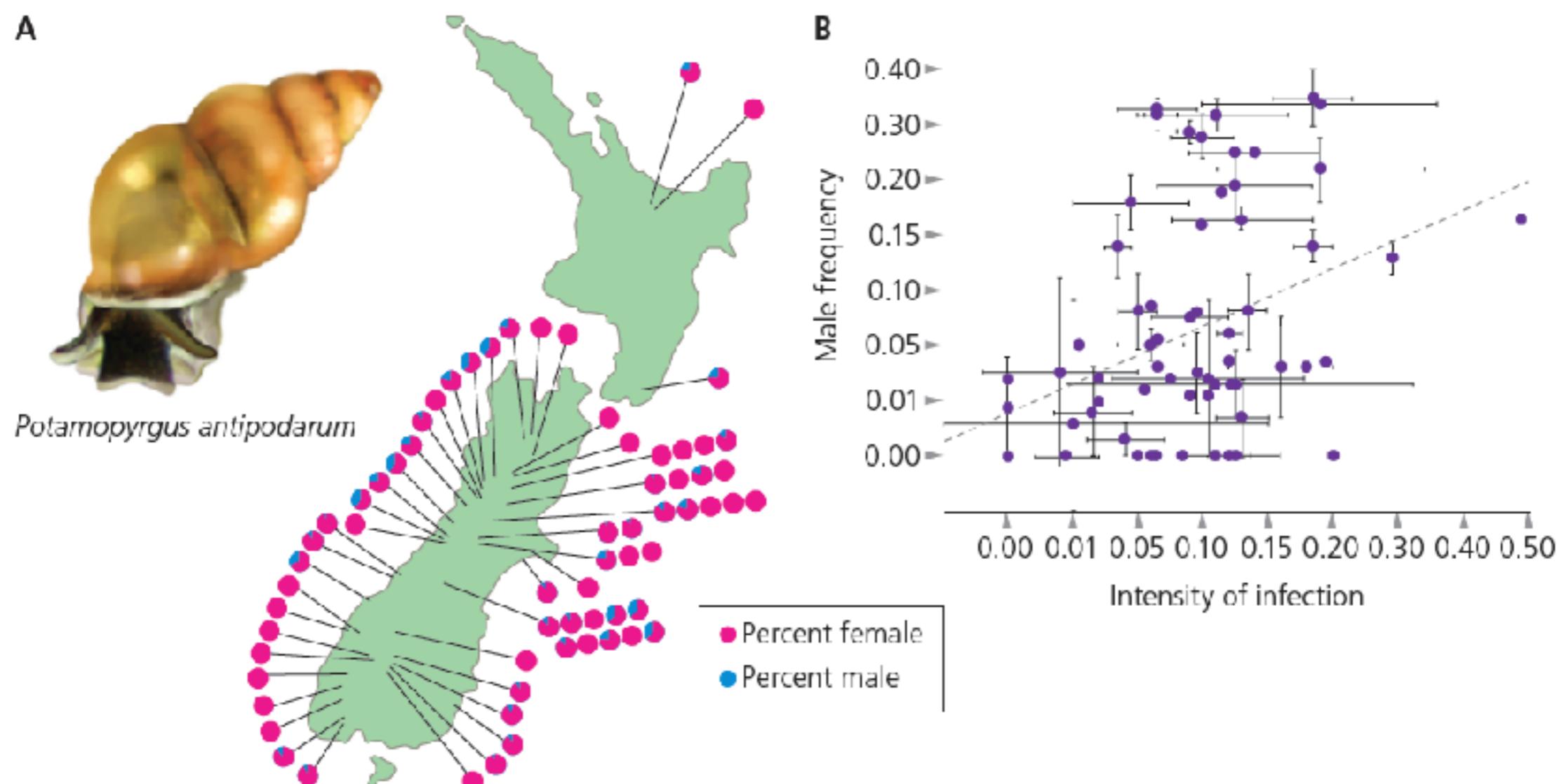
All groups for which data exist go extinct at a rate that is constant for a given group. When this is recent in ecological form (the effective environment of any homogeneous group of organisms deteriorates at a stochastically constant rate), no definite exceptions exist although a few are possible. Extinction rates are similar within some very broad categories and vary regularly with size of area inhabited. A new unit of rates for discrete phenomena, the *macarthur*, is introduced. Laws are appropriate in evolutionary biology. Truth needs more than correct predictions. The Law of Extinction is evidence for ecological significance and comparability of taxa. A non-Markovian hypothesis to explain the law invokes mutually incompatible optima within an adaptive zone. A self-perpetuating fluctuation results which can be stated in terms of an unstudied aspect of zero-sum game theory. The hypothesis can be derived from a view that momentary fitness is the amount of control of resources, which remain constant in total amount. The hypothesis implies that long-term fitness has only two components and that events of mutualism are rare. The hypothesis largely explains the observed pattern of molecular evolution.





<https://amandakylegibson.wordpress.com/infection-prevalence/>

# variación geográfica en sistemas reproductivos y la reina roja

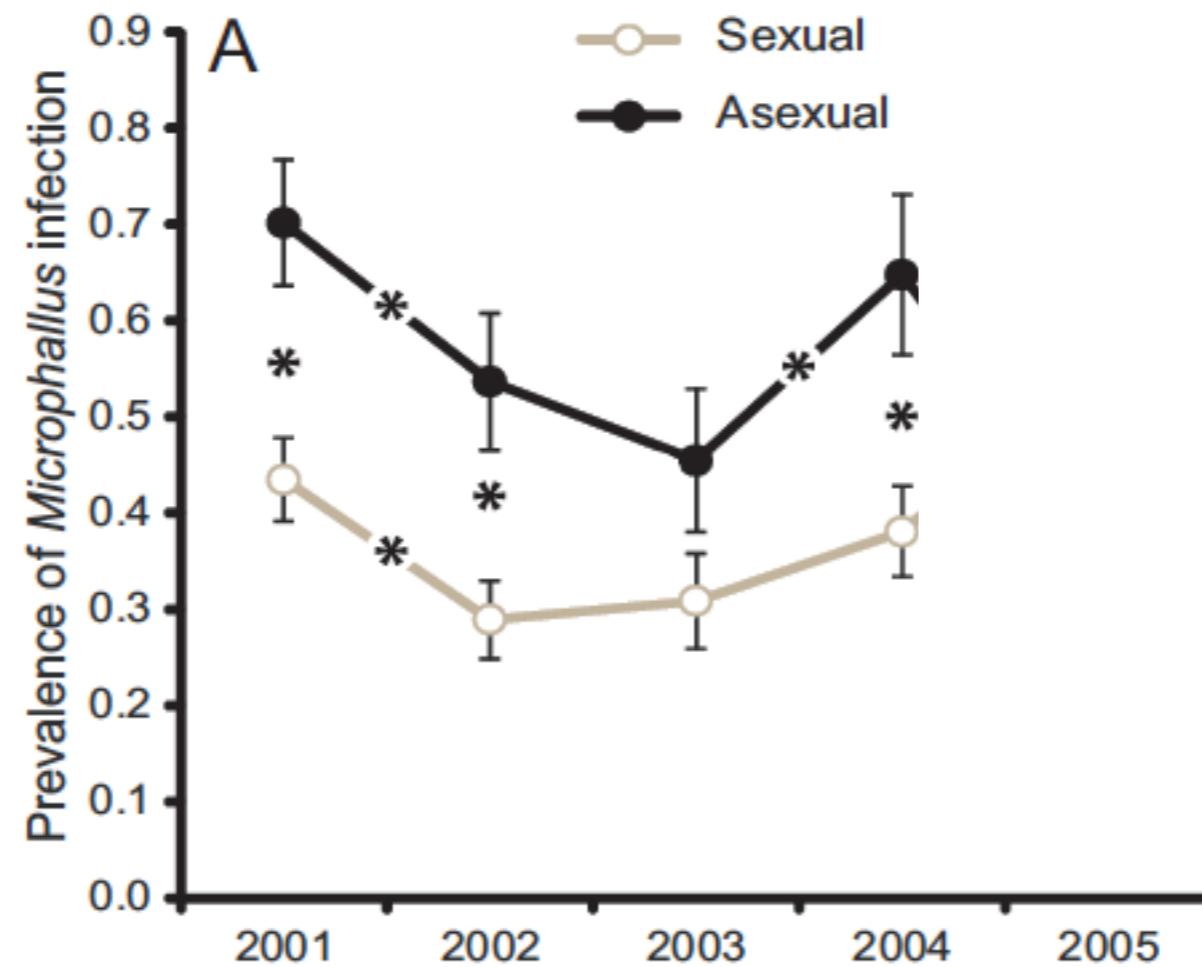


PARTHENOGENESIS IN A FRESHWATER SNAIL:  
REPRODUCTIVE ASSURANCE VERSUS PARASITIC RELEASE

CURTIS M. LIVELY

*Evolution*, 46(4), 1992, pp. 907–913

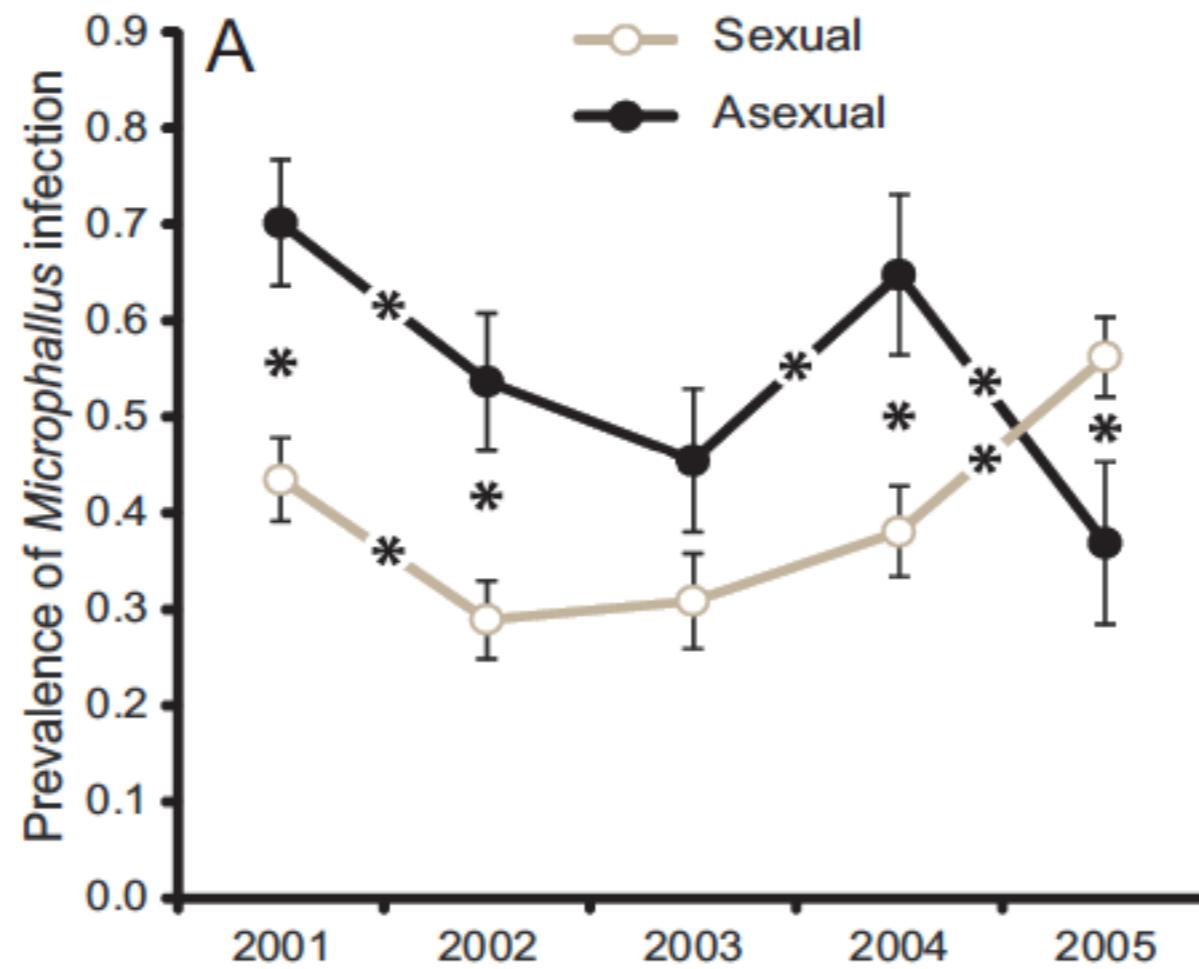
# evidencia a favor de la reina roja: menor parasitismo en hembras sexuales



## Infection Dynamics in Coexisting Sexual and Asexual Host Populations: Support for the Red Queen Hypothesis\*

Daniela Vergara,<sup>1</sup> Jukka Jokela,<sup>2</sup> and Curtis M. Lively<sup>1,†</sup>

# evidencia a favor de la reina roja: menor parasitismo en hembras sexuales



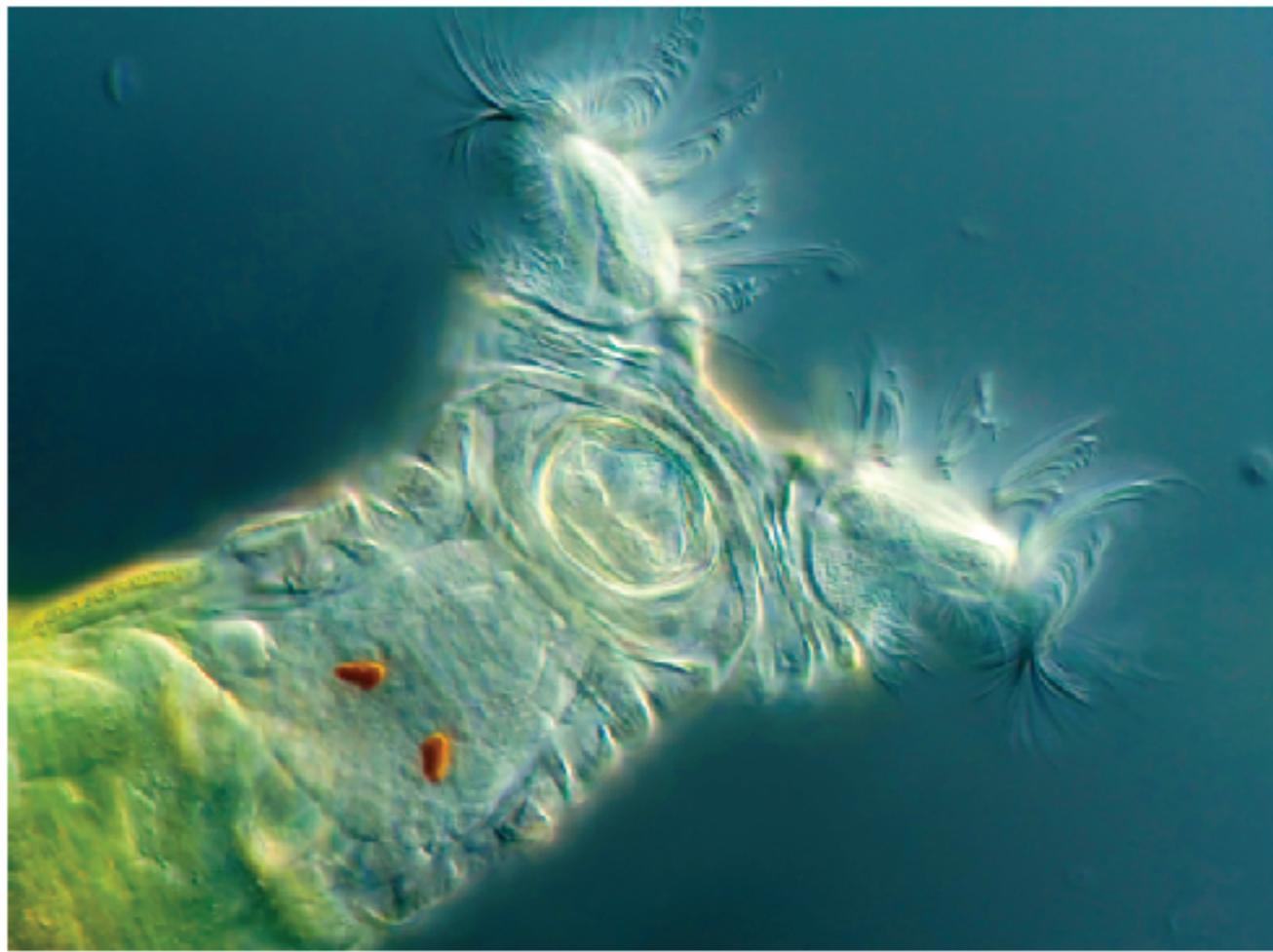
Infection Dynamics in Coexisting Sexual and Asexual Host Populations: Support for the Red Queen Hypothesis\*

Daniela Vergara,<sup>1</sup> Jukka Jokela,<sup>2</sup> and Curtis M. Lively<sup>1,†</sup>

**TABLE 11.1** Consequences of Sexual Reproduction

Disadvantages	Advantages
<b>Twofold Cost of Sex</b> Asexual lineages have an intrinsic capacity to grow more rapidly in each generation, because all progeny can produce offspring. In sexual populations, males cannot themselves produce offspring.	<b>Combining Beneficial Mutations</b> By combining alleles of genes from two different individuals, sexual reproduction can bring separate beneficial mutations together in a single individual faster than would be expected if they had to arise spontaneously in the same genome.
<b>Search Cost</b> Males and females must locate each other in order to mate. This can involve time, energy, and risk of predation.	<b>Generation of Novel Genotypes</b> Through recombination, meiosis provides an opportunity for paired chromosomes to cross over, creating gametes with unique combinations of alleles.
<b>Reduced Relatedness</b> Sexually reproducing organisms pass only half of their alleles to their offspring, because meiosis generates gametes that are haploid. This halves the relatedness between parents and their progeny.	<b>Faster Evolution</b> Offspring of sexual parents will be more genetically variable than offspring of asexually reproducing parents. This can speed the evolutionary response to selection of sexual populations and is critical for maintaining resistance to parasites (the Red Queen effect).
<b>Risk of Sexually Transmitted Diseases</b> Mating between males and females provides an effective means of transmission for many pathogens. Asexual populations do not mate and so avoid this risk.	<b>Clearance of Deleterious Mutations</b> Sexual populations can purge themselves of harmful mutations because recombination can generate individuals with allelic combinations that exclude deleterious mutations. Asexual populations cannot do so, and they steadily and irreversibly accumulate mutations until a lineage is driven extinct (Muller's ratchet).

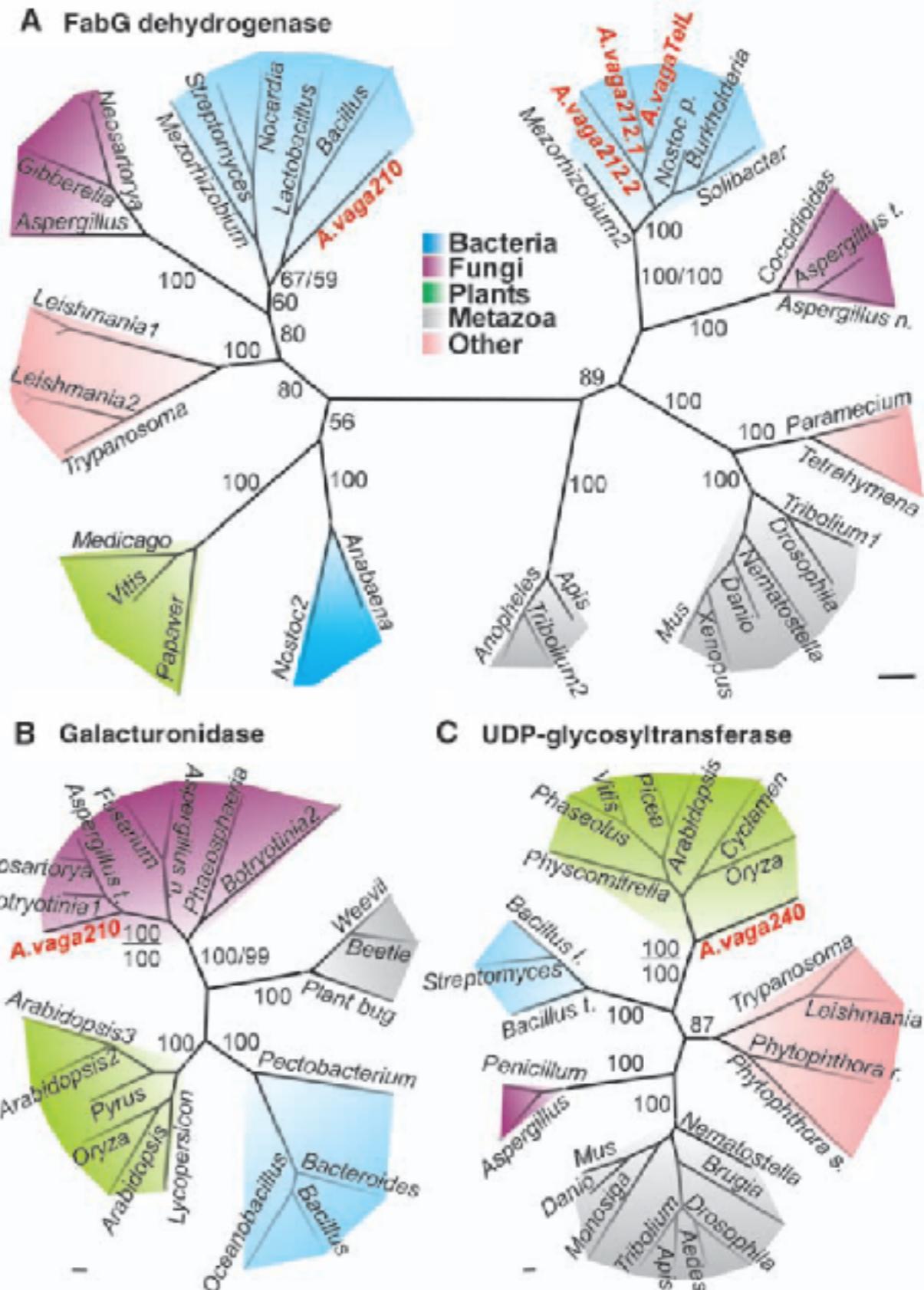
# "sexo" tras bambalinas



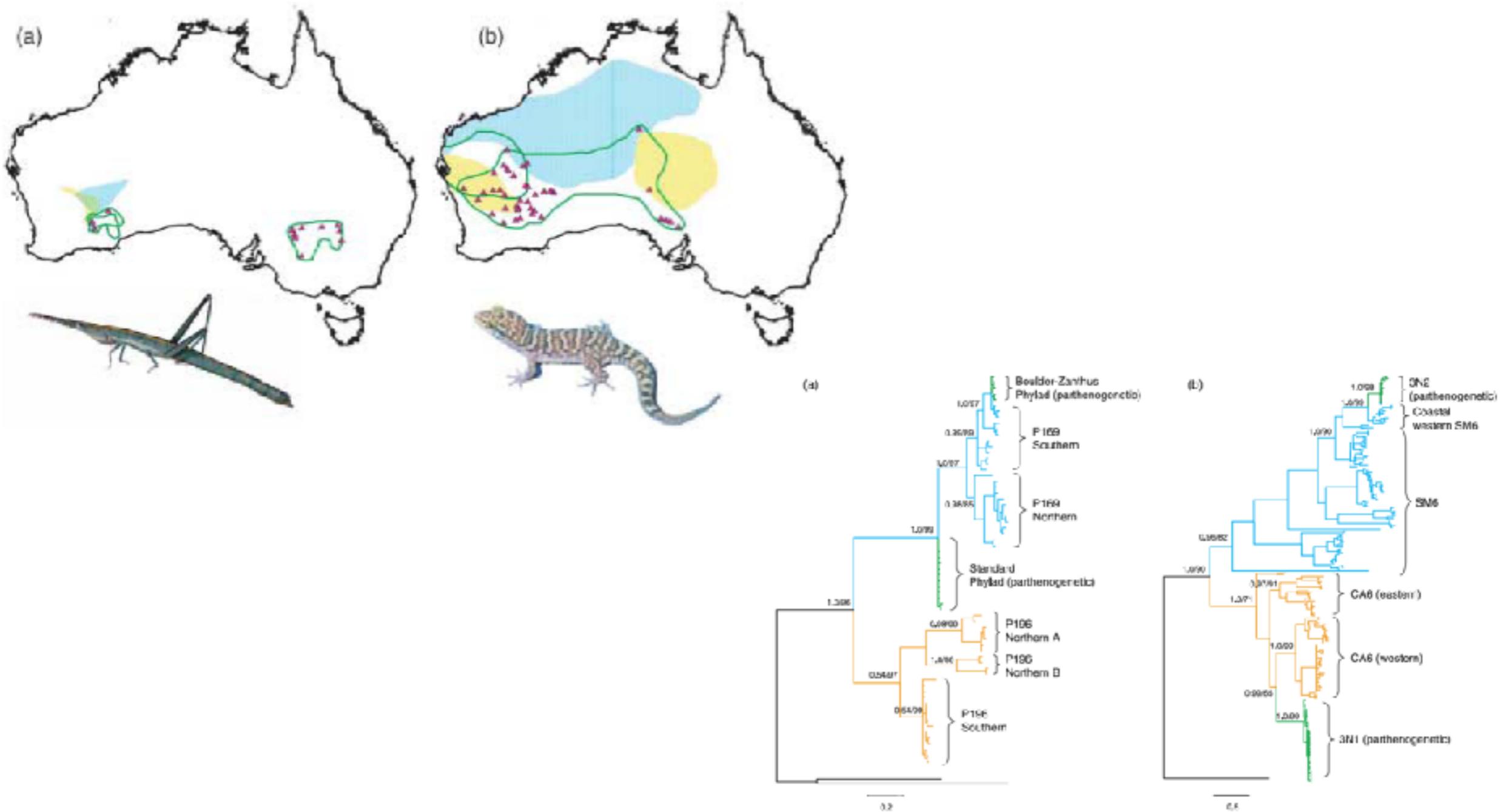
30 MAY 2008 VOL 320 SCIENCE

## Massive Horizontal Gene Transfer in Bdelloid Rotifers

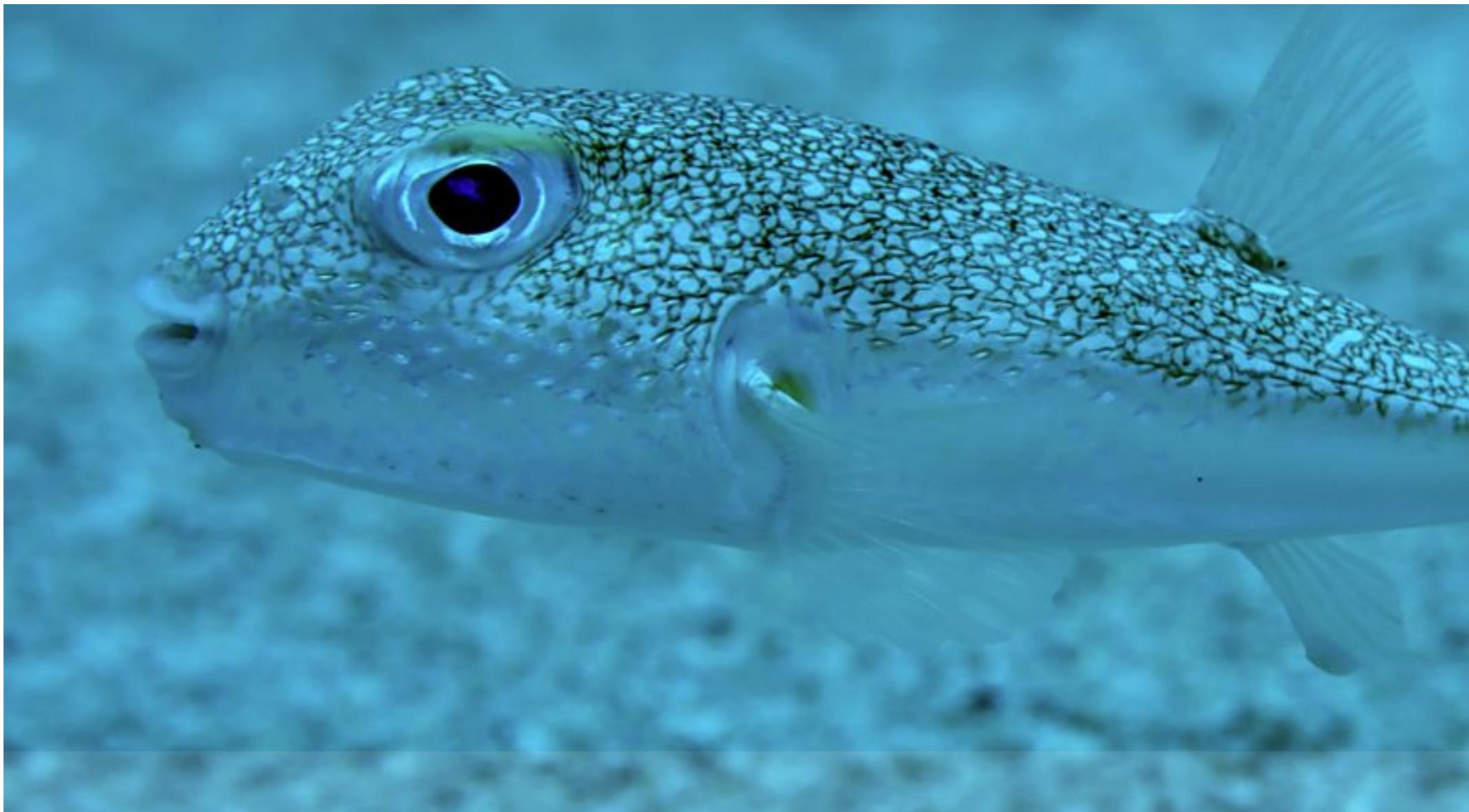
Eugene A. Gladyshev,<sup>1</sup> Matthew Meselson,<sup>1,2\*</sup> Irina R. Arkhipova<sup>1,2\*</sup>



# la reproducción asexual puede ser adaptativa



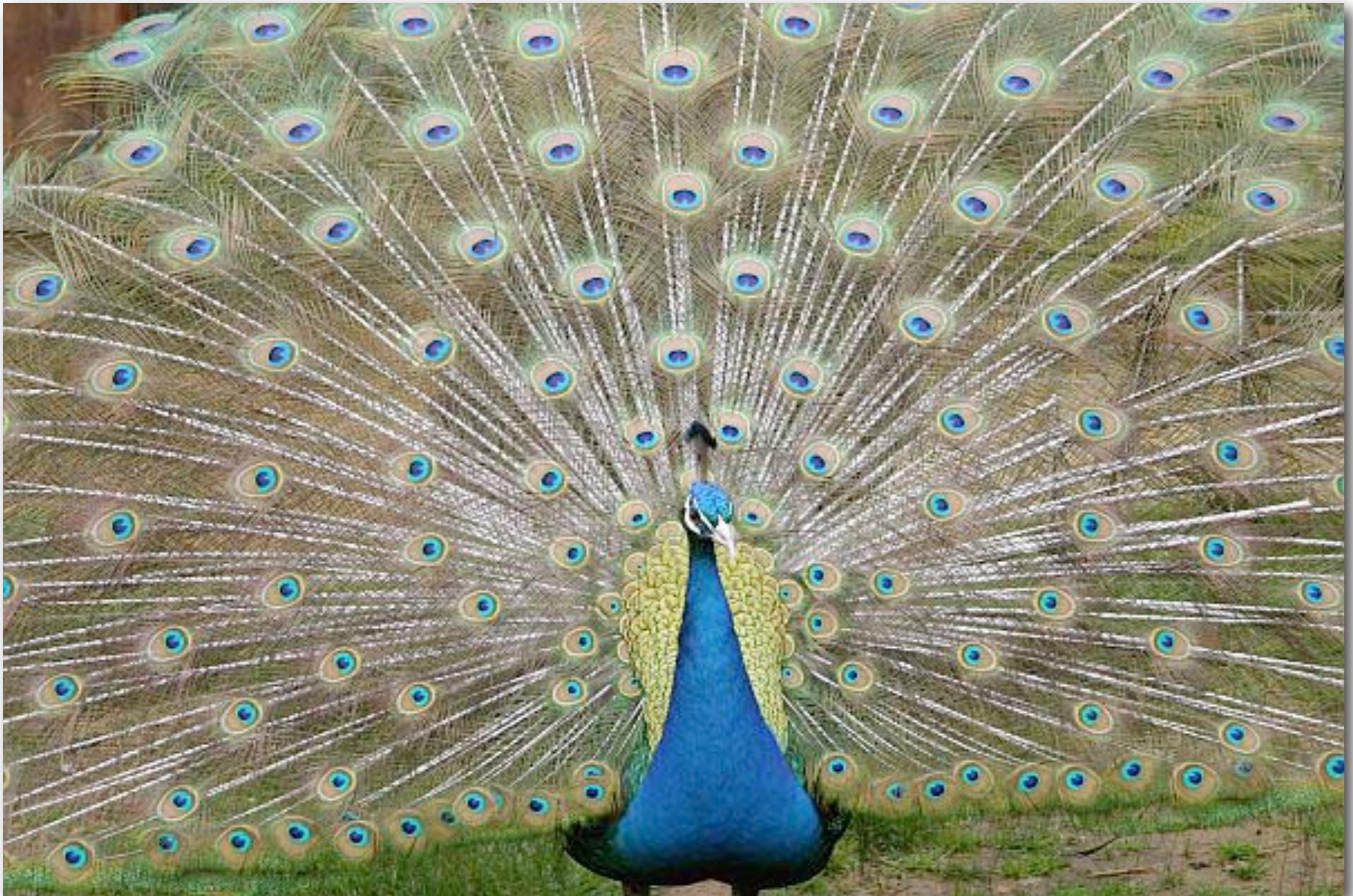
**Waves of parthenogenesis in the desert: evidence for the parallel loss of sex in a grasshopper and a gecko from Australia**



[https://youtu.be/VQr8xDk\\_UaY](https://youtu.be/VQr8xDk_UaY)



[http://www.youtube.com/watch?feature=player\\_embedded&v=GPbWJPsbPdA](http://www.youtube.com/watch?feature=player_embedded&v=GPbWJPsbPdA)



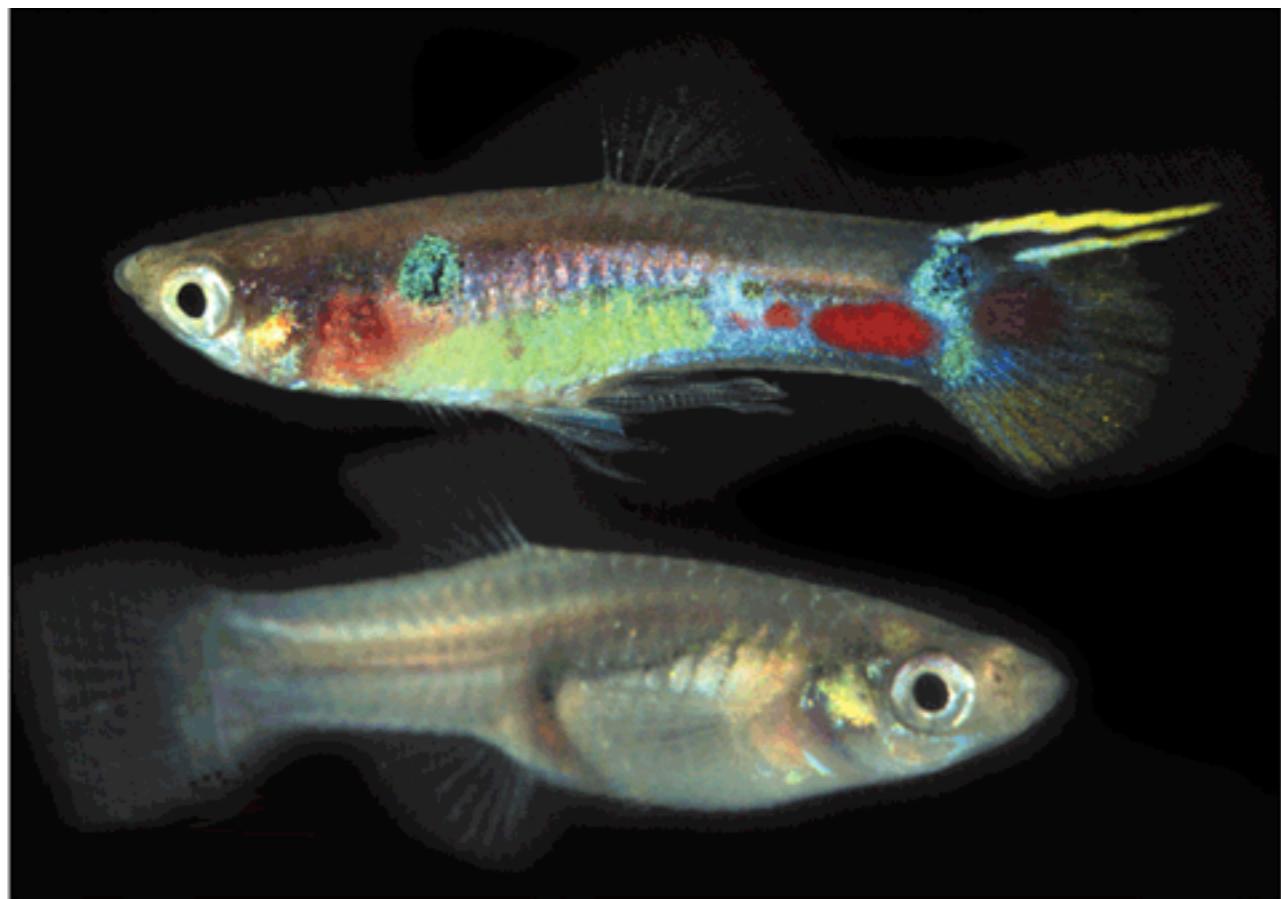
*'The sight of a feather in a peacock's tail, whenever I gaze at it, makes me sick!' (C. Darwin)*



## Diversity in the Weapons of Sexual Selection: Horn Evolution in Dung Beetles

DOUGLAS EMLEN

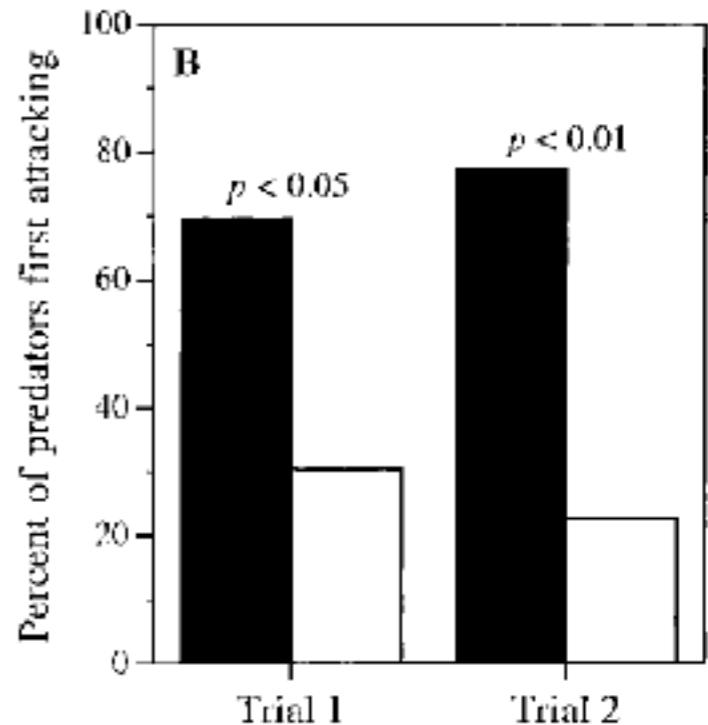
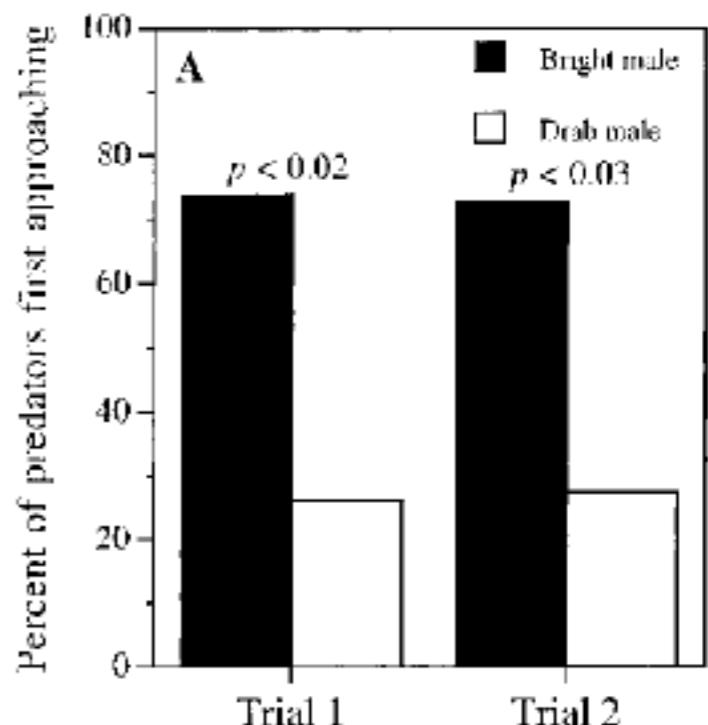
# el costo de los ornamentos



Nature Reviews | Genetics

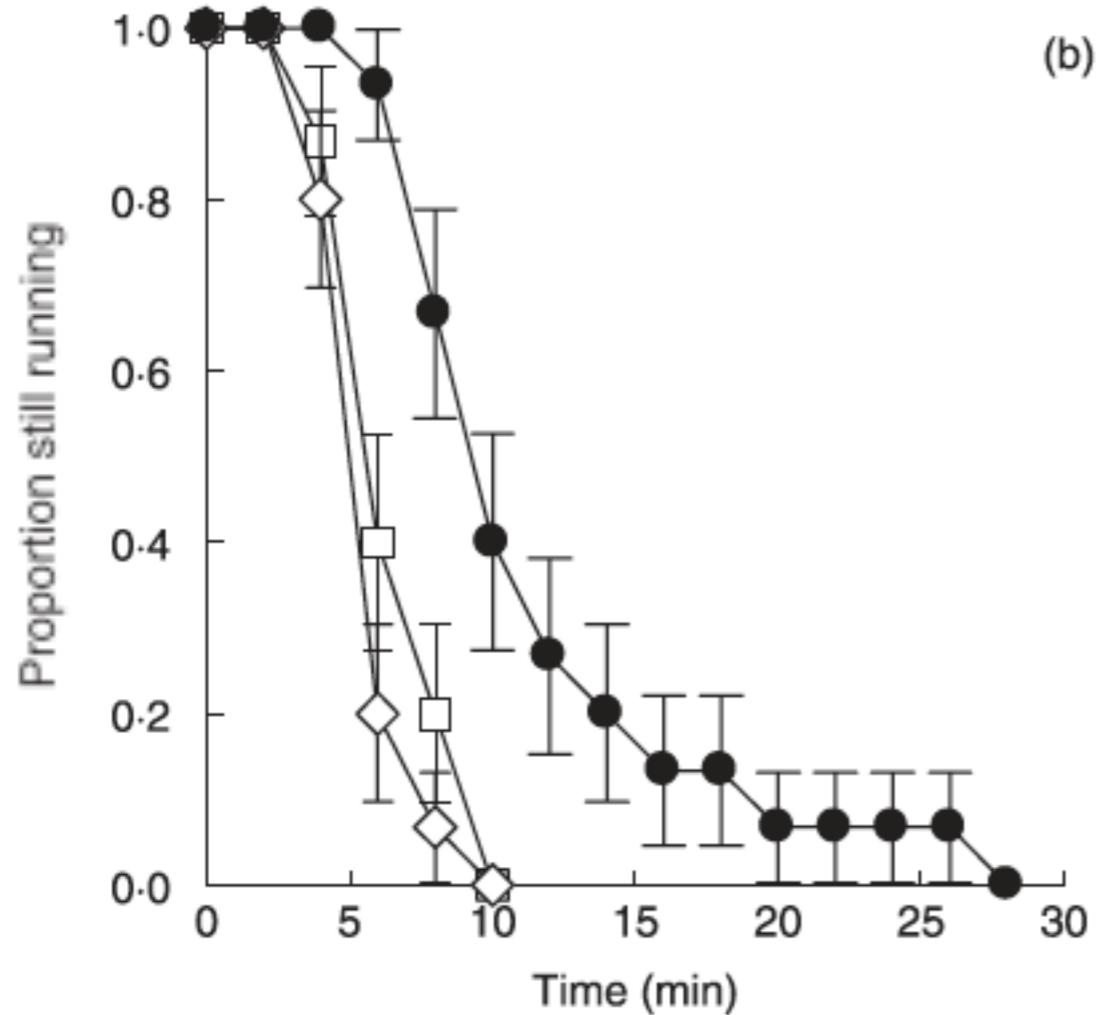
Predator preference for brightly colored males in the guppy: a viability cost for a sexually selected trait

Jean-Guy J. Godin and Heather E. McDonough



Behavioral Ecology Vol. 14 No. 2: 194–200

# el costo de las armas



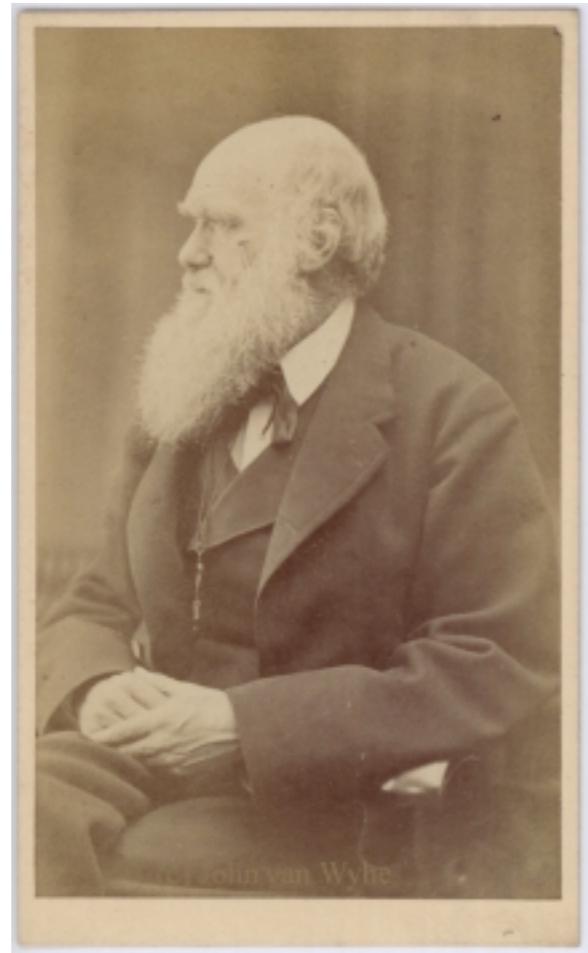
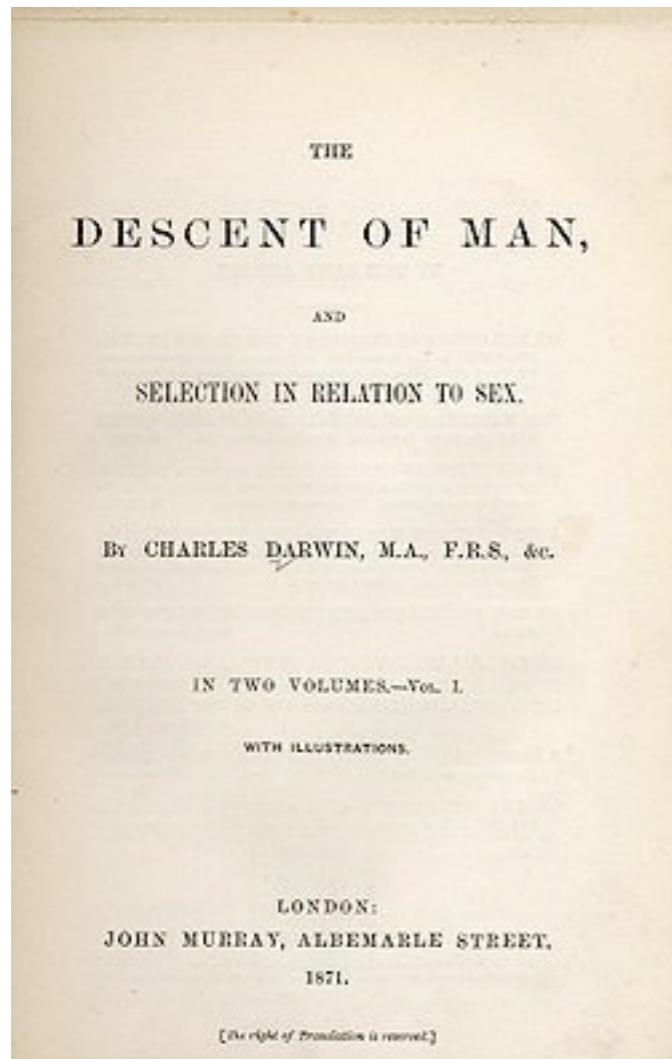
**Costs of bearing a sexually selected ornamental weapon in a fiddler crab**

BENGT J. ALLEN† and JEFFREY S. LEVINTON

*Functional  
Ecology* 2007  
21, 154–161

# selección sexual

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*"We are, however, here concerned only with that kind of selection, which I have called sexual selection. This depends on the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction."*

Darwin (1871)

# **preferencias sexuales de hembras en palabras de Darwin**

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*"With the great majority of animals, however, the taste for the beautiful is confined to the attractions of the opposite sex. The sweet strains poured forth by many male birds during the season of love, are certainly admired by the females . . . If female birds had been incapable of appreciating the beautiful colours, the ornaments, and voices of their male partners, all the labour and anxiety by the latter in displaying their charms before the females would have been thrown away; and this is impossible to admit..."*

*"[Male birds] charm the female by vocal and instrumental music of the most varied kinds."*

# *preferencias sexuales de hembras en palabras de Darwin*

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*"The case of the male Argus Pheasant is eminently interesting, because it affords good evidence that the most refined beauty may serve as a sexual charm, and for no other purpose."*

[http://farm5.static.flickr.com/4018/4487639471\\_05479ed6e8.jpg](http://farm5.static.flickr.com/4018/4487639471_05479ed6e8.jpg)

# si lo dice Darwin ...

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*"On the whole, birds appear to be the most aesthetic of all animals, excepting of course man, and they have nearly the same taste for the beautiful as we have."* (Darwin 1871)



R. A. Fisher (1930):  
las preferencias sexuales de las hembras son rasgos heredables  
*Fisherian runaway selection: "selección en fuga"*

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THE GENETICAL THEORY OF  
NATURAL SELECTION  
A Complete Variorum Edition

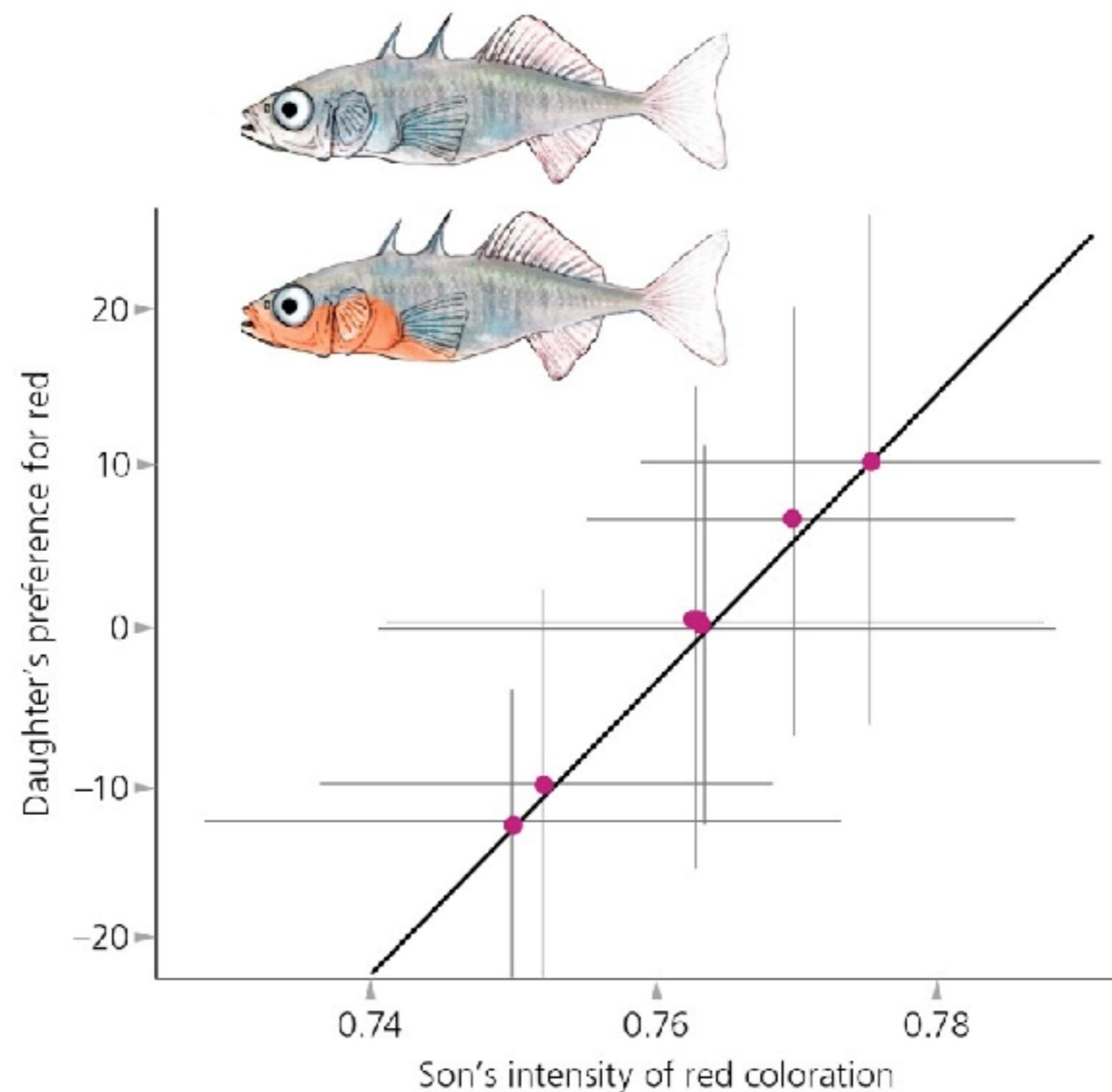


R. A. FISHER

Edited with an introduction and notes by Henry Bennett



# lo que puede pasar cuando rasgos y preferencias van ligados



NATURE · VOL 363 · 20 MAY 1993

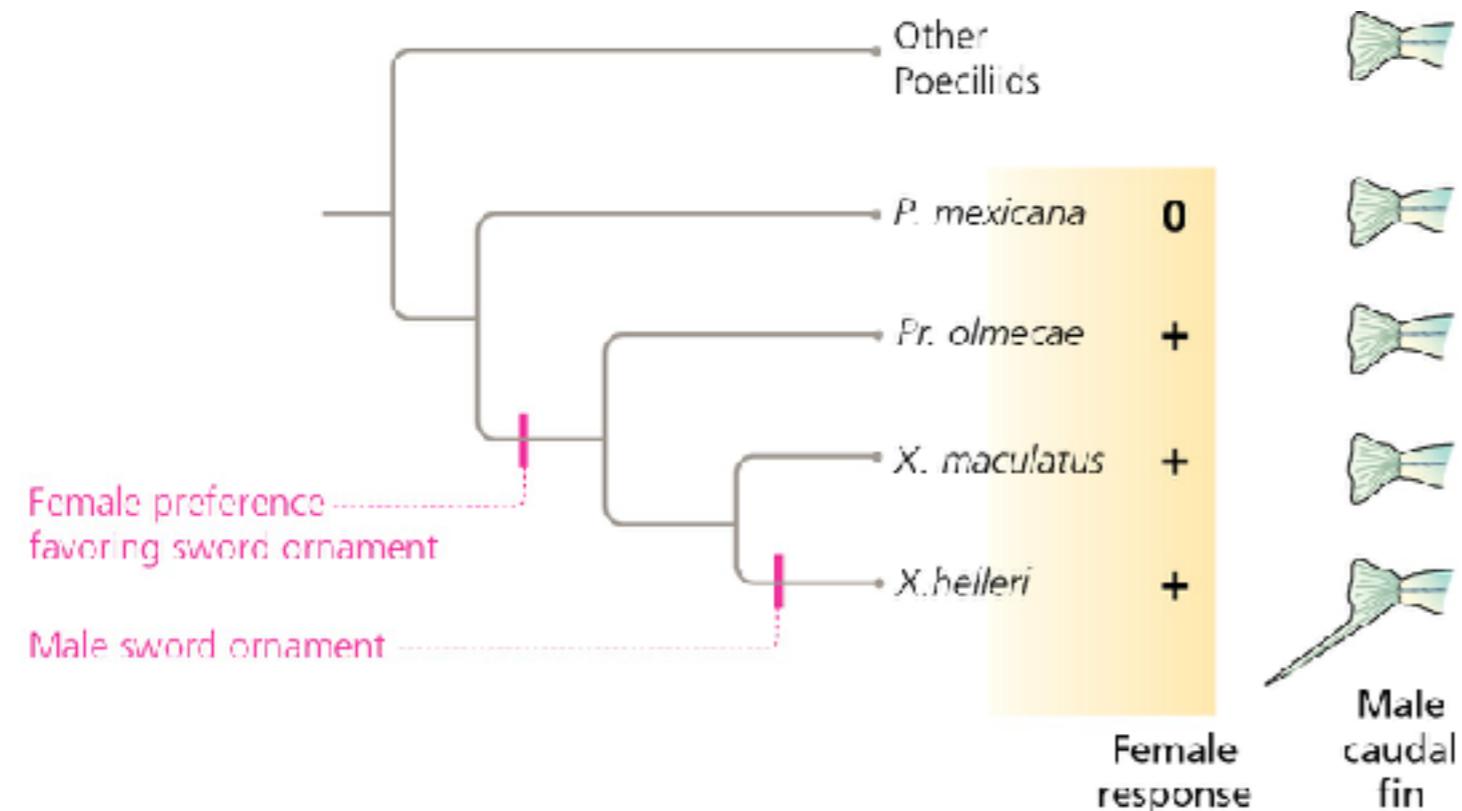
**Positive genetic correlation  
between female preference  
and preferred male ornament  
in sticklebacks**

Theo C. M. Bakker

# sesgos preexistentes y la evolución de ornamentos

## Female Preference Predates the Evolution of the Sword in Swordtail Fish

ALEXANDRA L. BASOLO\*

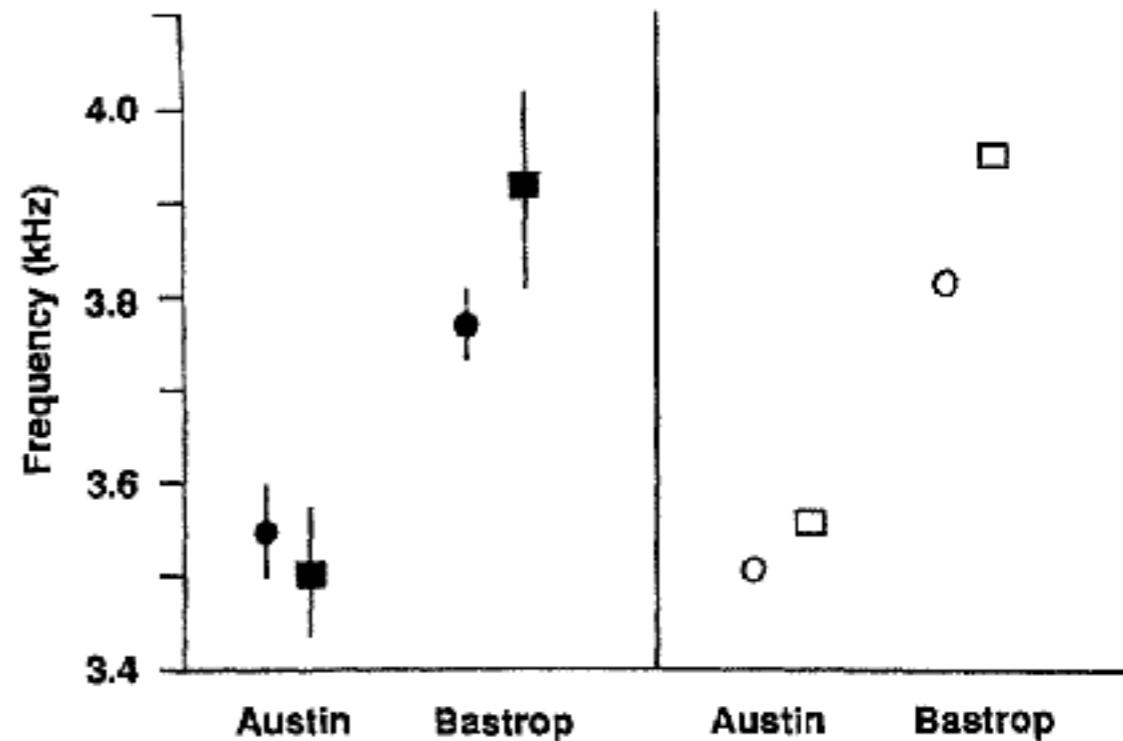


# possible ejemplo de selección sexual Fisheriana



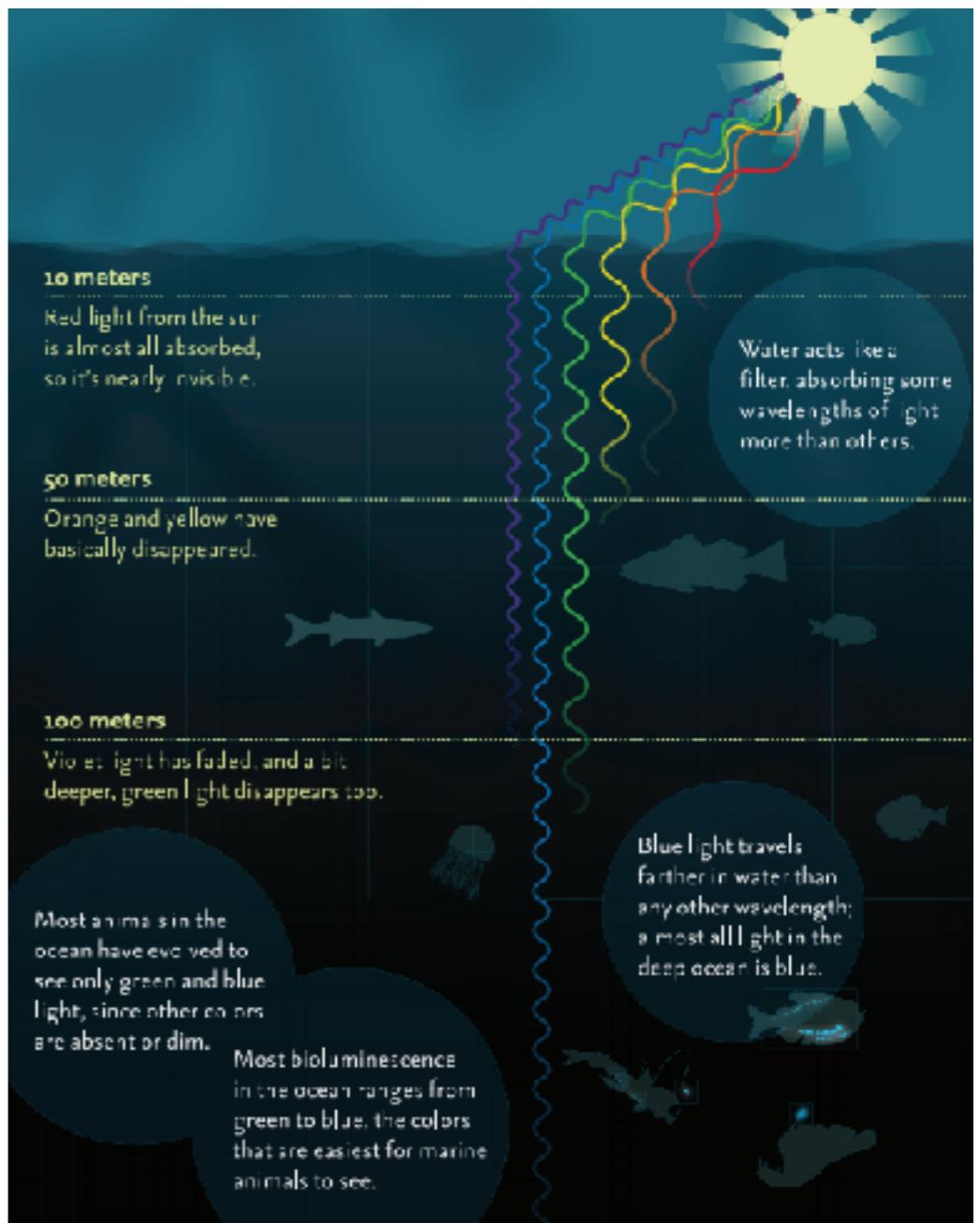
## Coevolution of Sender and Receiver: Effect on Local Mate Preference in Cricket Frogs

MICHAEL J. RYAN AND WALTER WILCZYNSKI



**Fig. 1.** The mean  $\pm$  1 SE of the dominant frequency of the call ( $n = 10$ , solid circles) and best excitatory frequency of the basilar papilla ( $n = 4$ , solid boxes) for cricket frogs from Austin and Bastrop. The open figures are the analogous means after being adjusted for body size (see Table 1).

# ¿son los sesgos en preferencias arbitrarios o tienen una explicación?



## Speciation through sensory drive in cichlid fish

Ole Seehausen<sup>1,2</sup>, Yohey Terai<sup>3</sup>, Isabel S. Magalhaes<sup>1,2</sup>, Karen L. Carleton<sup>4</sup>, Hillary D. J. Mross<sup>5</sup>, Ryutaro Miyagi<sup>6</sup>, Inke van der Sluijs<sup>6†</sup>, Maria V. Schneider<sup>2†</sup>, Martine E. Maan<sup>6†</sup>, Hidenori Tachida<sup>7</sup>, Hiroo Imai<sup>8</sup> & Norihiro Okada<sup>9</sup>

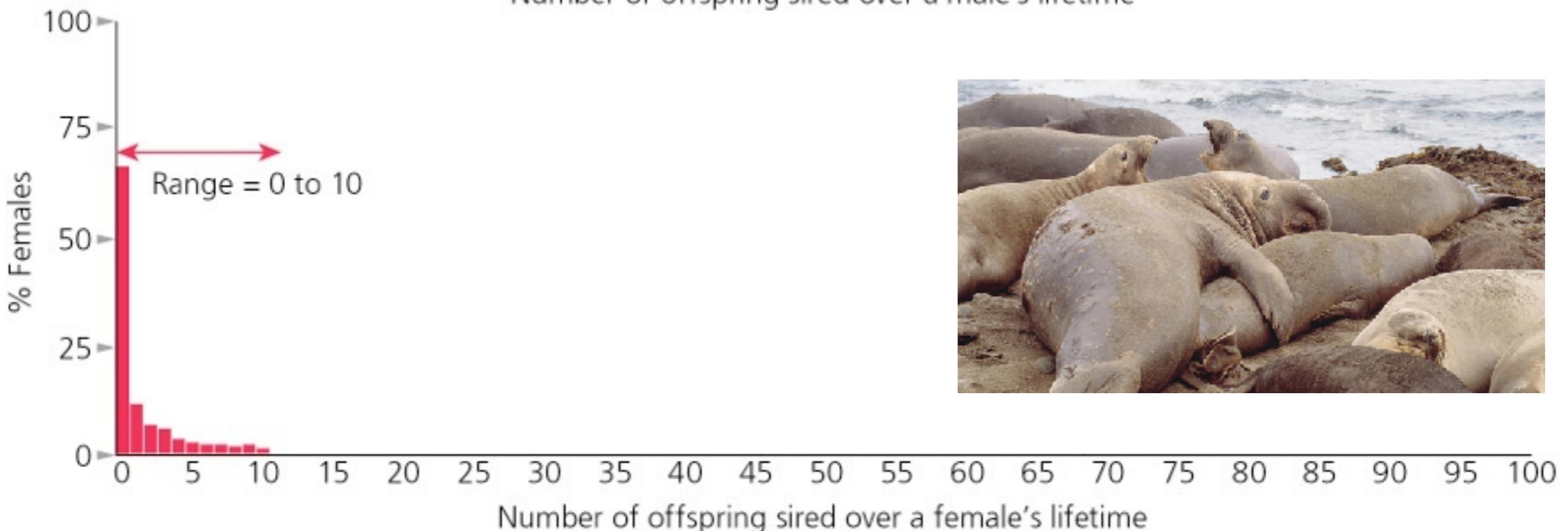
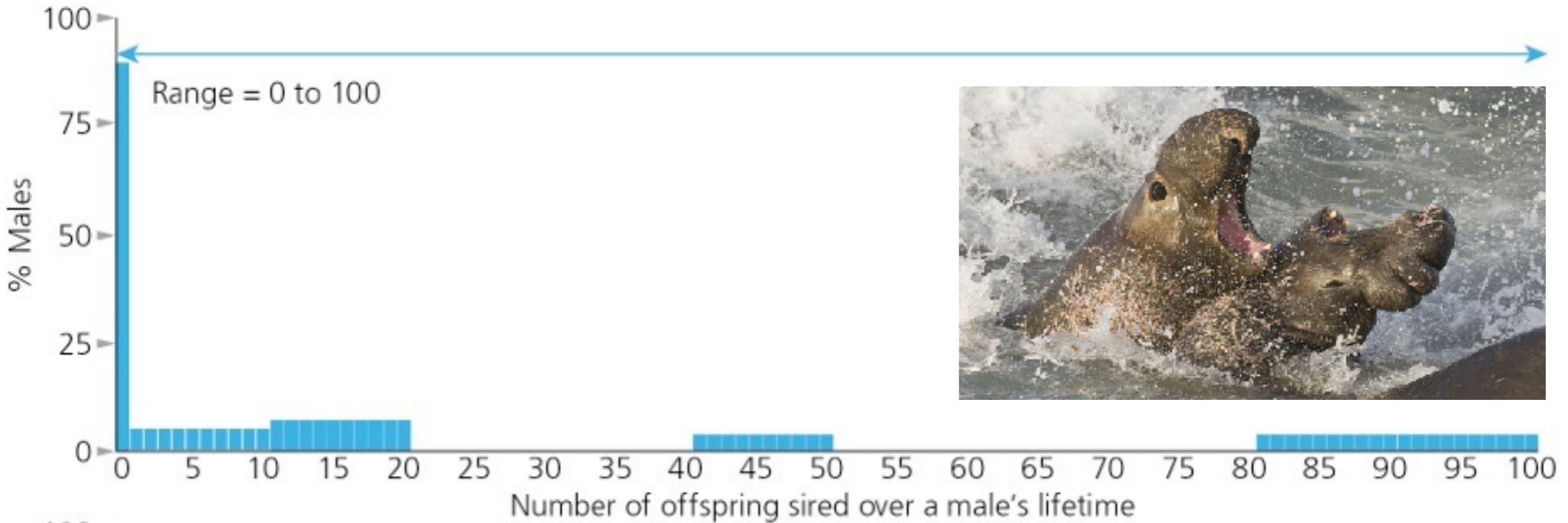
| doi:10.1038/nature07285

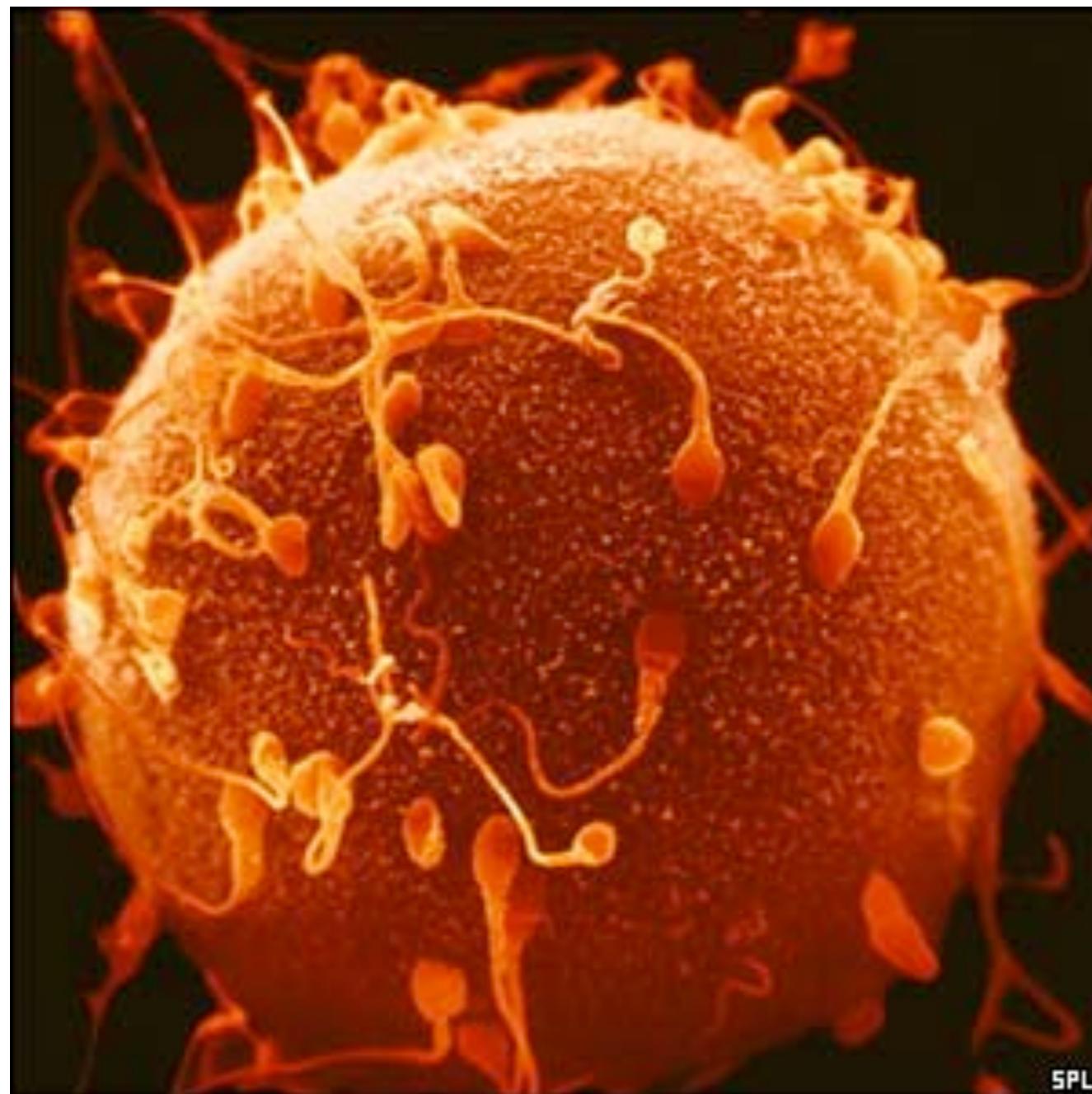
# dogma: "cheap sperm and costly eggs" y sus consecuencias



Robert Trivers (1972)

# sesgo reproductivo y su variación entre los sexos





**At best, Bateman's principles should be considered hypotheses and approached with great care.**

## Repetition of Bateman challenges the paradigm

# *preferencias sexuales de hembras en palabras de Darwin*

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*"With the great majority of animals, however, the taste for the beautiful is confined to the attractions of the opposite sex. The sweet strains poured forth by many male birds during the season of love, are certainly admired by the females ... If female birds had been incapable of appreciating the beautiful colours, the ornaments, and voices of their male partners, all the labour and anxiety by the latter in displaying their charms before the females would have been thrown away; and this is impossible to admit..."*

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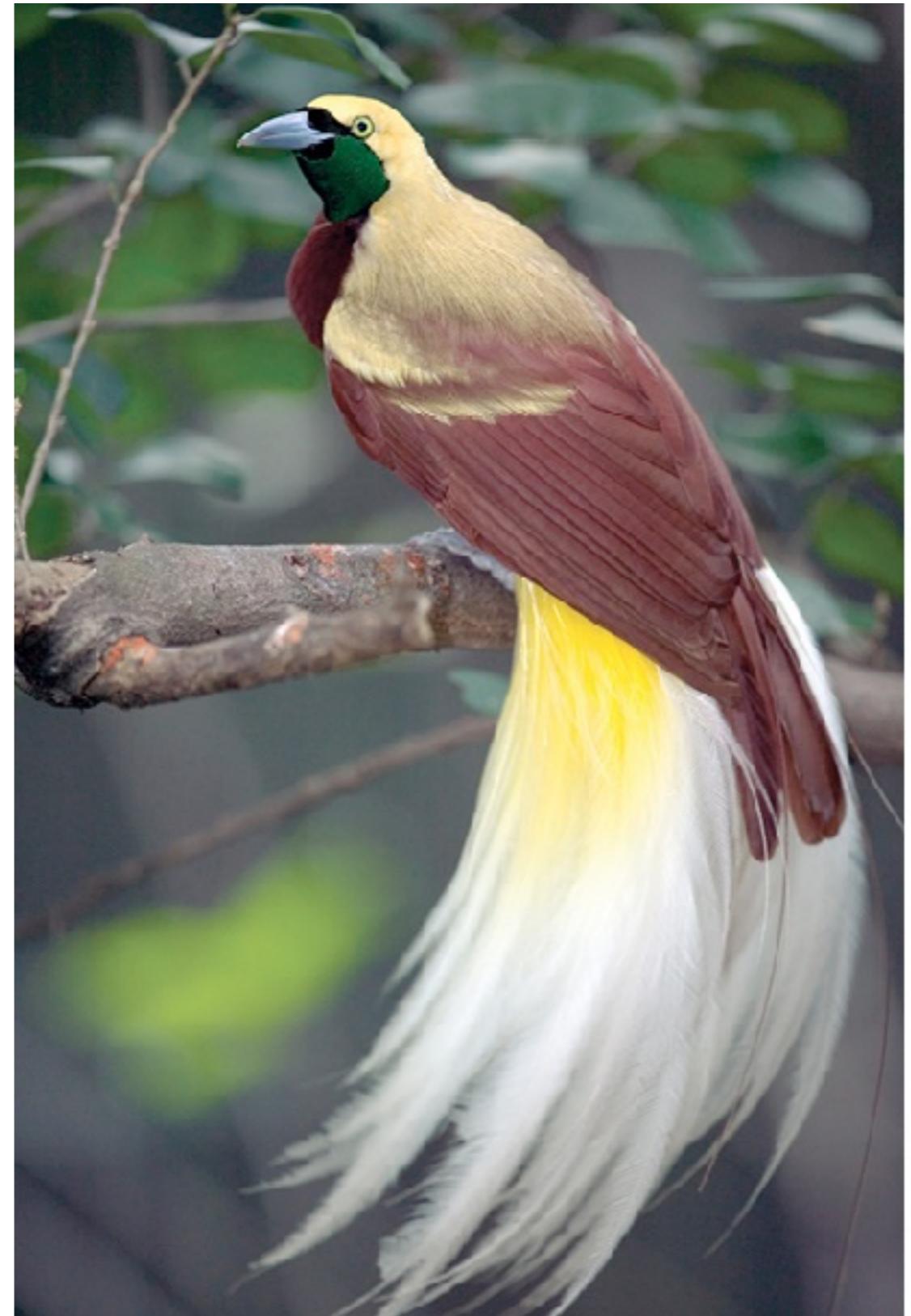
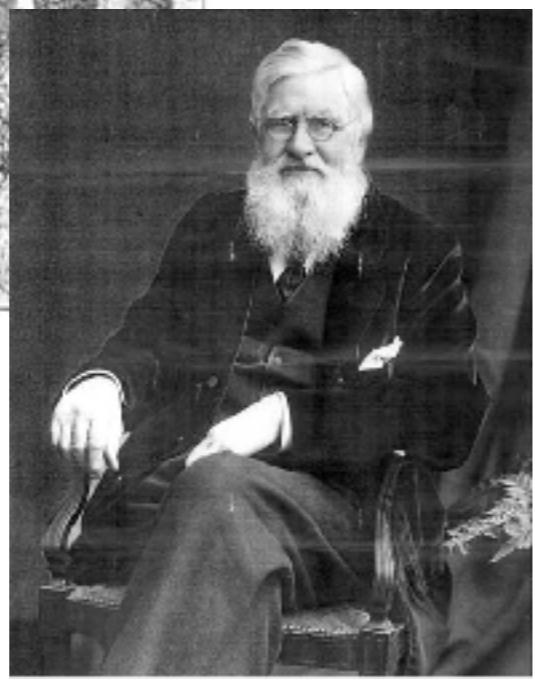


*"The case of the male Argus Pheasant is eminently interesting, because it affords good evidence that the most refined beauty may serve as a sexual charm, and for no other purpose."*

[http://farm5.static.flickr.com/4018/4487639471\\_05479ed6e8.jpg](http://farm5.static.flickr.com/4018/4487639471_05479ed6e8.jpg)

# Alfred Russel Wallace

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<http://www.birdsofparadiseproject.org/>

# WALLACE ONLINE

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*Wallace Online* is the first complete edition of the writings of naturalist and co-founder of the theory of evolution Alfred Russel Wallace. Including a comprehensive compilation of his specimens - much of it never before seen. The project is directed by John van Wyhe, assisted by Kees Rookmaaker, at the National University of Singapore, in collaboration with the [Wallace Page](#) by Charles H. Smith.

[Biography](#)

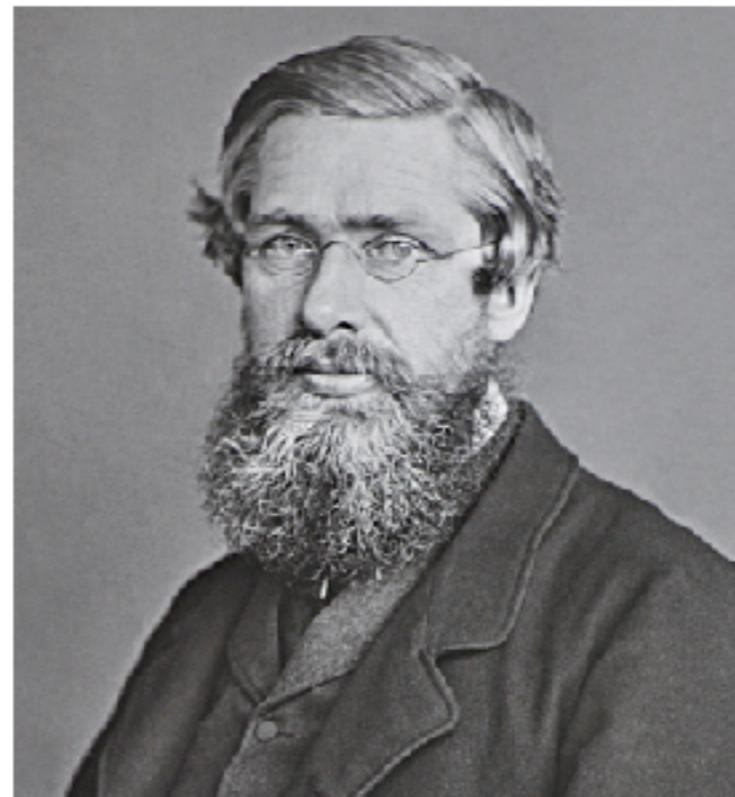
[Wallace in Singapore](#)

[Illustrations](#)

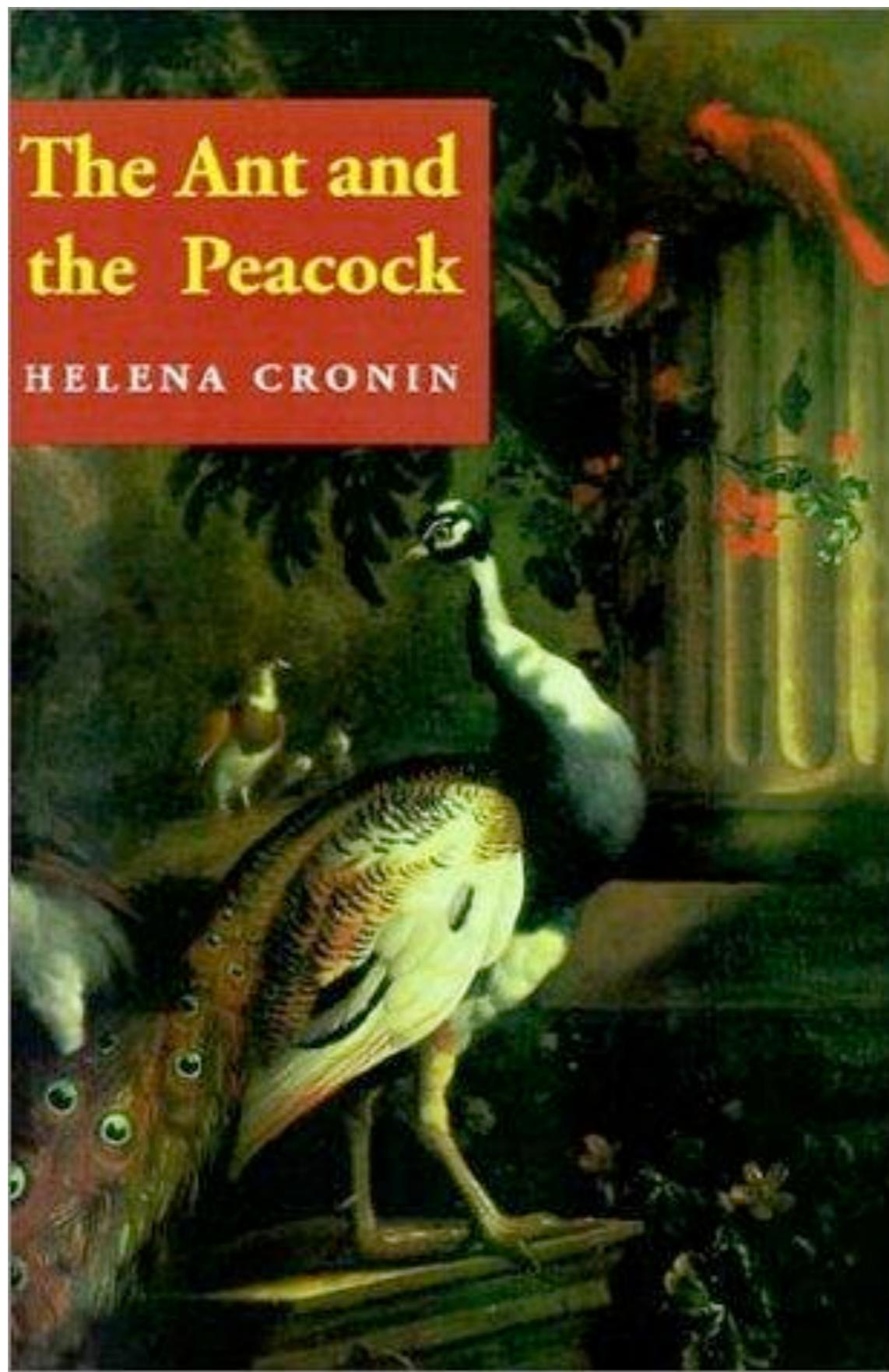
[About the project](#)

[Acknowledgements](#)

**Quick links:** [Amazon](#), [Sarawak law](#), [Darwin-Wallace paper](#), [Malay Archipelago](#), [Darwinism](#), [My Life](#), [Letters and reminiscences](#).



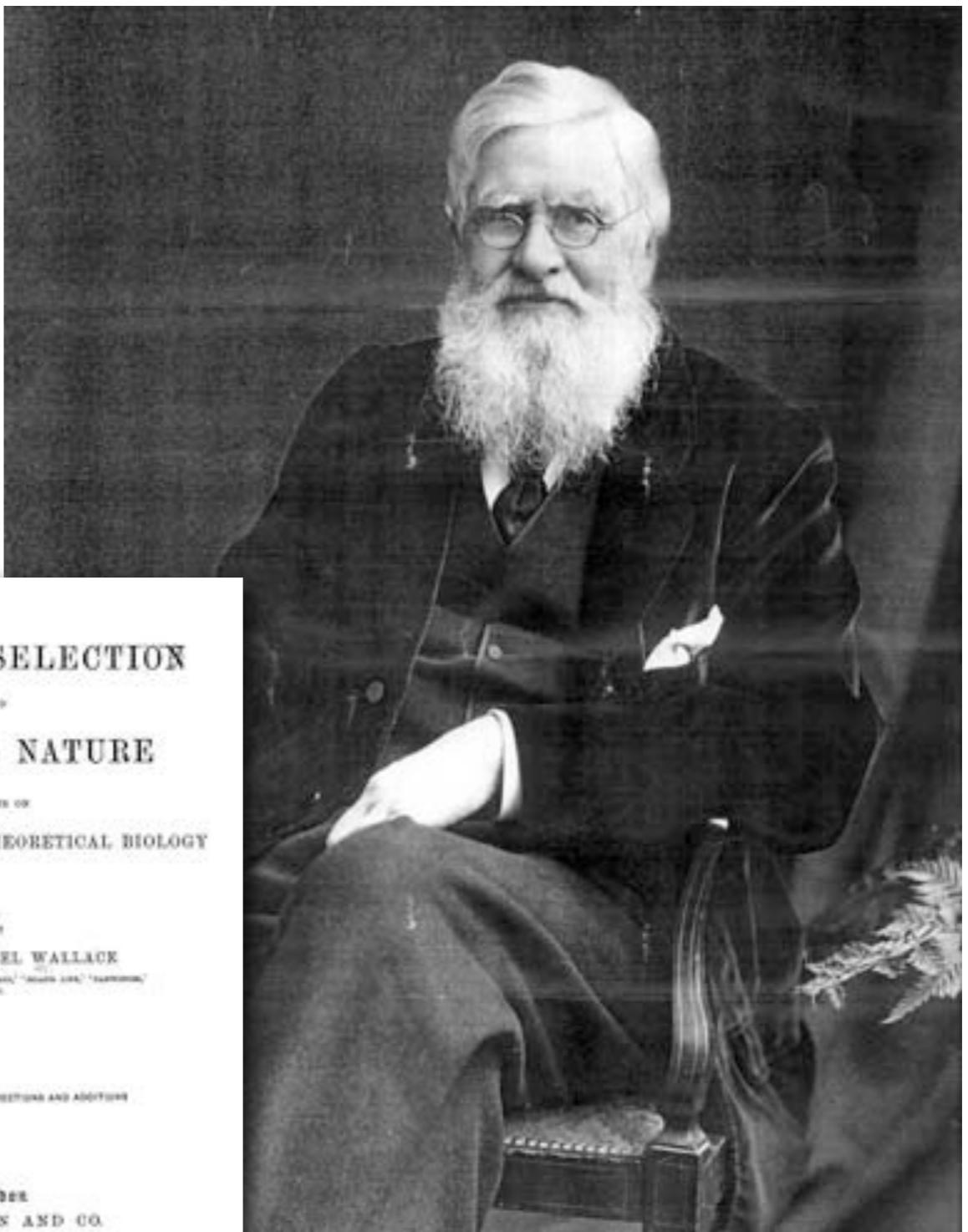
<http://wallace-online.org/>



# habla Wallace (1895)

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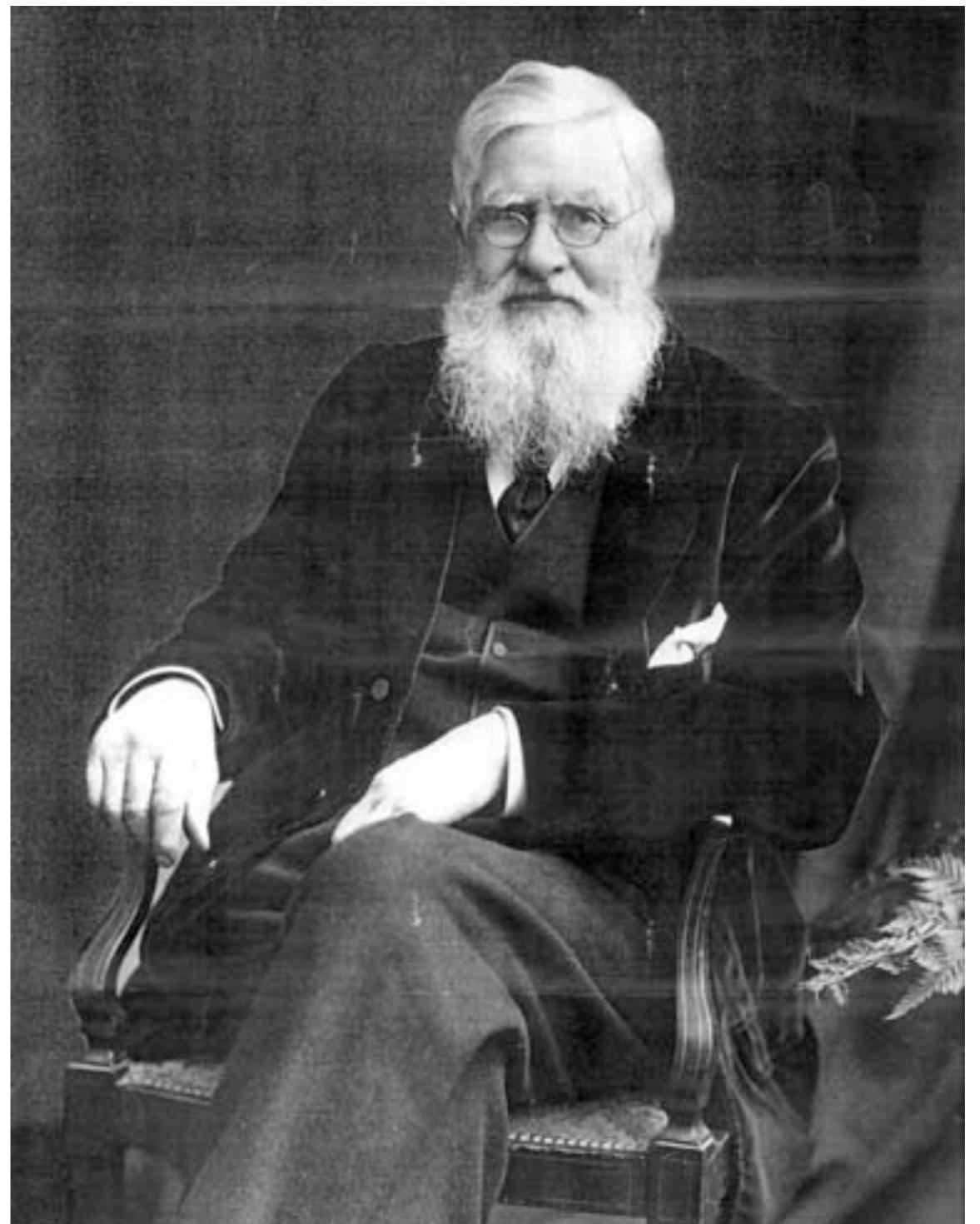
*"The only way in which we can account for the observed facts is by supposing that colour and ornament are strictly correlated with health, vigor, and general fitness to survive."*



## habla Wallace (1889)

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*“Even in rejecting that phase  
of sexual selection  
depending on female  
choice, I insist on the greater  
efficacy of natural selection.  
This is pre-eminently the  
Darwinian doctrine and I  
therefore claim for my book  
the position of being the  
advocate of pure  
Darwinism”*



# Zahavi (1975) y el principio del “handicap”

## Mate Selection --A Selection for a Handicap

AMOTZ ZAHAVI

*"An individual with a well developed sexually selected character [such as a peacock's flashy tail] is an individual which has survived a test. A female which could discriminate between a male possessing a sexually selected character, from one without it, can discriminate between a male which has passed a test and one which has not been tested. Females which selected males with the most developed characters can be sure that they have selected from among the best genotypes of the male population."*

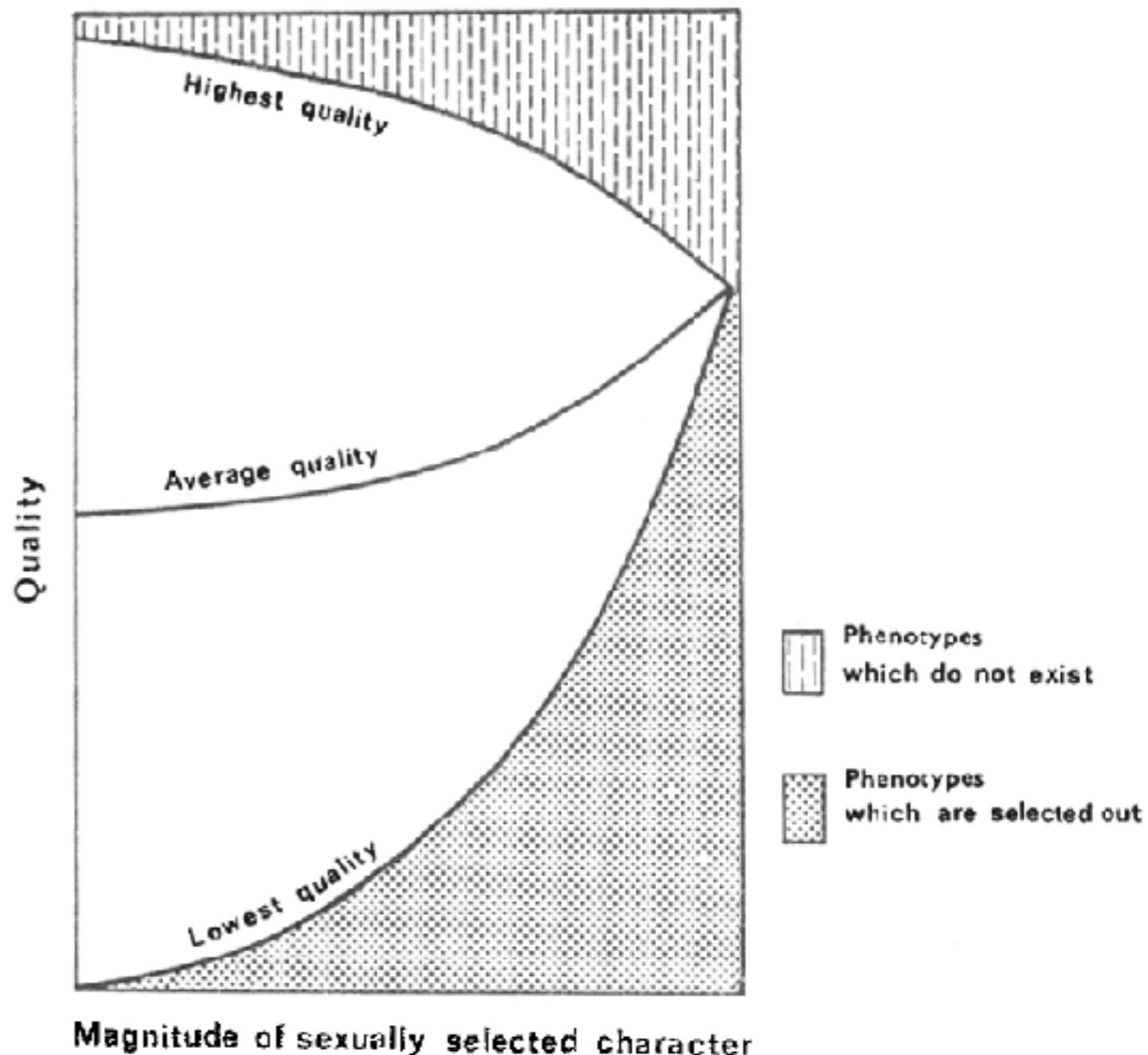
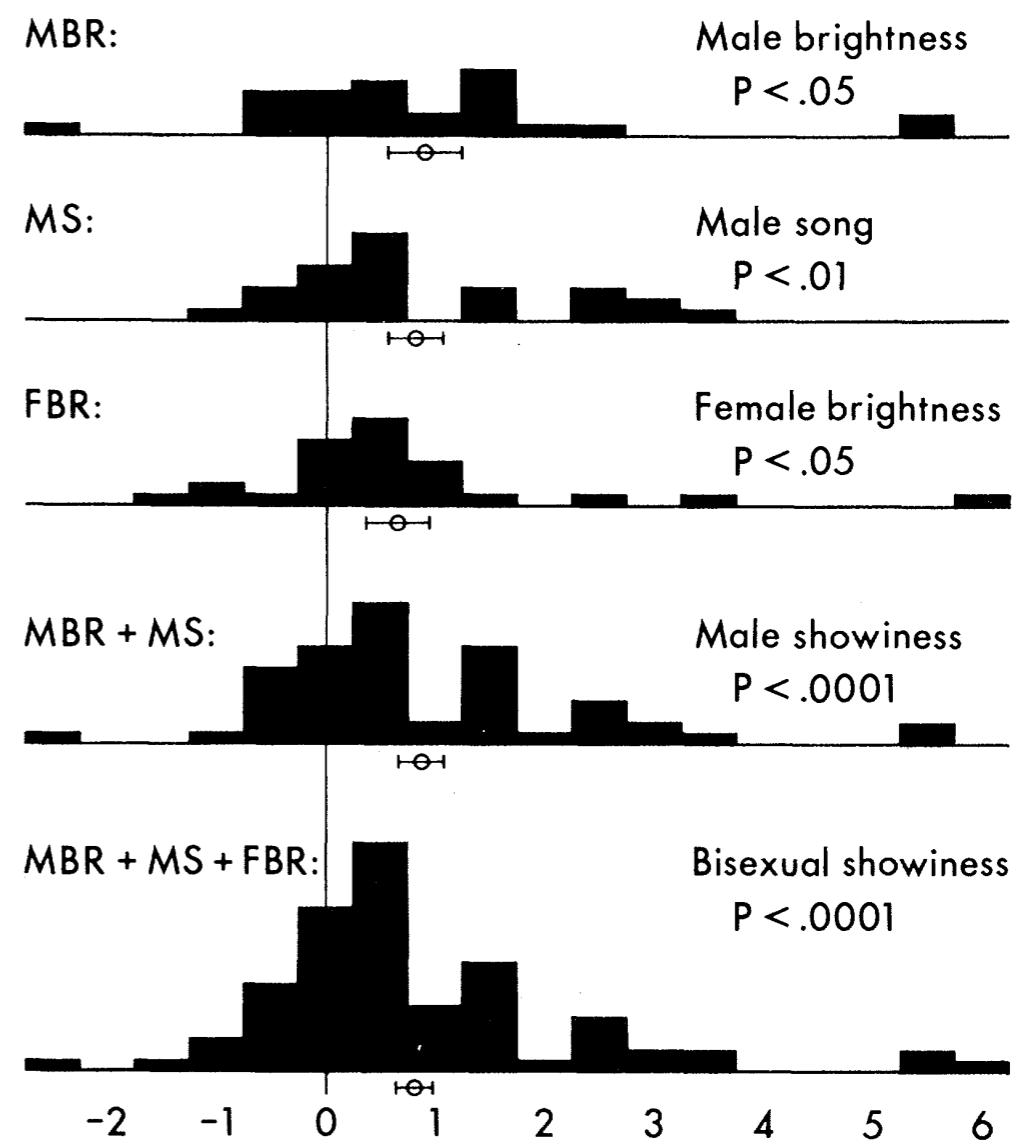
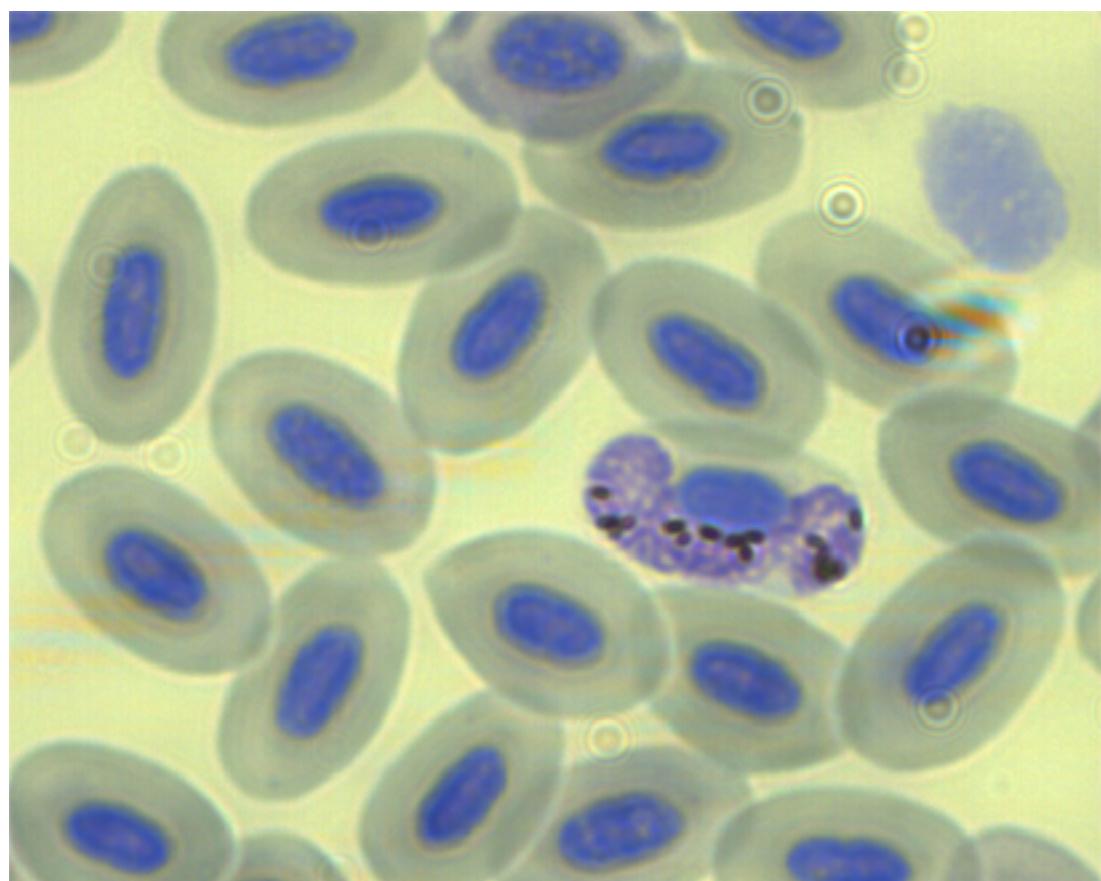


FIG. 1. The effects of mate preference on the evolution of a sexually attractive character. Quality in the mate is plotted on the vertical axis while the size of the attractive character (which is considered to be a handicap) is plotted on the horizontal axis. At the intersection of the axes the character is of the size which fits best the selection pressure of natural selection. An increase in the character (hence in the handicap) eliminates low quality individuals (lower hatched area in the diagram). The selecting sex cannot distinguish quality among potential mates with equally developed attractive character. Note that the more developed the attractive character the higher the average quality of a potential mate.

# Heritable True Fitness and Bright Birds: A Role for Parasites?

WILLIAM D. HAMILTON  
MARLENE ZUK



*Abstract.* Combination of seven surveys of blood parasites in North American passerines reveals weak, highly significant association over species between incidence of chronic blood infections (five genera of protozoa and one nematode) and striking display (three characters: male "brightness," female "brightness," and male song). This result conforms to a model of sexual selection in which (i) coadaptational cycles of host and parasites generate consistently positive offspring-on-parent regression of fitness, and (ii) animals choose mates for genetic disease resistance by scrutiny of characters whose full expression is dependent on health and vigor.

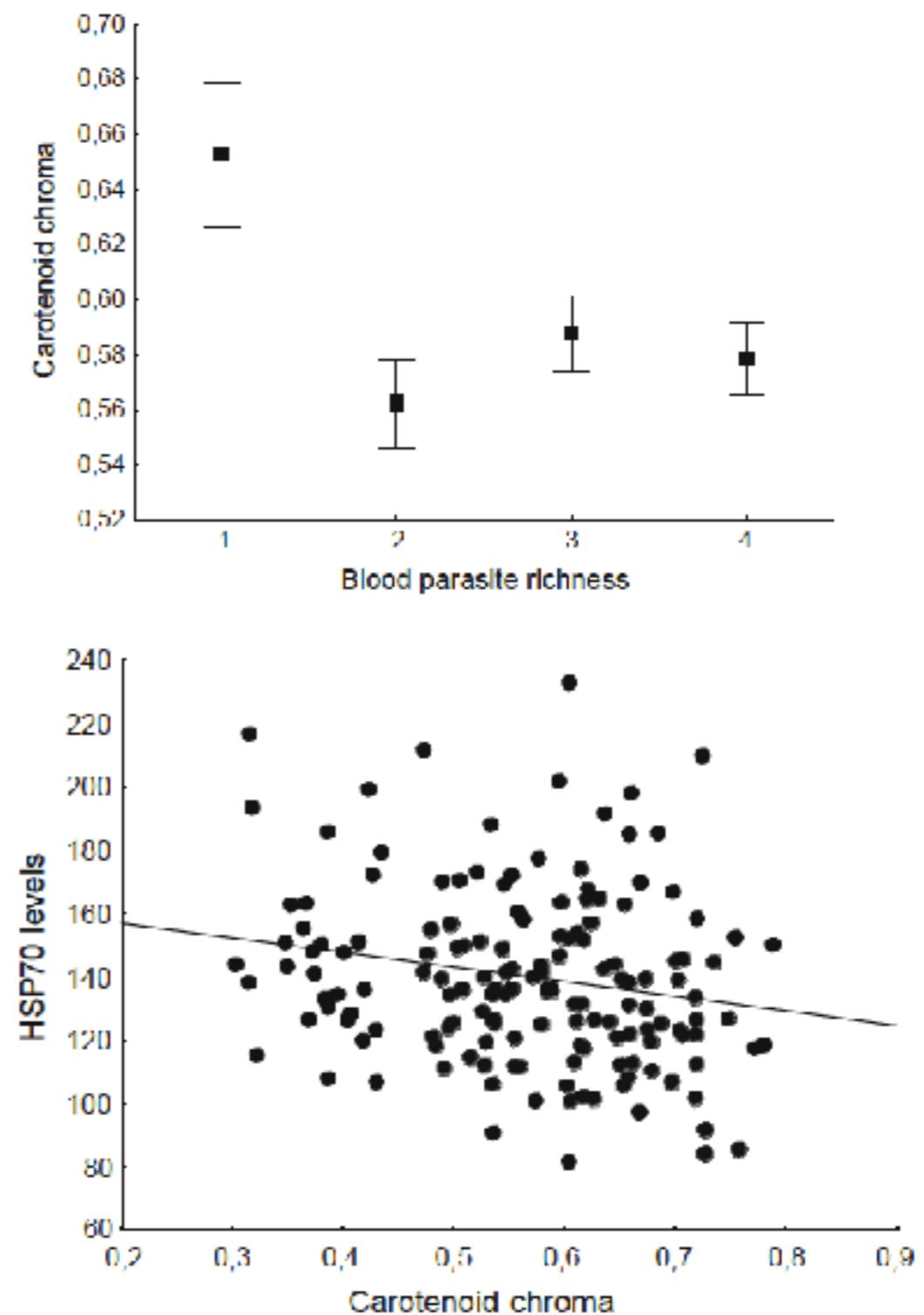
# Hamilton & Zuk (1982) y el papel de los parásitos

Oecologia (2010) 162:825–835



**Carotenoid-based plumage colouration is associated with blood parasite richness and stress protein levels in blue tits (*Cyanistes caeruleus*)**

Sara del Cerro · Santiago Merino · Josué Martínez-de la Puente · Elisa Lobato ·  
Rafael Ruiz-de-Castañeda · Juan Rivero-de Aguilar · Javier Martínez ·  
Judith Morales · Gustavo Tomás · Juan Moreno

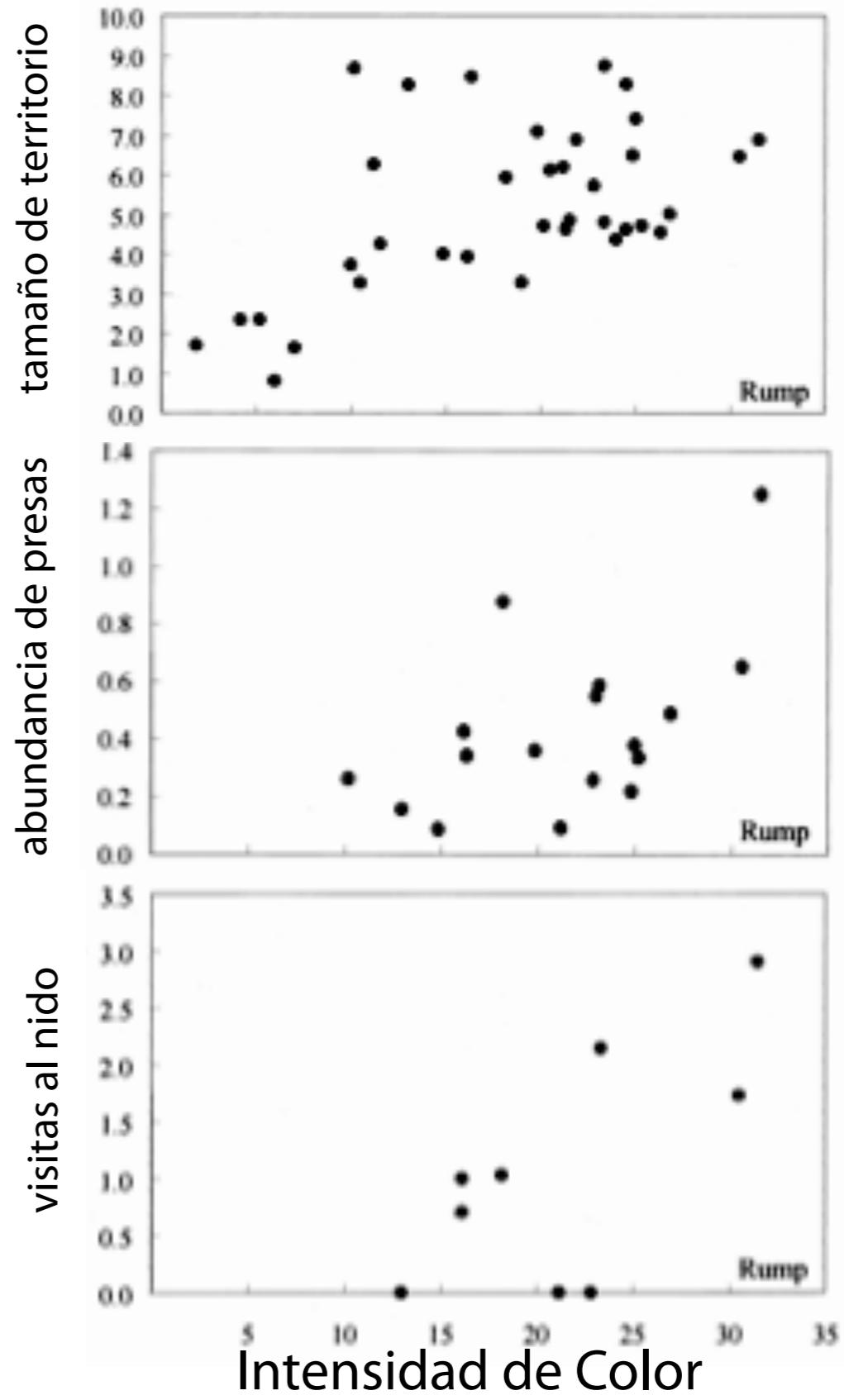


**Fig. 3** Relationship between heat shock protein (HSP) 70 levels and carotenoid chroma of breast plumage colour of blue tits in 2004

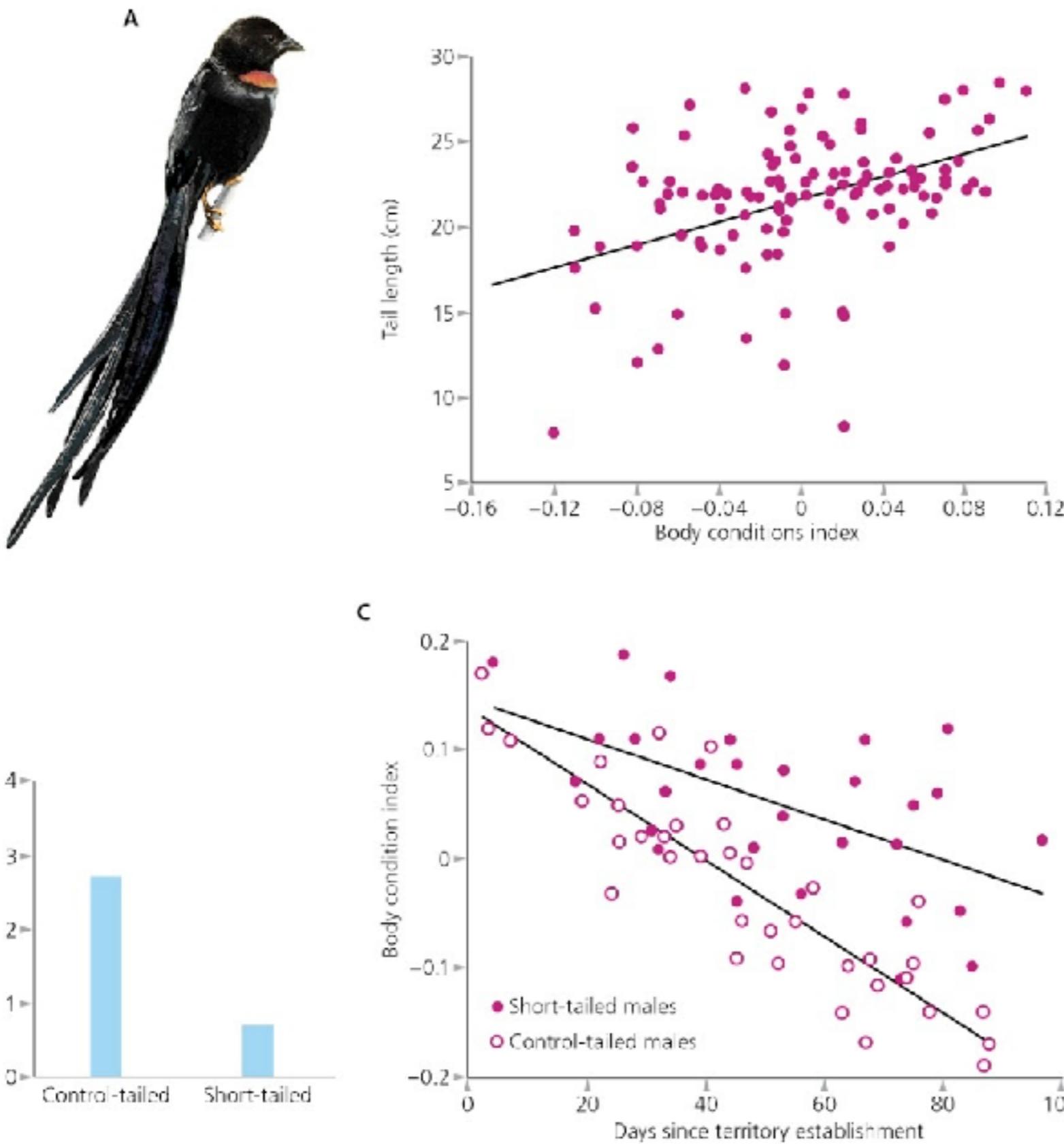
# señales sexuales como indicadores honestos: beneficios directos para las hembras



Structurally based plumage coloration is an honest signal of quality in male blue grosbeaks



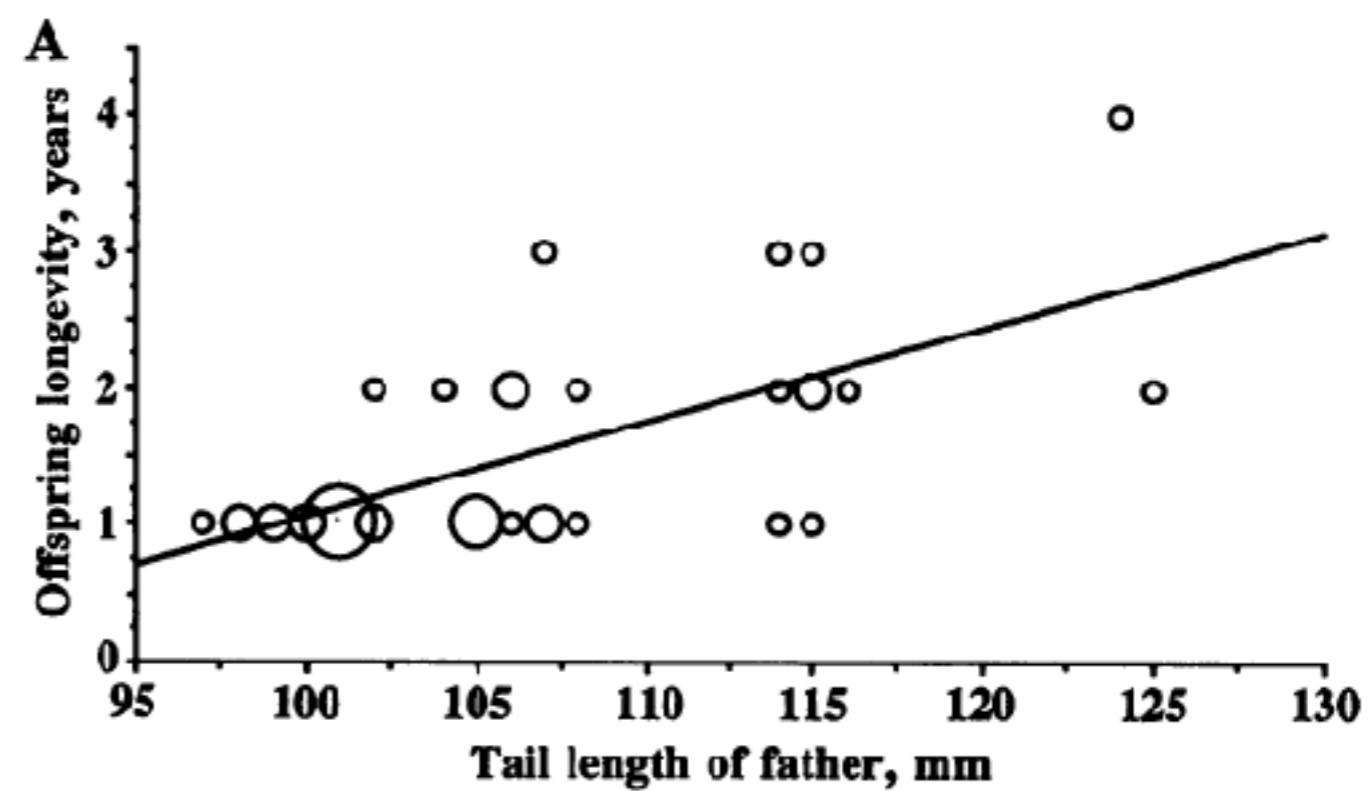
# señales sexuales como indicadores honestos: buenos genes y beneficios indirectos - “sexy sons”



Pryke et al. (2001)

Pryke & Andersson (2005)

# señales sexuales como indicadores honestos: buenos genes y beneficios indirectos - progenie más apta



*Proc. Natl. Acad. Sci. USA*  
Vol. 91, pp. 6929–6932, July 1994

## Male ornament size as a reliable cue to enhanced offspring viability in the barn swallow

(female choice/good genes models/sexual selection)

ANDERS PAPE MØLLER

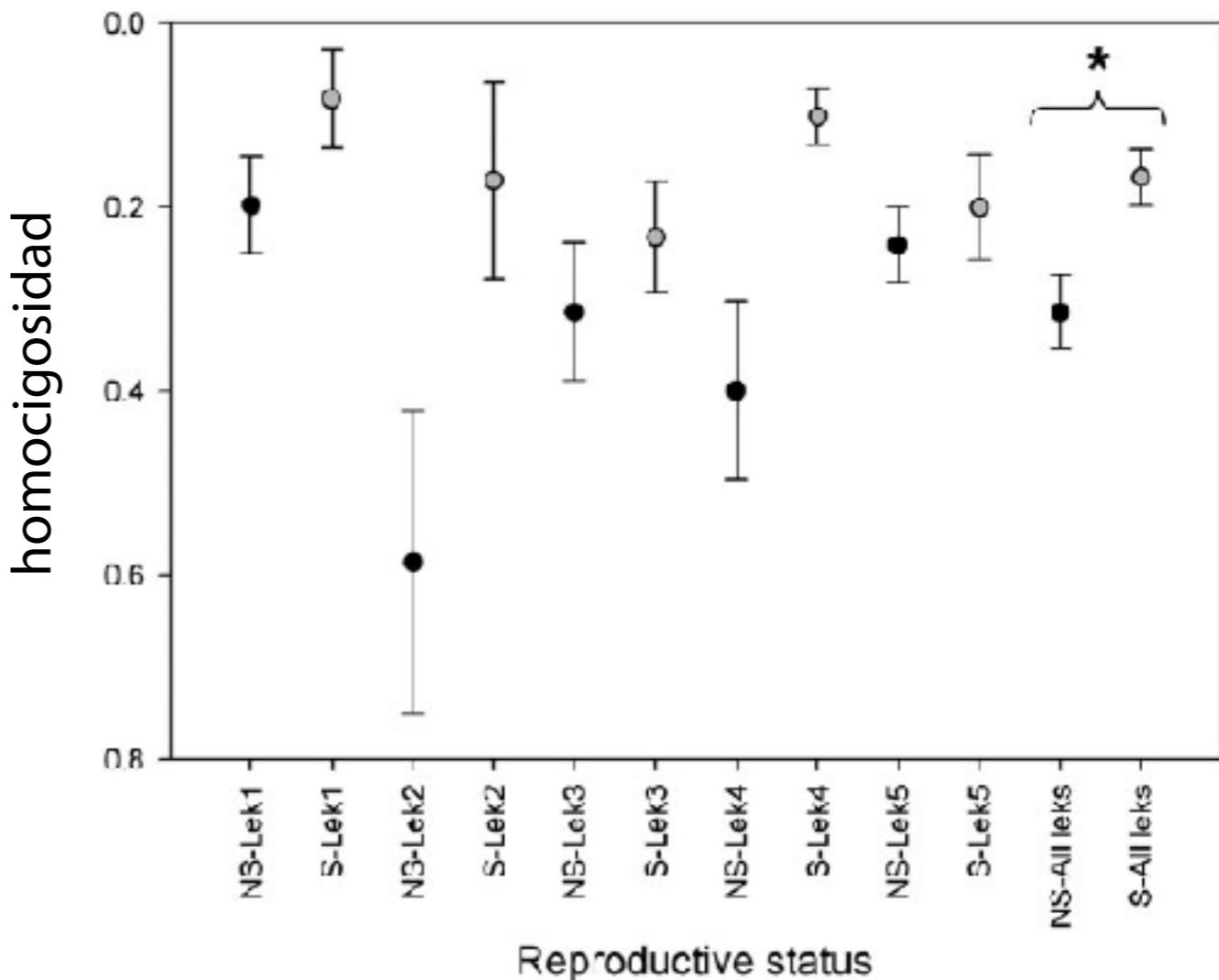
# buenos genes y beneficios indirectos - progenie con mayor variabilidad



(*Behav Ecol* 21:203–210 (2010))

Mate choice for genetic quality: a test of the heterozygosity and compatibility hypotheses in a lek-breeding bird

T.B. Ryder, W.P. Tori, J.G. Blake, B.A. Loiselle, and P.G. Parker



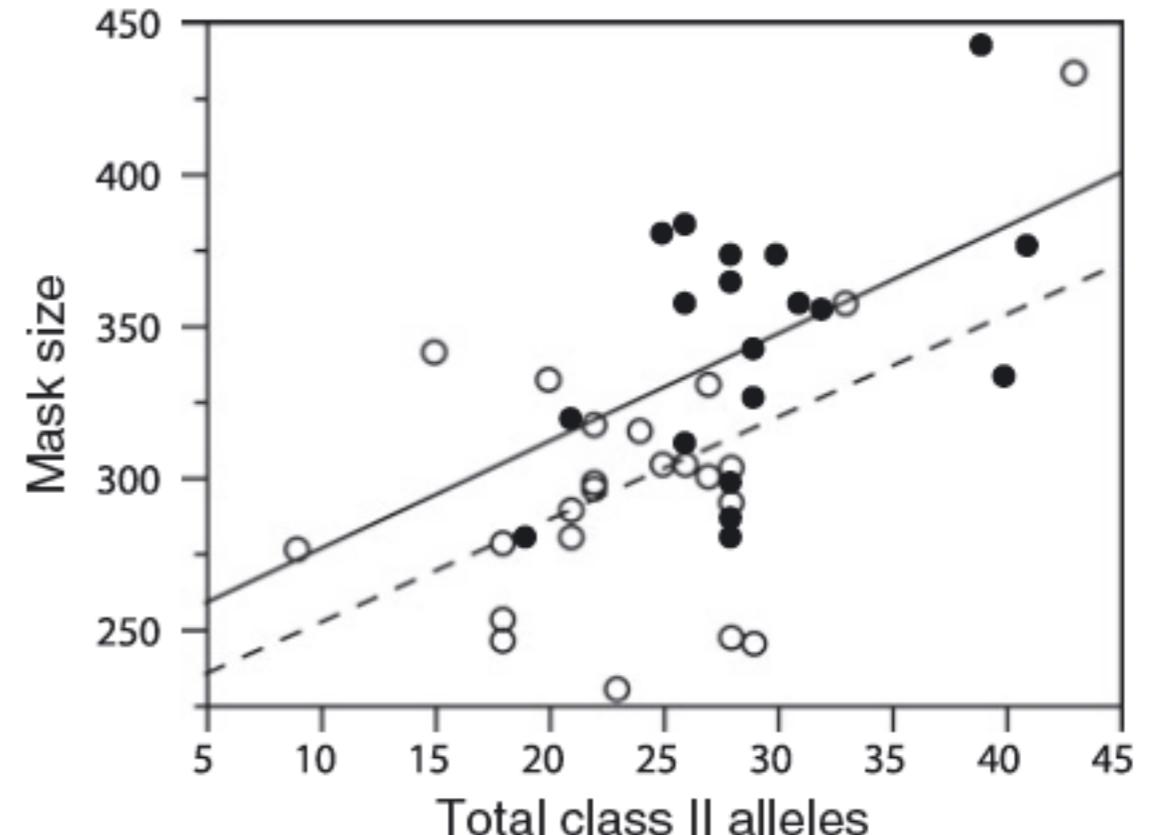
# señales sexuales como indicadores honestos: beneficios indirectos - progenie con mayor variabilidad en genes de rta inmune



Evolution 67-3: 679–687

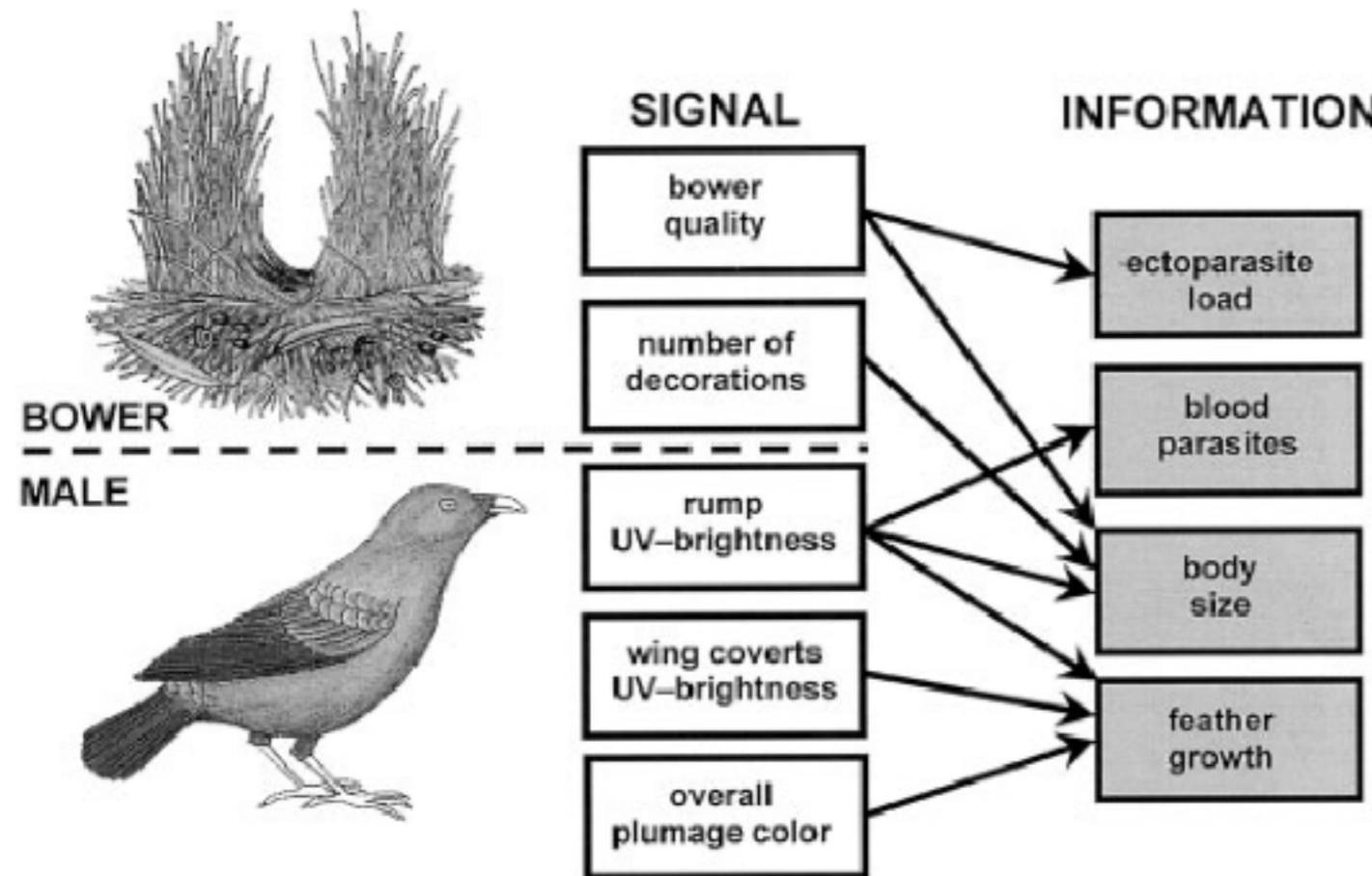
## MHC VARIATION IS RELATED TO A SEXUALLY SELECTED ORNAMENT, SURVIVAL, AND PARASITE RESISTANCE IN COMMON YELLOWTHROATS

Peter O. Dunn,<sup>1,2</sup> Jennifer L. Bollmer,<sup>1</sup> Corey R. Freeman-Gallant,<sup>3</sup> and Linda A. Whittingham<sup>1</sup>



**Figure 1.** Males with larger masks have more MHC class II alleles ( $F_{1,39} = 13.15, P < 0.001$ ), even after controlling for breeding experience ( $F_{1,39} = 4.46, P = 0.041$ ; overall model  $R^2 = 0.42$ ). Males with prior breeding experience are indicated by solid dots and line ( $N = 19$ ), and males without prior breeding experience are indicated by open circles and dashed line ( $N = 23$ ).

# distintas señales sexuales y qué indican



Multiple sexual ornaments in satin bowerbirds:  
ultraviolet plumage and bowers signal different  
aspects of male quality



[http://www.youtube.com/watch?v=v\\_BurGW2rPU](http://www.youtube.com/watch?v=v_BurGW2rPU)

[http://www.youtube.com/watch?v=tJ32\\_ijdmLo](http://www.youtube.com/watch?v=tJ32_ijdmLo)

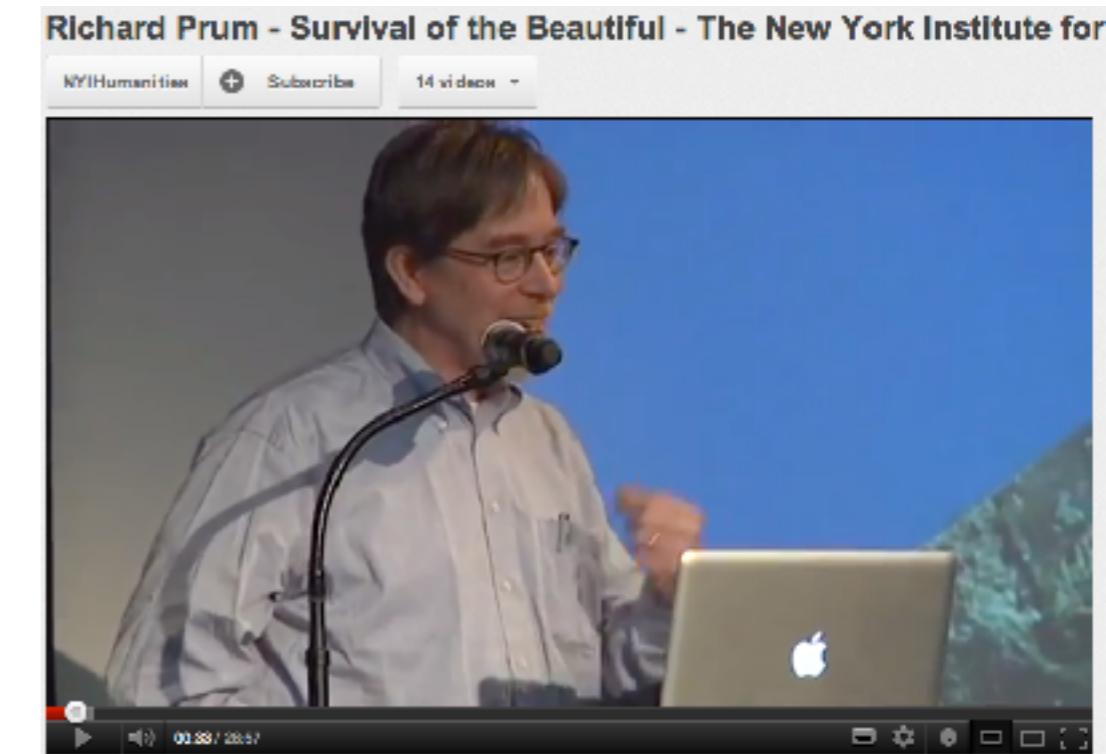
*Review*

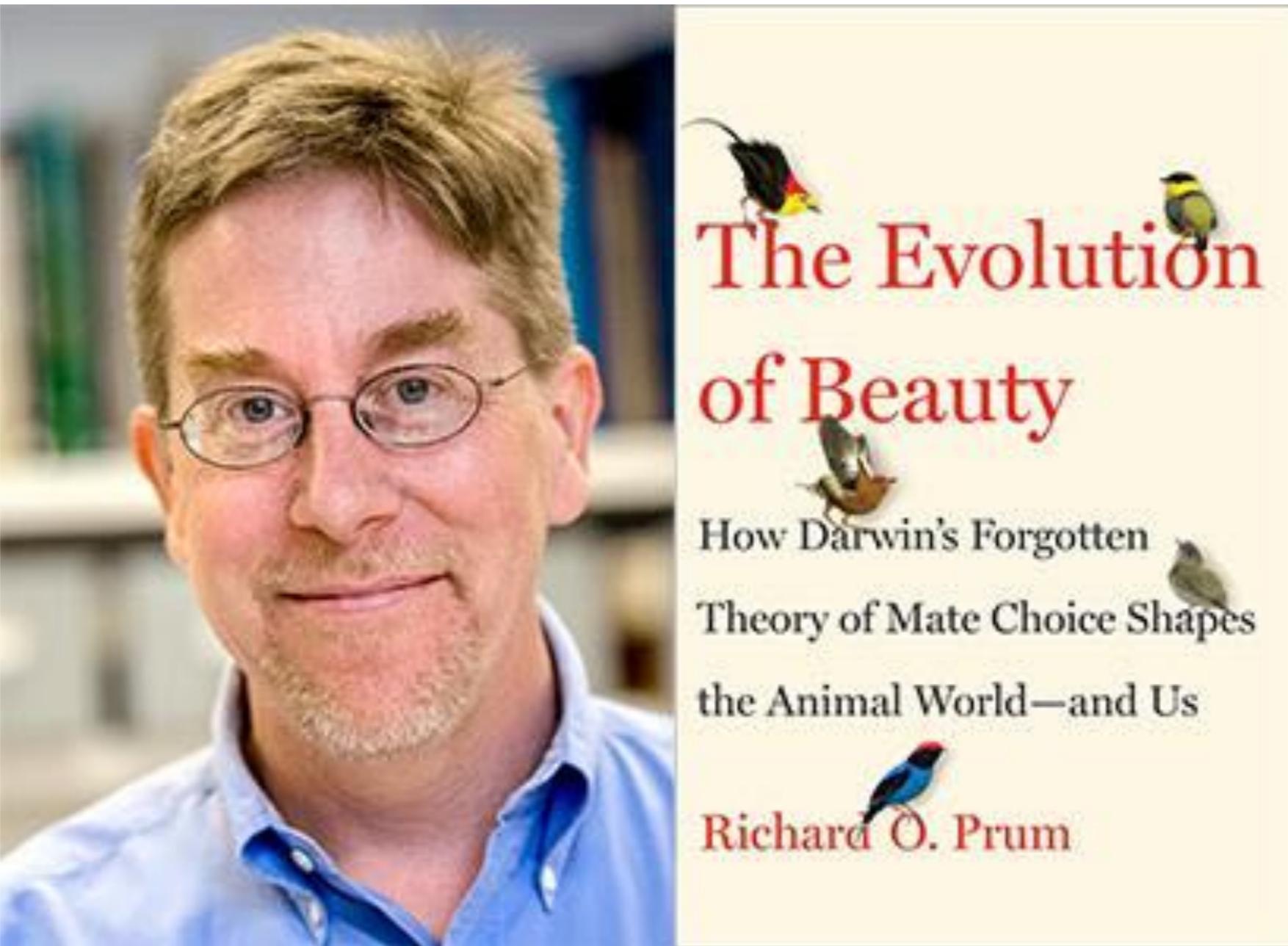
## Aesthetic evolution by mate choice: Darwin's *really dangerous idea*

Richard O. Prum\*

Department of Ecology and Evolutionary Biology, and Peabody Museum of Natural History,  
Yale University, New Haven, CT 06520, USA

Darwin proposed an explicitly aesthetic theory of sexual selection in which he described mate preferences as a ‘taste for the beautiful’, an ‘aesthetic capacity’, etc. These statements were not merely colourful Victorian mannerisms, but explicit expressions of Darwin’s hypothesis that mate preferences can evolve for arbitrarily attractive traits that do not provide any additional benefits to mate choice. In his critique of Darwin, A. R. Wallace proposed an entirely modern mechanism of mate preference evolution through the correlation of display traits with male vigour or viability, but he called this mechanism natural selection. Wallace’s honest advertisement proposal was strikingly anti-Darwinian and anti-aesthetic. Most modern sexual selection research relies on essentially the same Neo-Wallacean theory renamed as sexual selection. I define the process of aesthetic evolution as the evolution of a communication signal through sensory/cognitive evaluation, which is most elaborated through coevolution of the signal and its evaluation. Sensory evaluation includes the possibility that display traits do not encode information that is being assessed, but are merely preferred. A genuinely Darwinian, aesthetic theory of sexual selection requires the incorporation of the Lande–Kirkpatrick null model into sexual selection research, but also encompasses the possibility of sensory bias, good genes and direct benefits mechanisms.



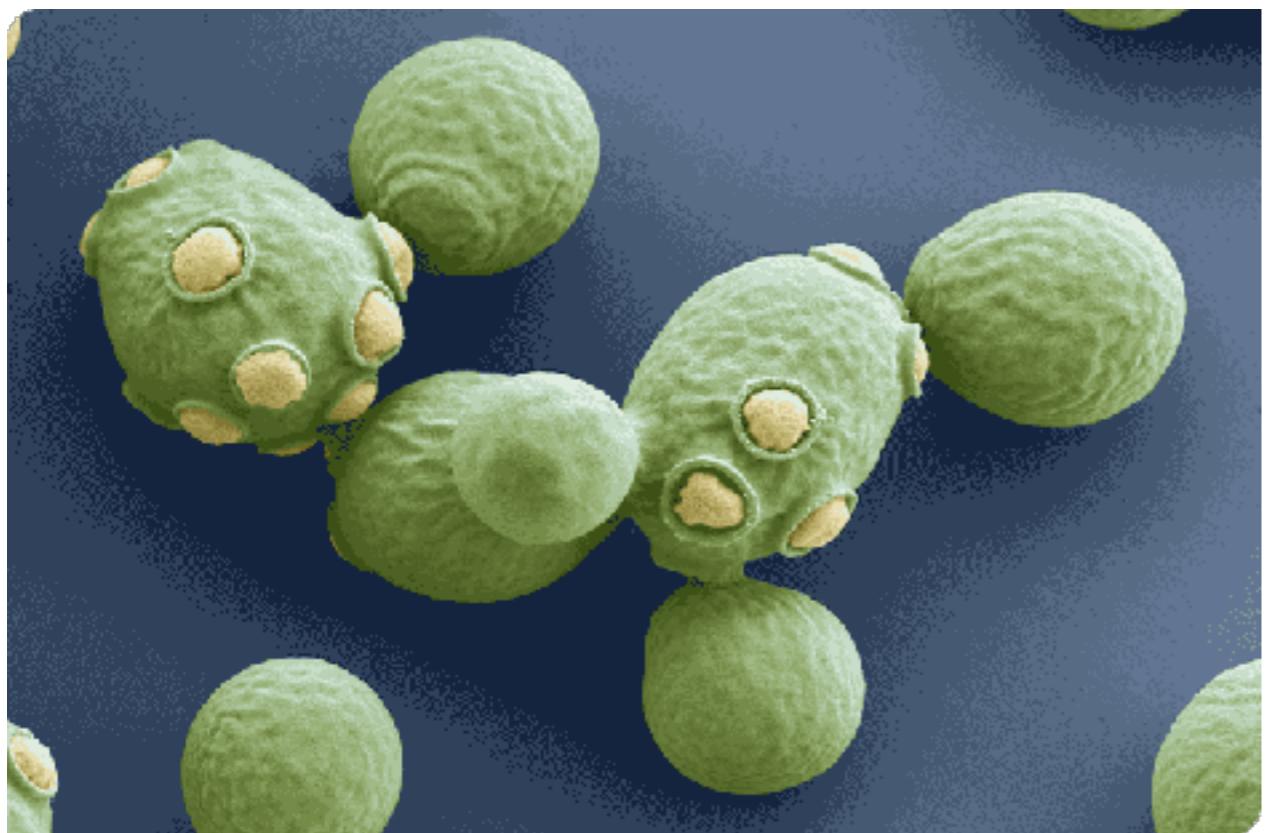


<https://www.nytimes.com/2017/05/29/science/evolution-of-beauty-richard-prum-darwin-sexual-selection.html>

<https://www.nytimes.com/2017/05/05/opinion/sunday/are-these-birds-too-sexy-to-survive.html>

<https://onlinelibrary.wiley.com/doi/abs/10.1111/evo.13629>

# selección sexual no ocurre sólo en animales



<http://www.microbiologyonline.org.uk/about-microbiology/introducing-microbes/fungi>

## Abstract

The significance of sexual selection, the component of natural selection associated with variation in mating success, is well established for the evolution of animals and plants, but not for the evolution of fungi. Even though fungi do not have separate sexes, most filamentous fungi mate in a hermaphroditic fashion, with distinct sex roles, that is, investment in large gametes (female role) and fertilization by other small gametes (male role). Fungi compete to fertilize, analogous to 'male-male' competition, whereas they can be selective when being fertilized, analogous to female choice. Mating types, which determine genetic compatibility among fungal gametes, are important for sexual selection in two respects. First, genes at the mating-type loci regulate different aspects of mating and thus can be subject to sexual selection. Second, for sexual selection, not only the two sexes (or sex roles) but also the mating types can form the classes, the members of which compete for access to members of the other class. This is significant if mating-type gene products are costly, thus signalling genetic quality according to Zahavi's handicap principle. We propose that sexual selection explains various fungal characteristics such as the observed high redundancy of pheromones at the *B* mating-type locus of Agaricomycotina, the occurrence of multiple types of spores in Ascomycotina or the strong pheromone signalling in yeasts. Furthermore, we argue that fungi are good model systems to experimentally study fundamental aspects of sexual selection, due to their fast generation times and high diversity of life cycles and mating systems.

## Sexual selection in fungi

# Sexual selection in plants

Jamie C. Moore and John R. Pannell

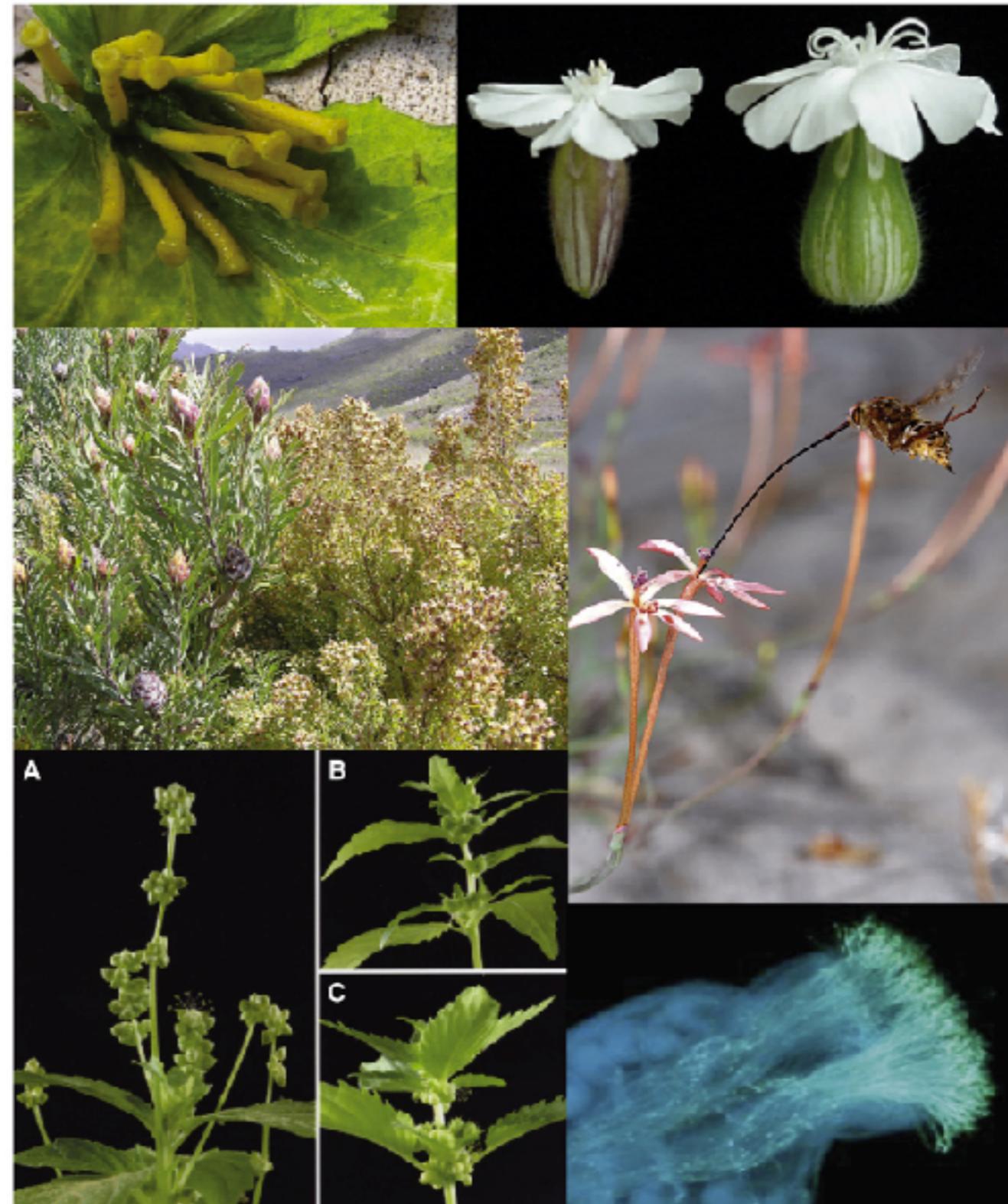


Figure 1. Potential examples of sexual selection in plants.

Bottom left: panels (A), (B) and (C) show the male, female and hermaphrodite inflorescences of the sexually polymorphic wind-pollinated species *Mercurialis annua* (Euphorbiaceae). Males have evolved stalked (pedunculate) inflorescences that confer a 60% siring advantage on their pollen grains compared to pollen grains dispersed by hermaphrodites (from Pannell et al. 2008, with permission from University of Chicago Press). Middle left: strong secondary sexual dimorphism in the wind-pollinated shrub *Leucadendron rubrum* (Proteaceae) in the fynbos of South Africa. Females (left) have larger leaves and thicker stems than males (right) (courtesy of Spencer C.H. Barrett). Top left: Extended stigmatic surfaces of gynodioecious *Dalechampia subternata* (Euphorbiaceae). The yellow stigmas, which are at the apex of much shorter non-stigmatic styles, increase the surface area over which pollen grains can be captured by the female organs (courtesy of W. Scott Armbruster). Top right: sexual dimorphism in the dioecious plant *Silene latifolia* (Caryophyllaceae), where staminate (male) flowers (left) are smaller, but much more numerous, than pistillate (female) flowers (right) (courtesy of Lynda F. Delph). Middle right: the long floral tube of the Cape fynbos species *Lapeirousia anceps* (Iridaceae), which is hypothesised to have co-evolved with the proboscis length of its pollinator *Moegistorhynchus longirostris* (Nemestrinidae; shown) (courtesy of Anton Pauw). Bottom right: fluorescence microscopic image of pollen tubes growing down the style of *Arabidopsis thaliana* in a race to fertilize the ovules (courtesy of James Doughty).

# Adaptation

## From Genes to Traits

### Learning Objectives

- Explain how the ancestors of Richard Lenski's *E. coli* lineages provided evidence for the development of the citrate-eating adaptation.
- Explain how mutations to a regulatory network may affect development of an organism.
- Describe two examples where proteins were co-opted for other functions.
- Explain why *Hox* genes are considered part of the "genetic toolkit."
- Explain how changes in the timing and location of the expression of developmental genes can affect the appearance of important traits like legs and beak size.
- Analyze how a mutation that affects an upstream element in a gene network can alter a phenotype.
- Describe three important steps in the evolution of the vertebrate eye.
- Distinguish the outcomes between a mutation in a pleiotropic gene and a non-pleiotropic gene.
- Analyze the imperfections of a familiar complex adaptation.
- Explain the relationship between homology and convergent evolution.

**To study evolution,** Bryan Fry puts his life on the line. Fry, a biologist at the University of Melbourne, studies the evolution of snake venom, and that means he has to make intimate contact with some of the most lethal animals in the world, from deadly sea snakes to king cobras. Fry is an admitted adrenaline junkie, but he's not reckless. He prepares himself for every encounter so that he comes home safe and sound. It helps to understand snake behavior. Fry knows, for example, that a king cobra signals its dominance over other king cobras by extending up and touching the tops of their heads. To trap a king cobra, Fry first shows it who's boss by tapping it on the head. The cobra briefly bows down in submission, and Fry takes the opportunity to slip it into a bag.

Once back in his lab at the University of Melbourne, Fry can get a close look at the biology that makes this snake so deadly. At the back of their mouths, venomous snakes have glands that produce venom. The cells in the glands express a set of venom genes, build the corresponding proteins, and pump the venom into the surrounding fluid. A king cobra opens its jaws and stabs its fangs into its victim. Muscles squeeze down on the glands, and the venom shoots down a pair of tubes leading

