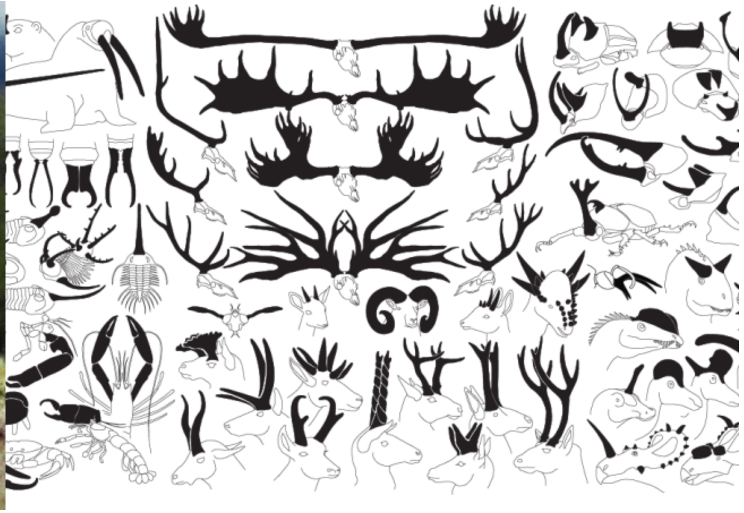
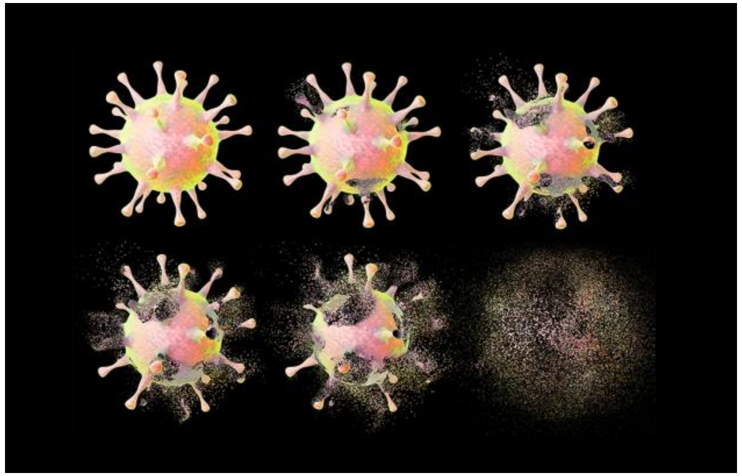
Antagonistic co-evolution, arm race and red queen

Anup Shah/Minden Pictures/Getty





- selection – imposed by environment
- environment – abiotic and **biotic** factors

- **Coevolution**, the process of reciprocal evolutionary change that occurs between pairs of species or among groups of species as they interact with one another.
- Coevolution can happen within the species as well!

Intra and inter specific interactions in which arm race occur

- Herbivores and plants
- Pollinators and plants
- Predators and prey
- Parasites and hosts
- Mutualism, symbiosis
- Sex

AGONISTIC OR ANTAGONISTIC

"It is this antagonistic dynamic between plants and their insects that has driven the diversity of these groups"

An ancient arms race has helped insects gain resistance to pesticides, again and again

A key genetic adaptation protection against plant toxins has independently evolved many times over 300 million years

17 JUL 2023 · 11:00 AM ET · BY ELIZABETH PENNISI

https://www.nature.com/articles/s41559-023-02127-4

Red queen hypothesis

“Well in our country,” said Alice, still panting a little. “you’d generally get to somewhere else-if you ran very fast for a long time as we’ve been doing.”

*“A slow sort of county!” said the Queen. “Now, here, you see, **it takes all the running you can do to keep in the same place**. If you want to get somewhere else, you must run at least twice as fast as that!”*

- **Van Valen 1973 - ‘Red Queen hypothesis’** (RQH) emphasized the **primacy of biotic interactions over abiotic forces in driving evolution**. This was a revolutionary advance in biological thinking on the sources and modes of selection driving evolutionary change.
- *Organisms must constantly adapt, evolve, and proliferate not merely to gain reproductive advantage, but also simply to survive while pitted against ever-evolving opposing organisms in a constantly changing environment*
- *In tightly coevolved interactions, evolutionary change by one species (e.g., a prey or host) could lead to extinction of other species (e.g. a predator or parasite), and that the probability of such changes might be reasonably independent of species age*. Van Valen named the idea "the Red Queen hypothesis," because, under this view, **species had to "run" (evolve) in order to stay in the same place**

- **Cessation of change might lead to extinction!**

Sexual conflict

https://youtu.be/iMCtE2-YsLc

Trivers 1972 “even when ostensibly cooperating in a joint task **male and female interests are rarely identical**”.

This divergence in reproductive interest between the sexes stems from anisogamy (differences in size between male and female gametes). This creates an asymmetry between the sexes, where **male reproductive success is limited by the number of mating partners, while female reproductive success is limited by the resources invested in reproduction** (Bateman 1948).

To reach a completely conflict-free relationship between a male and female, there will have to be life long monogamy with no chances of re- mating again even if one partner dies, a scenario that with the help of molecular techniques has proven to be extremely rare

Garter snakes - males produce plugs that block the female's cloacas (multipurpose genital openings) to prevent any subsequent males from inseminating a female he got to first - the effort males put into this devotes up to 18 per cent of their daily energy expenditure in producing these plugs.

PROCEEDINGS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Sexual conflict over mating in red-sided garter snakes (*Thamnophis sirtalis*) as indicated by experimental manipulation of genitalia

Christopher R. Friesen, Emily J. Uhrig, Mattie K. Squire, Robert T. Mason and Patricia L. R. Brennan

Proc. R. Soc. B 2014 **281**, 20132694, published 13 November 2013

Males have a **basal spine that hooks into the female to keep a grip on her**, allowing him to extend mating after she was done with him.

The females have apparently responded by developing an **extremely muscular cloaca** whose contractions can get rid of males that have overstayed their welcome, while possibly also squeezing plugs out. Females also body roll to shake off unwanted suitors.

EXPERIMENT - manipulating the genitals of both male and female snakes.

...**removed the spines of the males** and **anesthetized the female cloacas** to see what happens when each sex loses its primary weapon. As expected, plugs were smaller when the males were trimmed, but the effect of anesthetizing the females was more complex, with sex lasting longer, but plugs not decreasing in size.

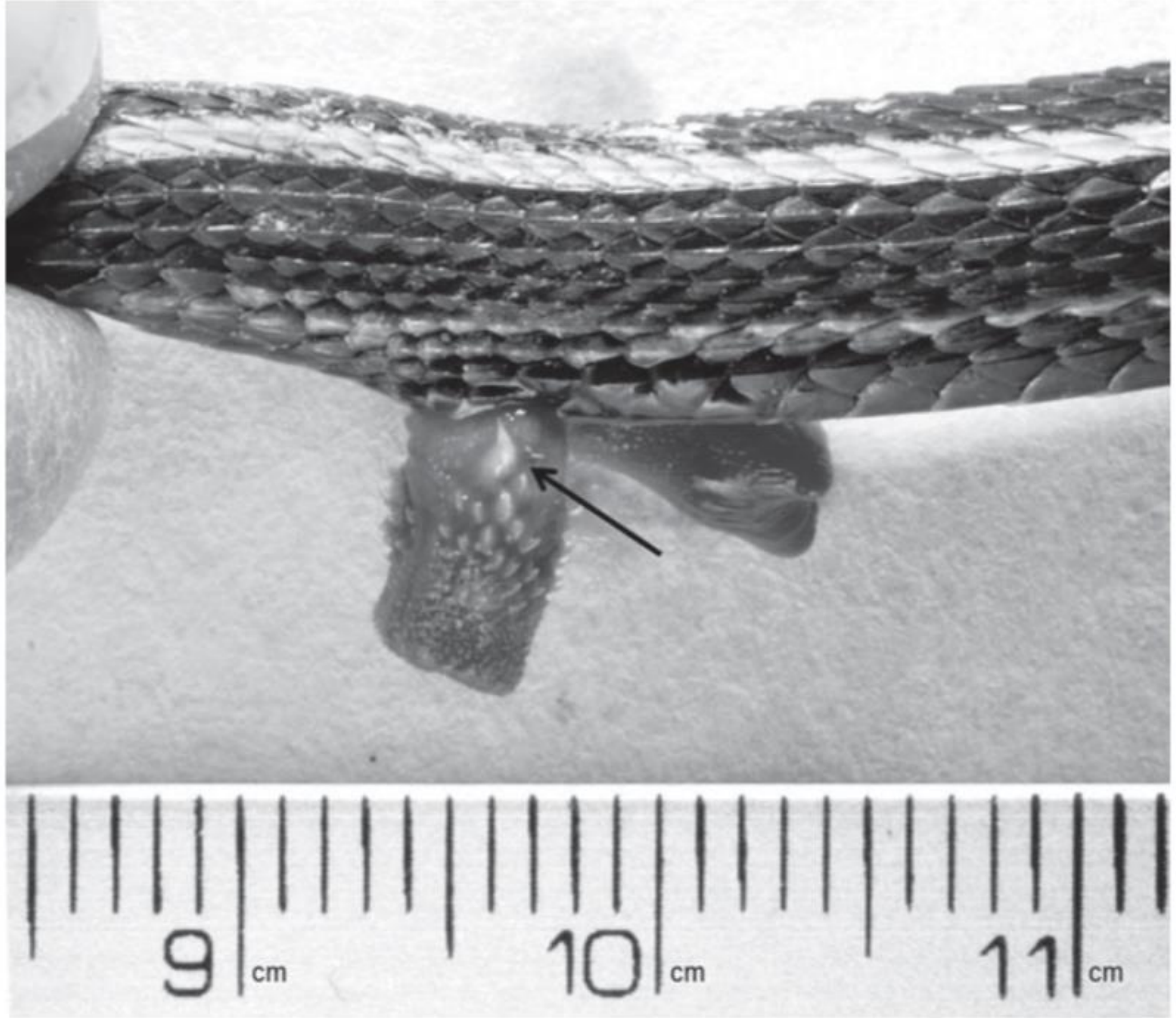


Figure 1. A photo of the basal spine on the right hemipene of *Thamnophis sirtalis parietalis*. The arrow indicates the basal spine.

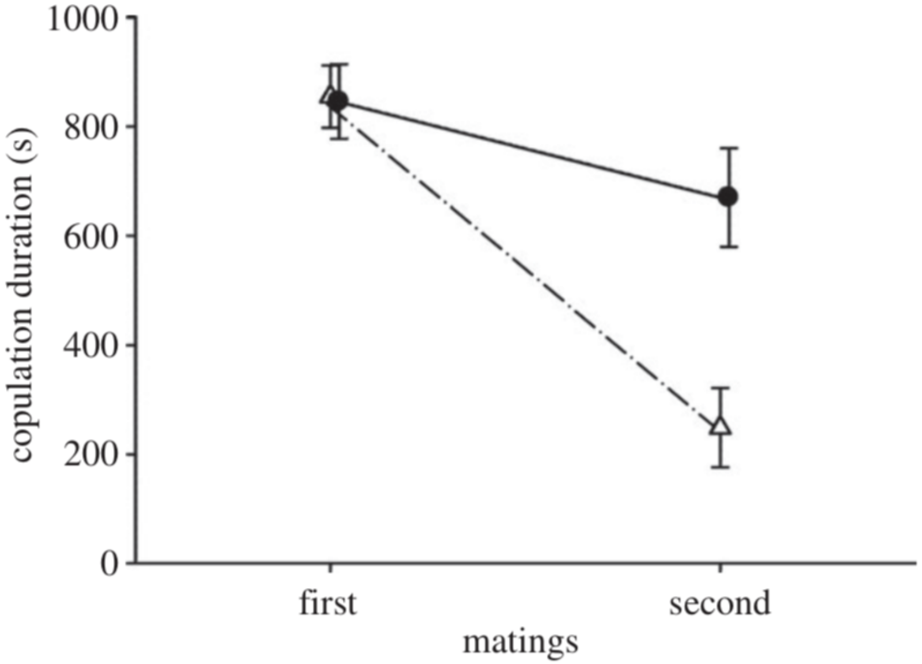


Figure 2. (*a*) Spine-ablated males (open triangles): copulation duration at first mating (pre-ablation) $\bar{X}$ (s.e.m.), 855 s (57 s); at second mating (post-ablation) 249 s (73 s). (*b*) Control males (filled circles): copulation duration at first mating $\bar{X}$ (s.e.m.), 819 s (68 s); at second mating 643 s (90 s).

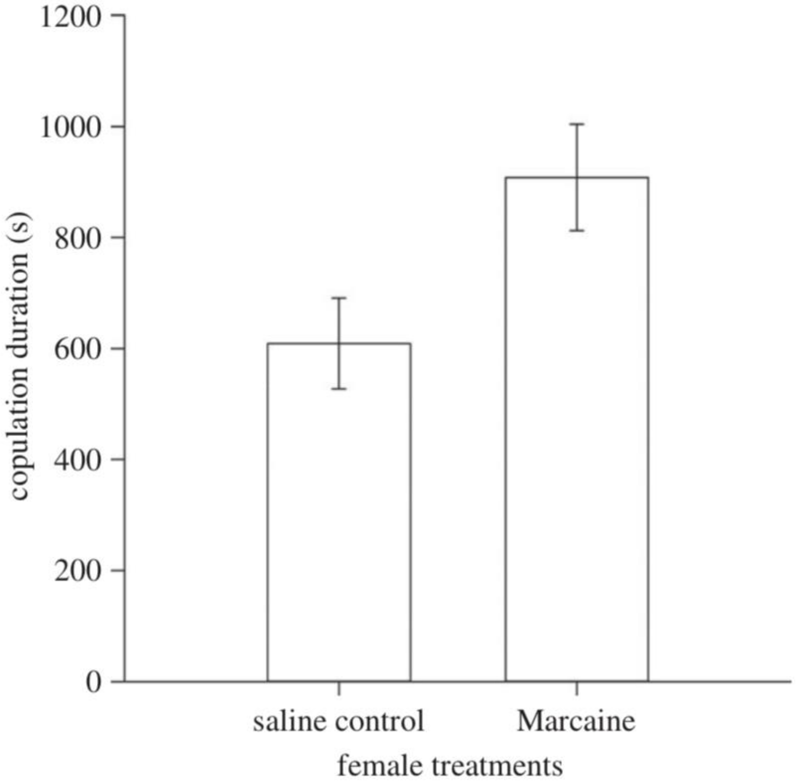


Figure 4. Copulation duration as a function of female treatment in locally anaesthetized females (Marcaine treated) versus saline-injected (control) females. Copulation was much longer in Marcaine-treated females. Bars in the graph represent the s.e.

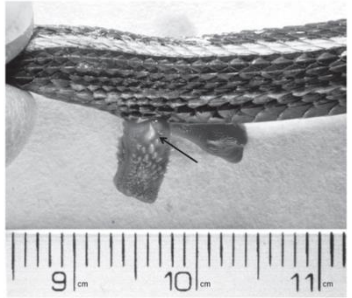


Figure 1. A photo of the basal spine on the right hemipene of *Thamnophis sirtalis parietalis*. The arrow indicates the basal spine.

COEVOLUTION OF PARASITISM

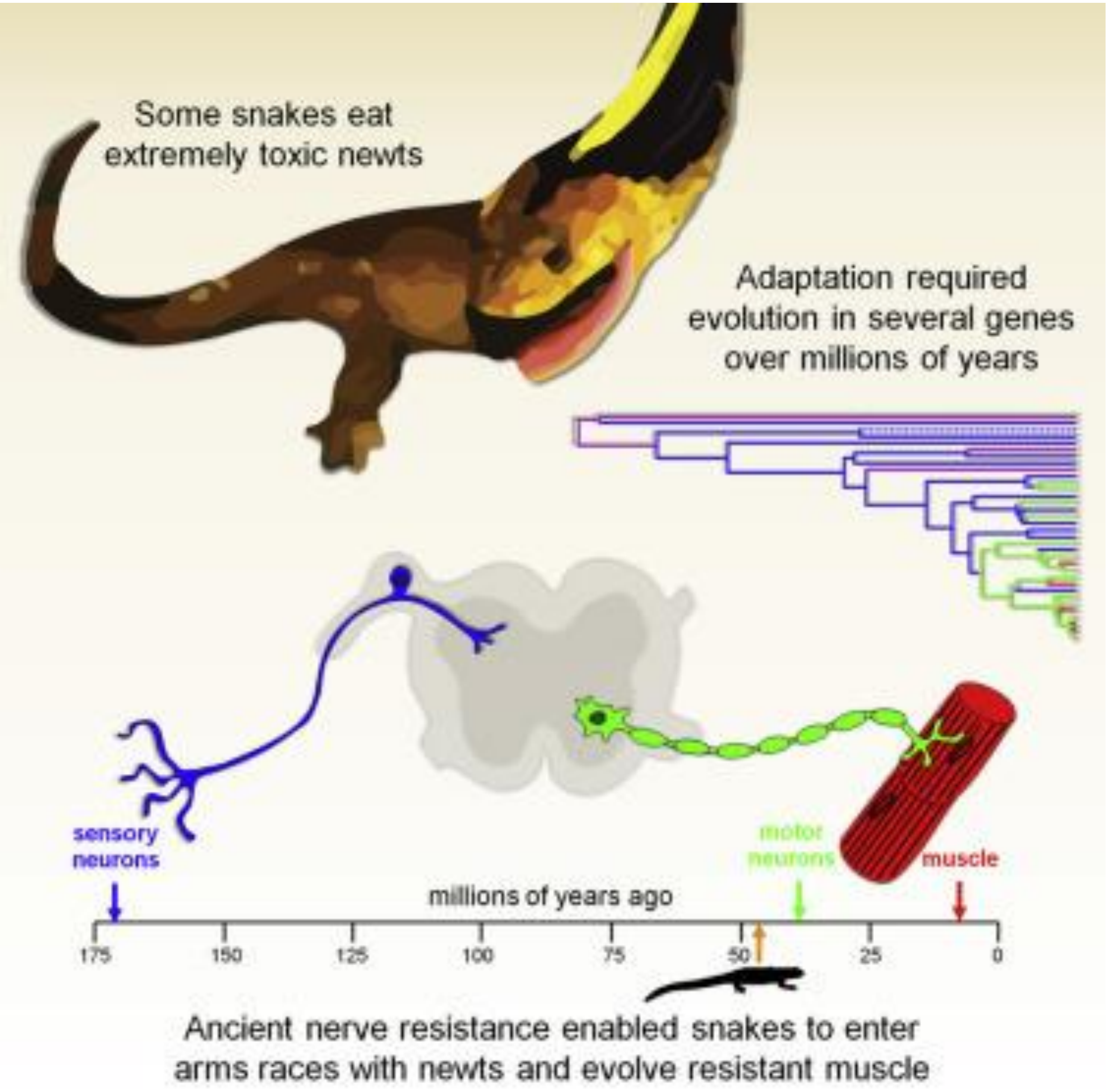
Cuckoo in Great Britain have 4 different hosts

- 3 cuckoo genotypes in population matching the phenotypes of eggs
- effective defence leads to relaxed selection, as nests are no longer targeted by cuckoos
- in Island, where cuckoo is novel species, non matching eggs are not excluded from the nests – evidence of evolved ability to reject cuckoo eggs

Why don't hosts discriminate against common cuckoo nestlings?

- *One possibility is* ***evolutionary lag****; hosts simply have yet to evolve this line of defence. Davies & Brooke (1988) advance a novel and insightful adaptive explanation as well. First, they point out that hosts of evictor parasites, like the common cuckoo, benefit much more by rejecting eggs early in the breeding season, thereby saving their brood from eviction, than by rejecting chicks much later. Therefore, it is not surprising that reed warblers discriminate against eggs rather than nestlings.*

Resistance to the blowfish poison, tetrodotoxin in Gartner snakes



Some snakes eat extremely toxic newts

Adaptation required evolution in several genes over millions of years

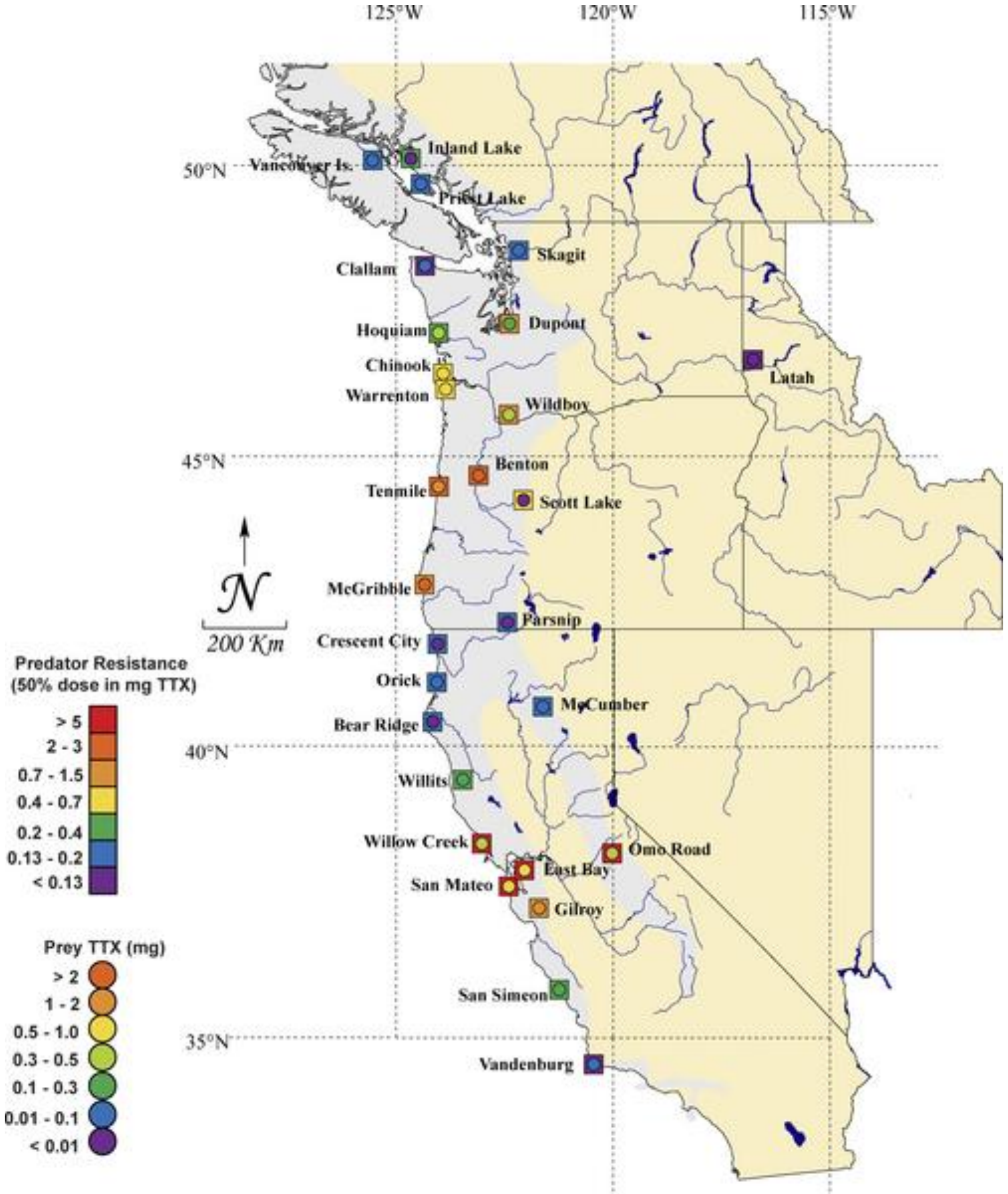
Ancient nerve resistance enabled snakes to enter arms races with newts and evolve resistant muscle

WHEN ONE CANT KEEP UP…

First adaptation in snakes themselves (the second nerve channel adaptation) happened about ***40 million years ago****, right around the time that newts came on the scene, and then happened again independently in another three snake lineages.* ***The most extreme resistance (the one that results from a mutated sodium channel in muscle cells) only came about around 12 million years ago****. Only five species of snake possess this mutation.*

doi:10.1371/journal.pbio. 0060060

Figure 1. The Geographic Distribution of TTX Resistance of Garter Snakes and TTX Toxicity of Newts in Western North America



In one third of the locations, the most toxic newt could still be eaten by the least resistant snake. This means that all snakes in the population do just as well regardless of their TTX resistance level, and there is no evolutionary pressure for the snakes to develop stronger resistance

While the most toxic newts had 14 to 15 milligrams of TTX, some garter snakes are resistant to up to 100 milligrams of TTX. To hold that much toxin, the tiny newts would be one part toxin to nine parts skin—a near physical impossibility

Hanifin CT, Brodie ED Jr, Brodie ED III (2008) Phenotypic Mismatches Reveal Escape from Arms-Race Coevolution. PLOS Biology 6(3): e60.
https://doi.org/10.1371/journal.pbio.0060060
https://journals.plos.org/plosbiology/article?id=10.1371/journal.pbio.0060060

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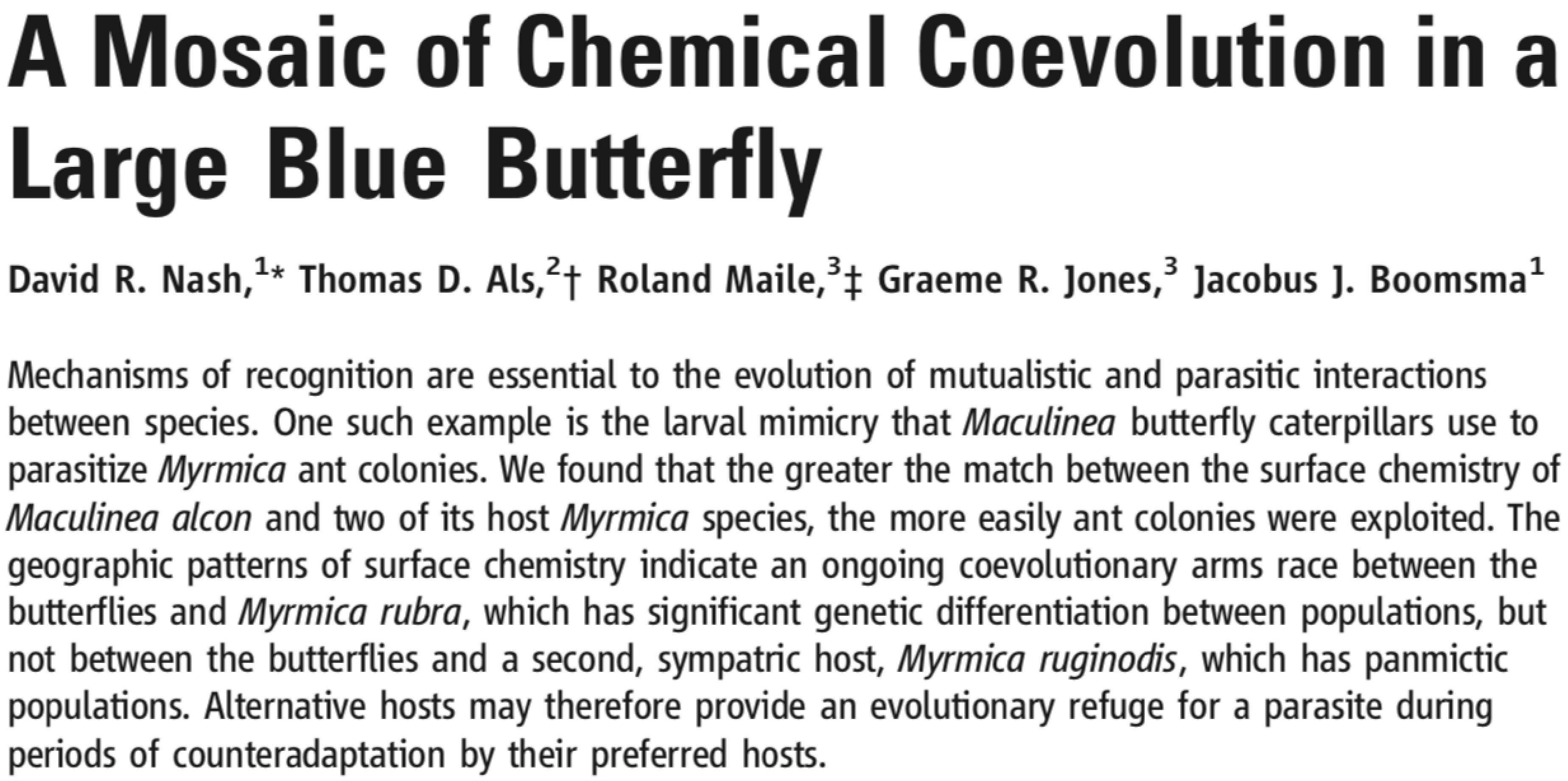


A Mosaic of Chemical Coevolution in a Large Blue Butterfly

David R. Nash,[1]* Thomas D. Als,[2]† Roland Maile,[3]‡ Graeme R. Jones,[3] Jacobus J. Boomsma[1]

Mechanisms of recognition are essential to the evolution of mutualistic and parasitic interactions between species. One such example is the larval mimicry that *Maculinea* butterfly caterpillars use to parasitize *Myrmica* ant colonies. We found that the greater the match between the surface chemistry of *Maculinea alcon* and two of its host *Myrmica* species, the more easily ant colonies were exploited. The geographic patterns of surface chemistry indicate an ongoing coevolutionary arms race between the butterflies and *Myrmica rubra*, which has significant genetic differentiation between populations, but not between the butterflies and a second, sympatric host, *Myrmica ruginodis*, which has panmictic populations. Alternative hosts may therefore provide an evolutionary refuge for a parasite during periods of counteradaptation by their preferred hosts.

The mimicry of caterpillars parasiting in ant nests showing chemical similarity in cuticular hydrocarbons with local ant populations

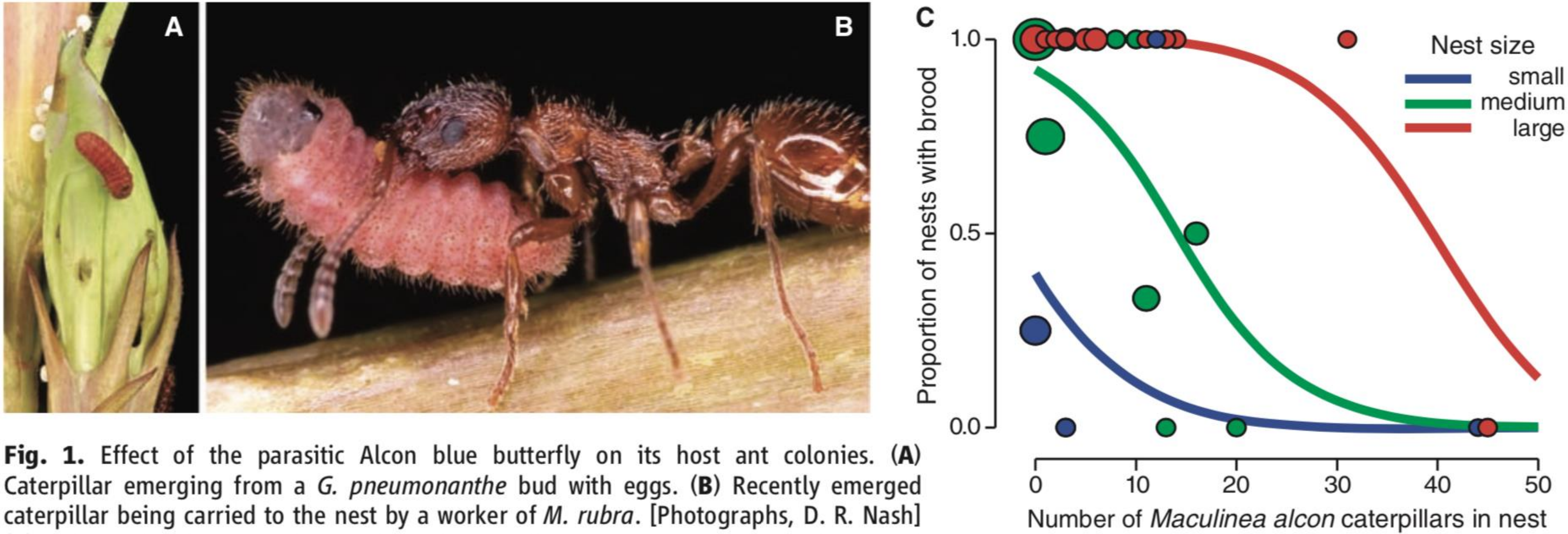


Fig. 1. Effect of the parasitic Alcon blue butterfly on its host ant colonies. (**A**) Caterpillar emerging from a *G. pneumonanthe* bud with eggs. (**B**) Recently emerged caterpillar being carried to the nest by a worker of *M. rubra*. [Photographs, D. R. Nash] (**C**) Relationship between the number of caterpillars present in small, medium, and large *M. rubra* nests (SOM text) in late spring and the probability of ant brood being present. The area of each symbol is proportional to the number of nests observed with that number of caterpillars. Lines are fitted logistic regressions.

The Alcon blue butterfly, Maculinea alcon, is socially parasitic on two species of Myrmica ants in Denmark. The butterfly’s caterpillars initially develop on marsh gentian plants, Gentiana pneumonanthe (Fig. 1A), before being “adopted” by a foraging Myrmica worker (Fig. 1B). Once inside the host ant nest, caterpillars are fed by the ants in preference to their own larvae, reducing host fitness, particularly in small colonies

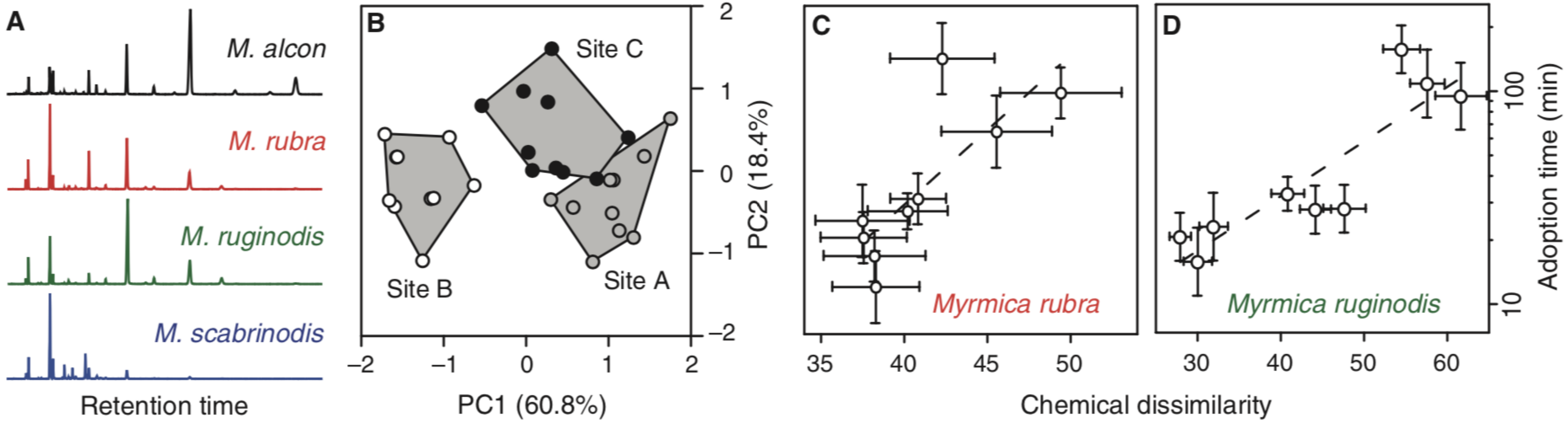
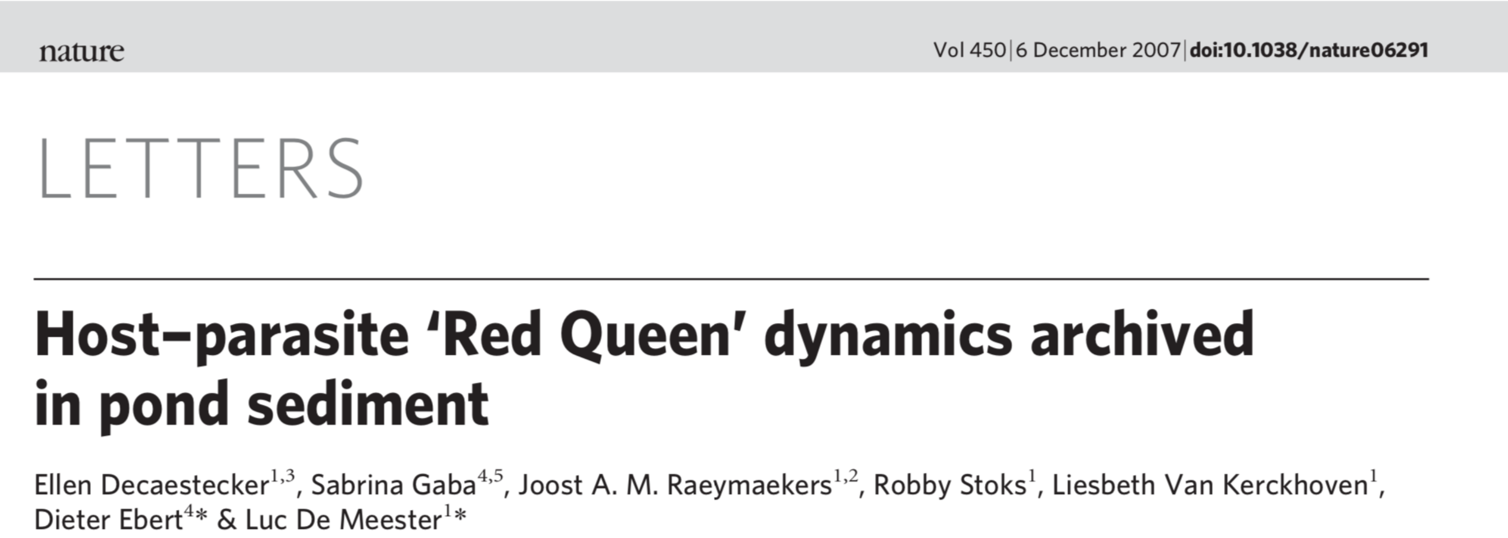


Fig. 2. Chemical mimicry of *Myrmica* ants by Alcon blue caterpillars. (**A**) Representative gas chromatograms for surface extracts of caterpillars of *M. alcon*, larvae of the host ants *M. rubra* and *M. ruginodis*, and larvae of the sympatric nonhost *M. scabrinodis*. (**B**) Ordination plots showing the first two principal components of the chemical profiles of *M. alcon* caterpillars from the three sample sites. Markers show the chemical profiles for individual caterpillars. The data for each study population are enclosed by a minimum convex polygon. (**C** and **D**) Relationship between adoption time (log scale) and dissimilarity in chemical profiles (Mahalanobis distance) between *M. alcon* caterpillars and larvae of *M. rubra* (C) and *M. ruginodis* (D). Each point is the mean ± SE of five observations for each of the nine combinations of butterflies and ants from the three infected sites (*17*). Lines are major axis regressions: for *M. rubra*, $r^2 = 0.62$, $P = 0.011$; for *M. ruginodis*, $r^2 = 0.78$, $P = 0.002$.

When parasites are common enough, selection on hosts to avoid being parasitized fuels coevolutionary arms races, in which parasites evolve better mimicry and hosts improve their recognition of parasites - mutual coadaptation is restricted to sites of intense and lasting interactions (hotspots), whereas parasites and hosts may evolve independently in other populations (coldspots).



nature Vol 450|6 December 2007|doi:10.1038/nature06291

LETTERS

Host–parasite ‘Red Queen’ dynamics archived in pond sediment

Ellen Decaestecker[1,3], Sabrina Gaba[4,5], Joost A. M. Raeymaekers[1,2], Robby Stoks[1], Liesbeth Van Kerckhoven[1],
Dieter Ebert[4]* & Luc De Meester[1]*

Antagonistic interactions between hosts and parasites are a key structuring force in natural populations, driving coevolution[1]

Here we use this fact to reconstruct rapid coevolutionary dynamics in a natural setting and show that the parasite rapidly adapts to its host over a period of only a few years. A coevolutionary model based on ***negative frequency-dependent selection*****, and designed to mimic essential aspects of our host– parasite system, corroborated these experimental results. In line with the idea of continuing host–parasite coevolution, temporal variation in parasite infectivity changed little over time. In contrast, from the moment the parasite was first found in the sediments, we observed a* ***steady increase in virulence over time, associated with higher fitness of the parasite****.*

**fitness decreases as the organism (phenotype) becomes more common*

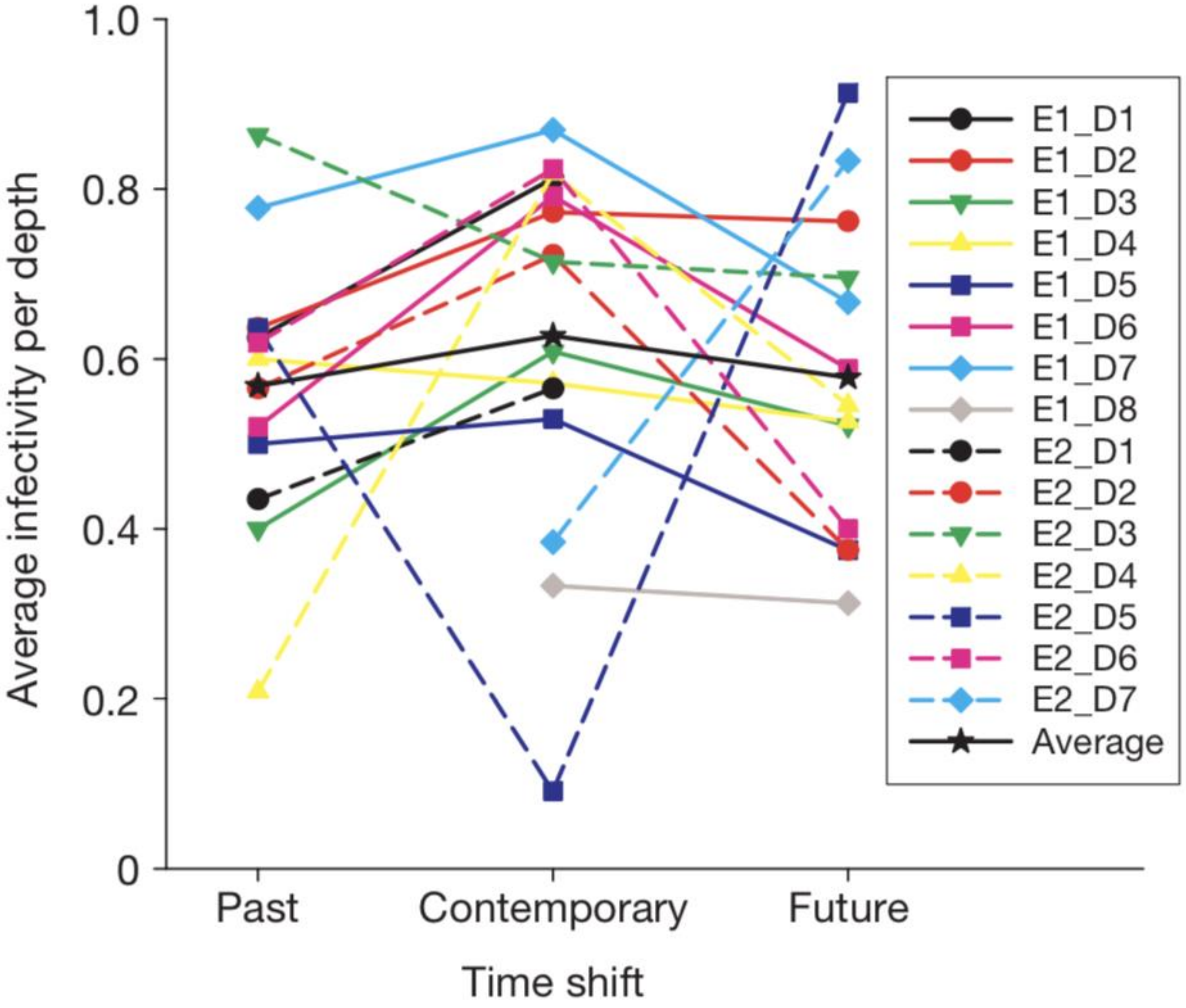


Figure 1 | Experimental results on temporal parasite adaptation. Average proportion of infected hosts when confronted with 'past', 'contemporary' and 'future' parasite isolates. Black stars, mean infectivity.

The oldest layer studied here (deepest depth 24 cm, a maximum of about 39 years old) represents the first time that both D. magna and P. ramosa co-occurred in this pond[18]*. In two cross-infection experiments, we exposed Daphnia clones from eight (experiment 1) or seven (experiment 2) depths to parasite isolates from the next layer down, the same layer and the next layer up. Thus, the host was exposed to 'past', 'contemporary' and 'future' parasite isolates (further referred to as a time shift of parasites relative to host populations).*

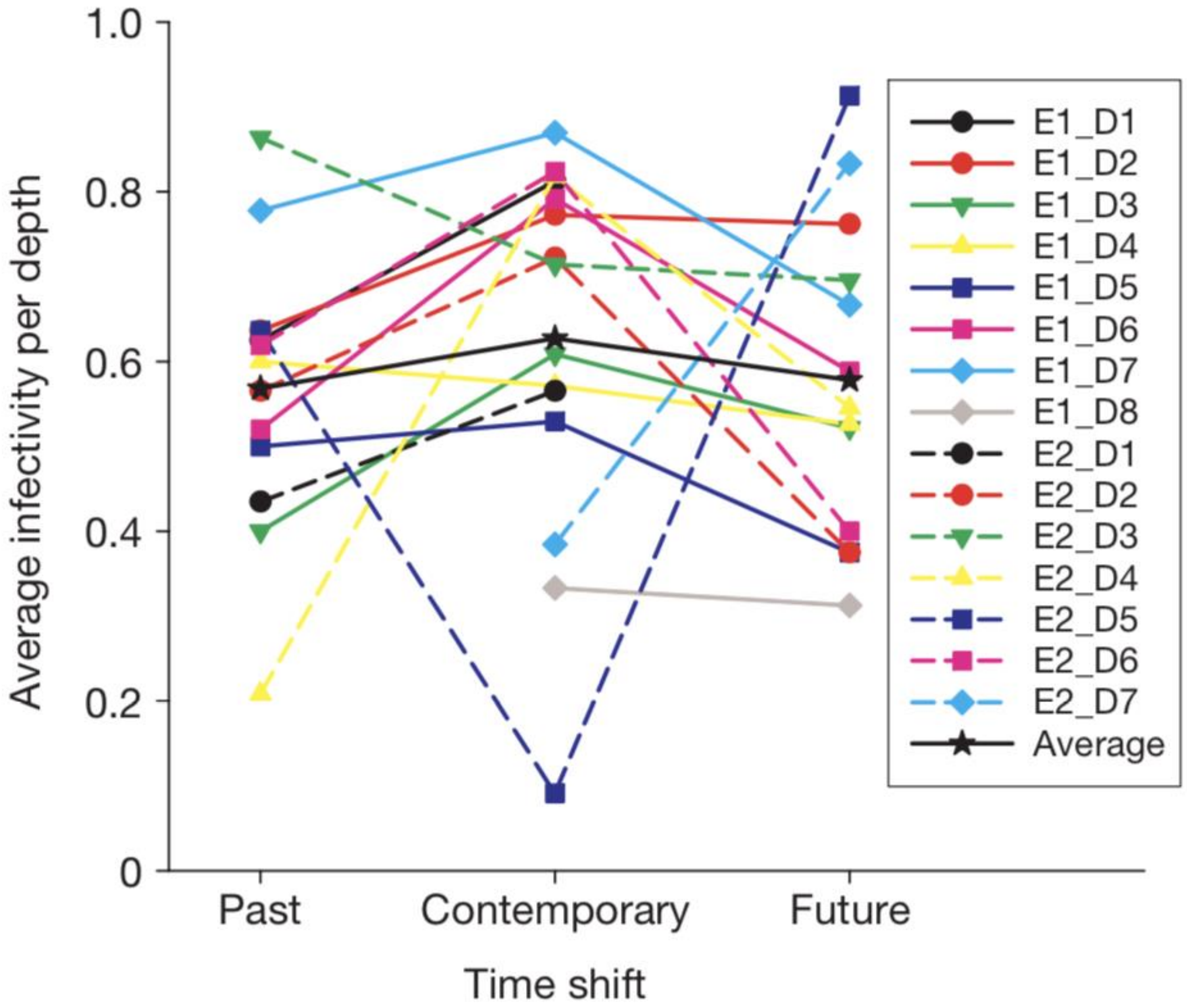


Figure 1 | Experimental results on temporal parasite adaptation. Average proportion of infected hosts when confronted with 'past', 'contemporary' and 'future' parasite isolates. Black stars, mean infectivity.

*On average, **infectivity was higher when Daphnia were exposed to contemporary** (average infectivity 0.65) parasites than to parasites from previous (average infectivity 0.55) growing seasons (Fig. 1). However, **parasite adaptation was quickly lost, because average parasite infectivity was lower when Daphnia clones were confronted with future parasites** (average infectivity 0.57) than with contemporary parasites (Fig. 1).*

The increase in spore production and virulence in Pasteuria over time (but not its infectivity) may reflect adaptation of the parasite to the host.