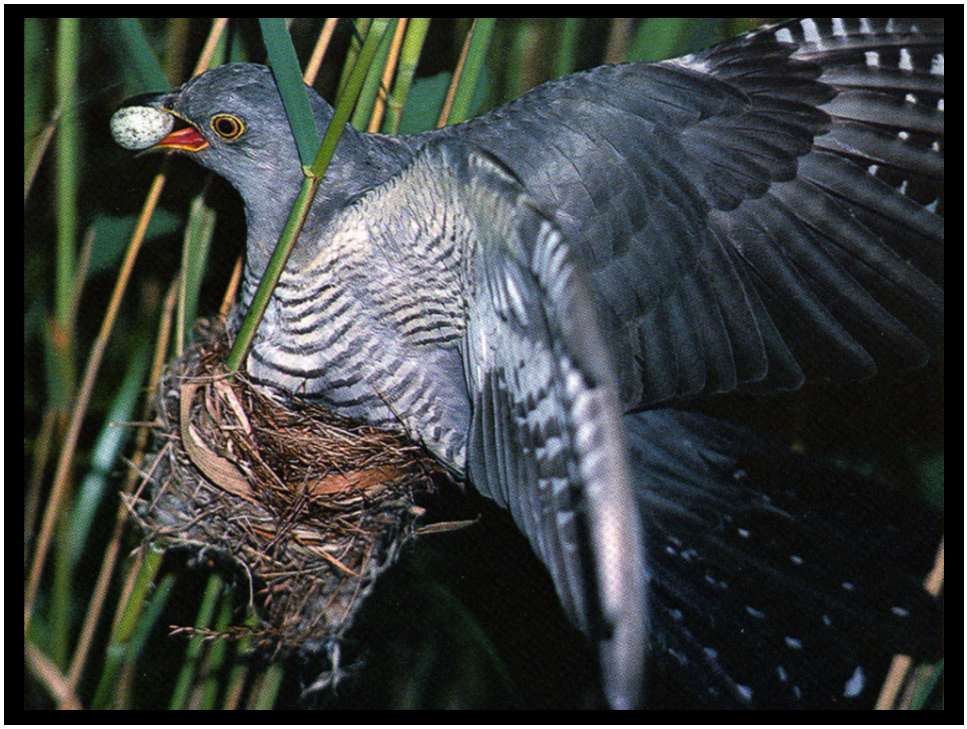
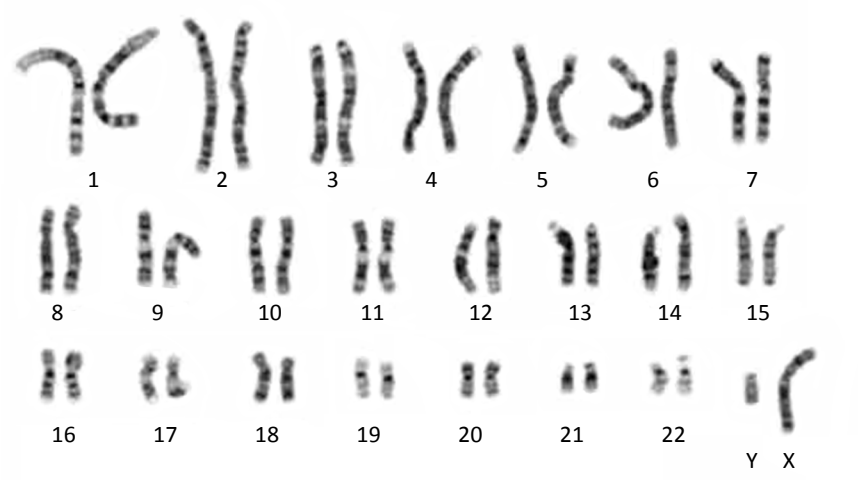
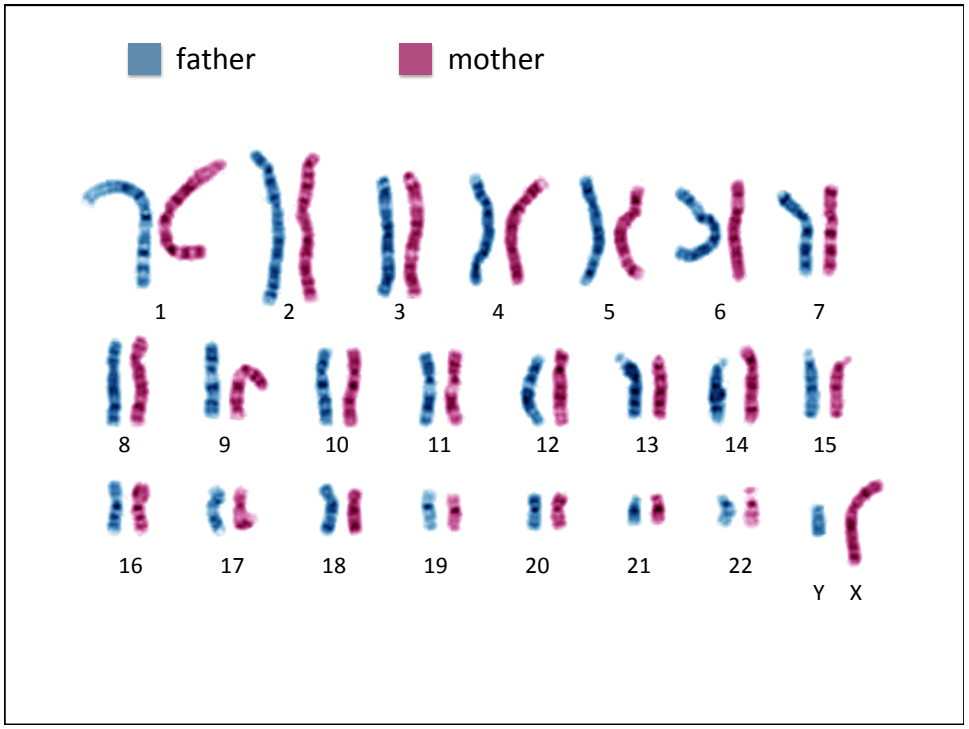


Brooke & Davies,
Nature 1989




father
mother
1
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Y
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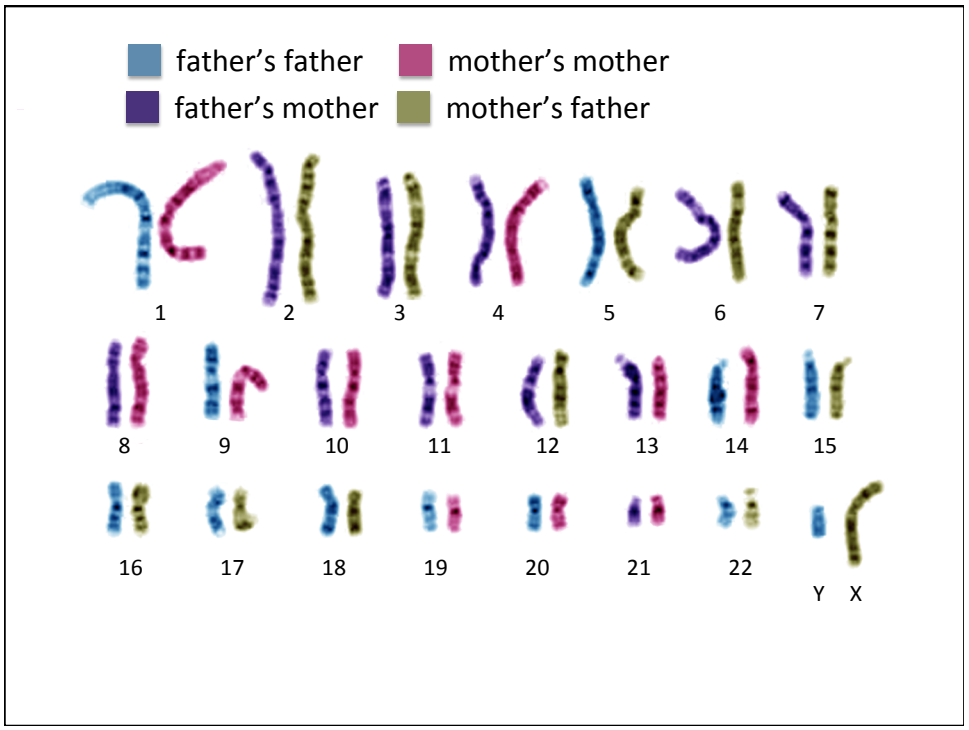
father's father
mother's mother
father's mother
mother's father
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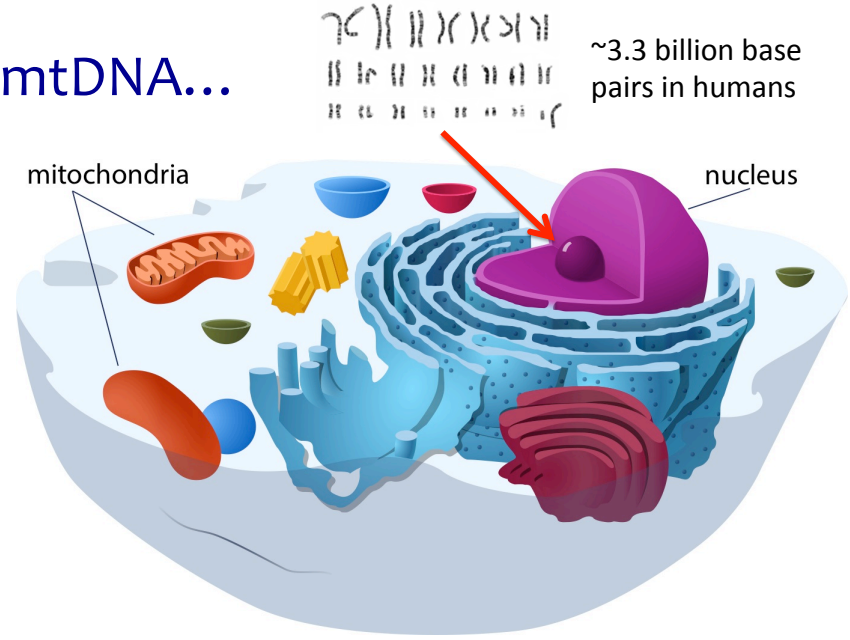
X

mtDNA...



mtDNA...

Mitochondrial DNA (mtDNA)

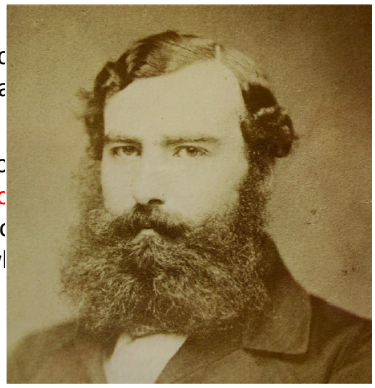
- ~17,000 base pairs in animals
- 13 protein-coding genes,2 rRNA genes, 22 transfer RNAs
- abundant in muscle or liver tissue, easy to amplify and sequenc
- **maternally inherited**
  - provides a record of matrilineal history
- an easy and, in most cases, highly informative *first look* at the history of species and speciation
  - relatively fast (1% per million years), "clock-like" evolution provides an approximate evolutionary timescale

How are multiple host-races (gentes) maintained within a single parasitic species?

Alfred Newton (1869) Cuckow's eggs. Nature 1: 74–76.
agreed with Baldamus (1853) that cuckoo eggs are similar in size and color to those of their hosts to minimize the likelihood of detection and went on to suggest that egg color was inherited and evolved via natural selection!

William Pycraft (1910, The History of Birds)
"A most serious objection, however, … is the c
Cuckoos' must frequently mate with male 'Wa

Reginald Punnett (1933, Nature)
"There is, however, another possibility… allelc
pattern in the Y –chromosome [= W chromosc
hypothesis every daughter of a hen cuckoo wc
character of the eggs laid by her, no matter wl

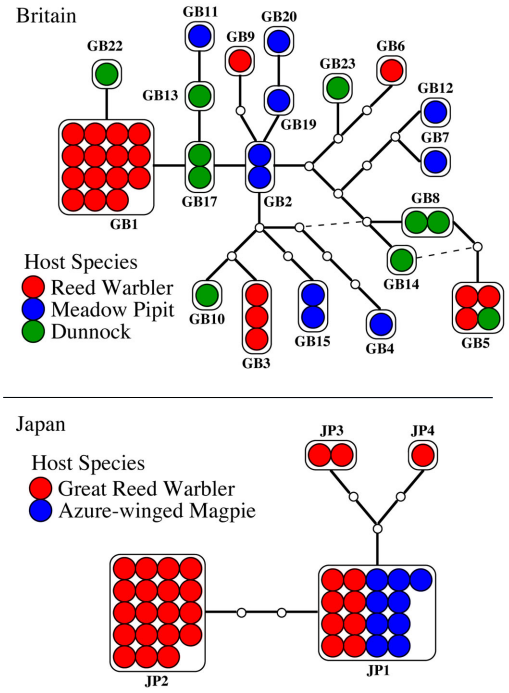


How are multiple host-races (gentes) maintained within a single parasitic species?

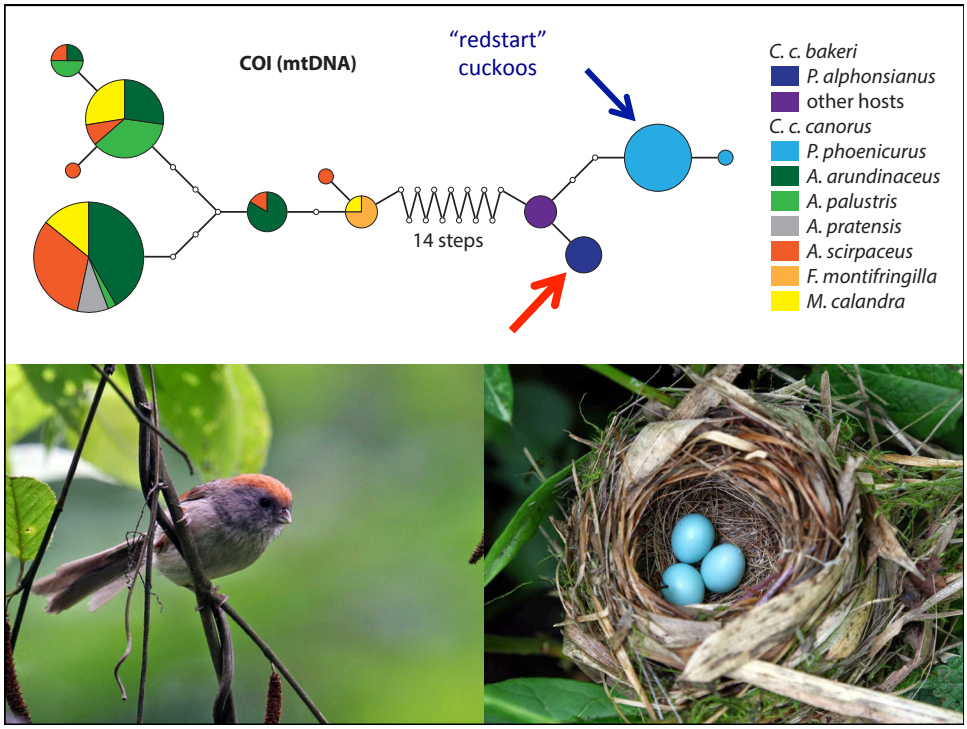
- "W-chromosome hypothesis" (maternal inheritance of egg traits)
  - in birds, females are ZW, males are ZZ
  - W has same genealogy/history as mtDNA
- adaptive divergence w/ gene flow
  - requires at least partial isolation of host races
- both hypotheses compatible with behavioral imprinting on host

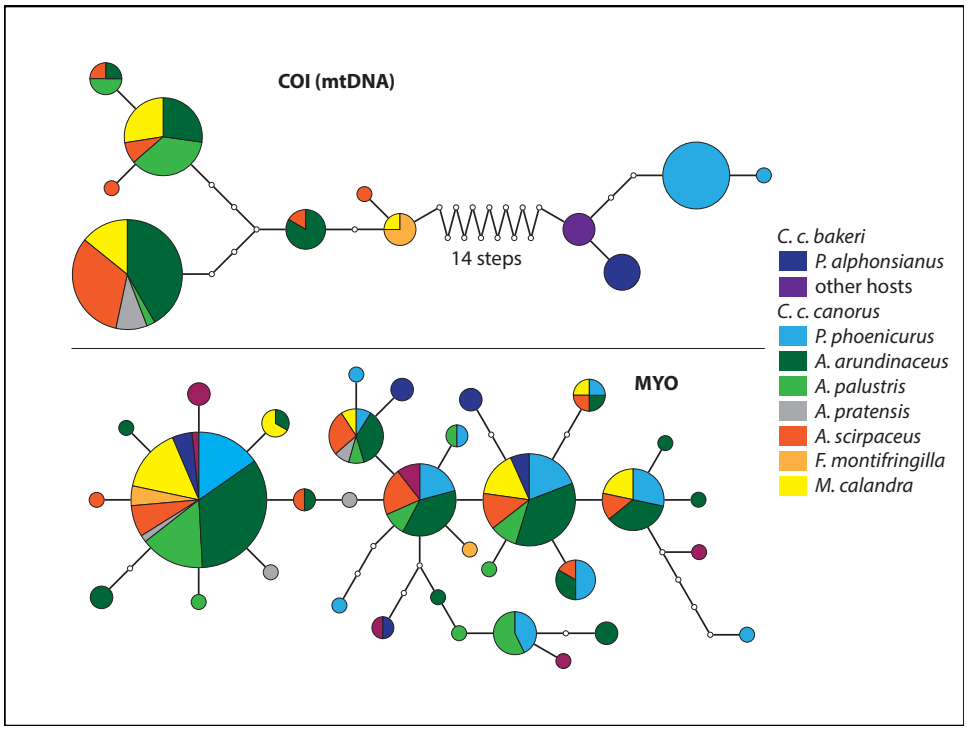
Network of common cuckoo (Cuculus canorus) mtDNA haplotypes

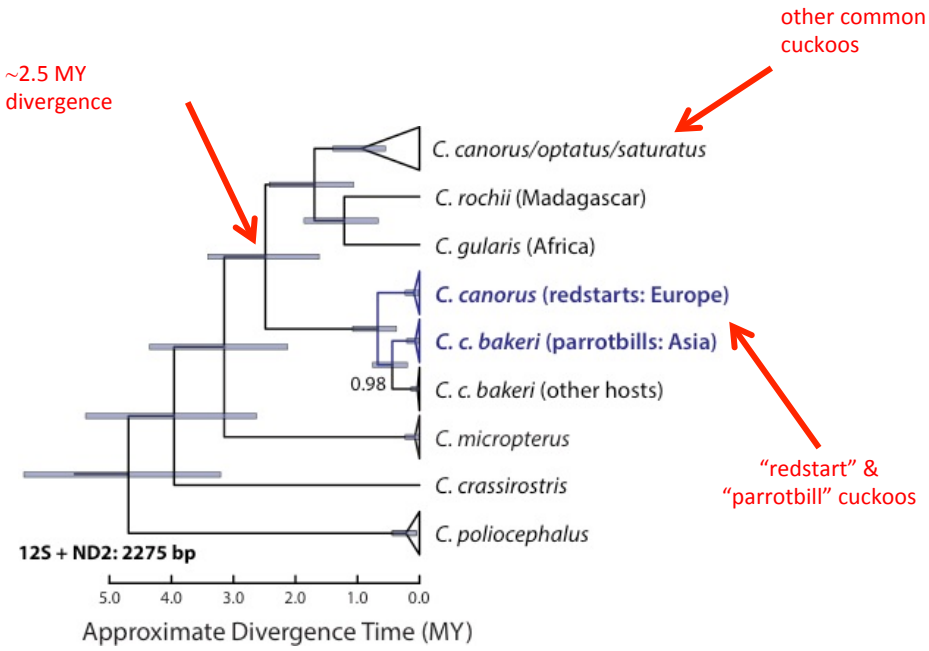
- significant differentiation in mtDNA haplotype frequencies among host races (F_{ST} = 0.18, p < 0.001)
- no significant differentiation in nuclear (bi-parentally inherited) microsatellites



Gibbs *et al.* 2000 *Nature*

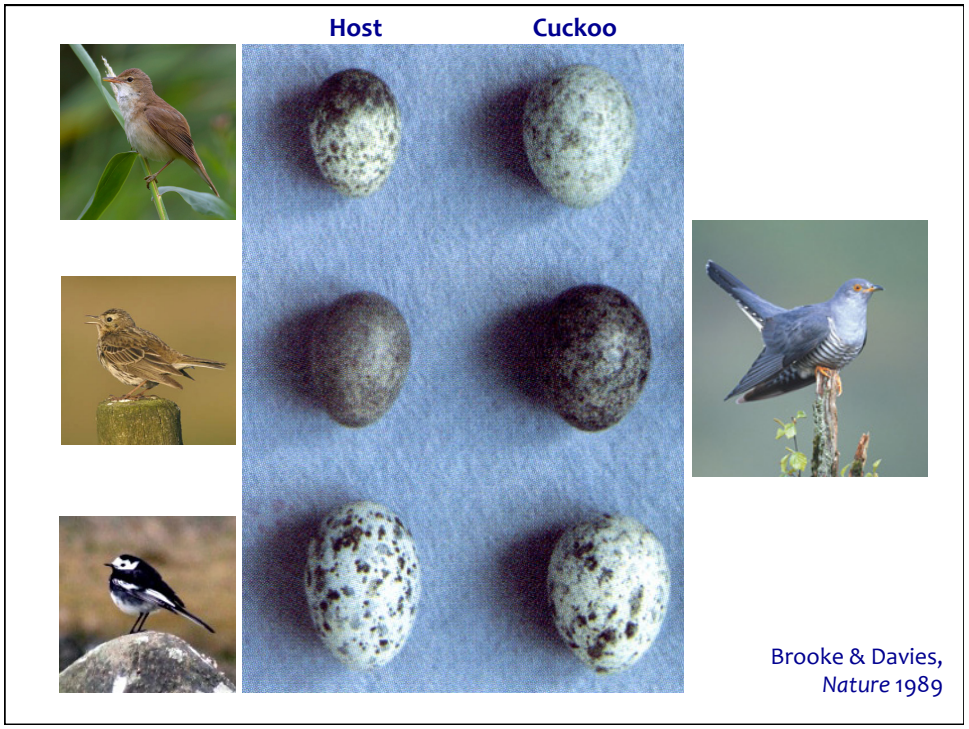

COI (mtDNA)
"redstart" cuckoos
14 steps
C. c. bakeri
P. alphonsianus
other hosts
C. c. canorus
P. phoenicurus
A. arundinaceus
A. palustris
A. pratensis
A. scirpaceus
F. montifringilla
M. calandra


COI (mtDNA)
14 steps
MYO
C. c. bakeri
P. alphonsianus
other hosts
C. c. canorus
P. phoenicurus
A. arundinaceus
A. palustris
A. pratensis
A. scirpaceus
F. montifringilla
M. calandra



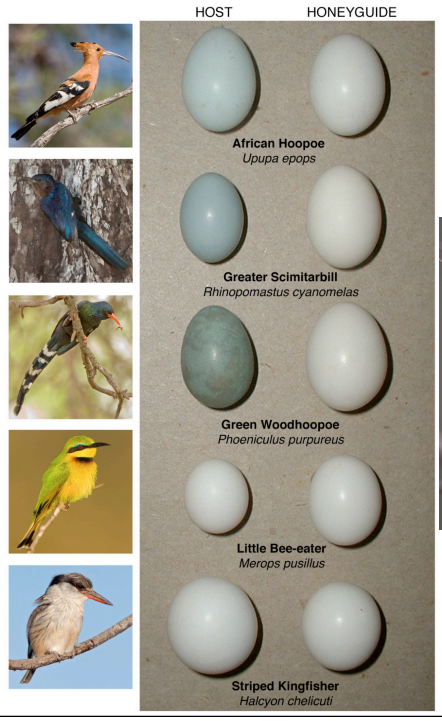
Cuckoo Conclusions

- female common cuckoos laying blue eggs belong to an ancient matriline, but are indistinguishable from other European cuckoos at nuclear loci
- the perfect association between mtDNA (maternal lineage) and blue eggs provides strong evidence that this trait is maternally inherited (W-chromosome)
- the blue egg matriline most likely originated in Asia, after which it expanded westwards as females laying blue eggs interbred with the existing European population, introducing an adaptive trait that expanded the range of potential hosts


Host
Cuckoo
Brooke & Davies,
Nature 1989


Claire Spottiswoode

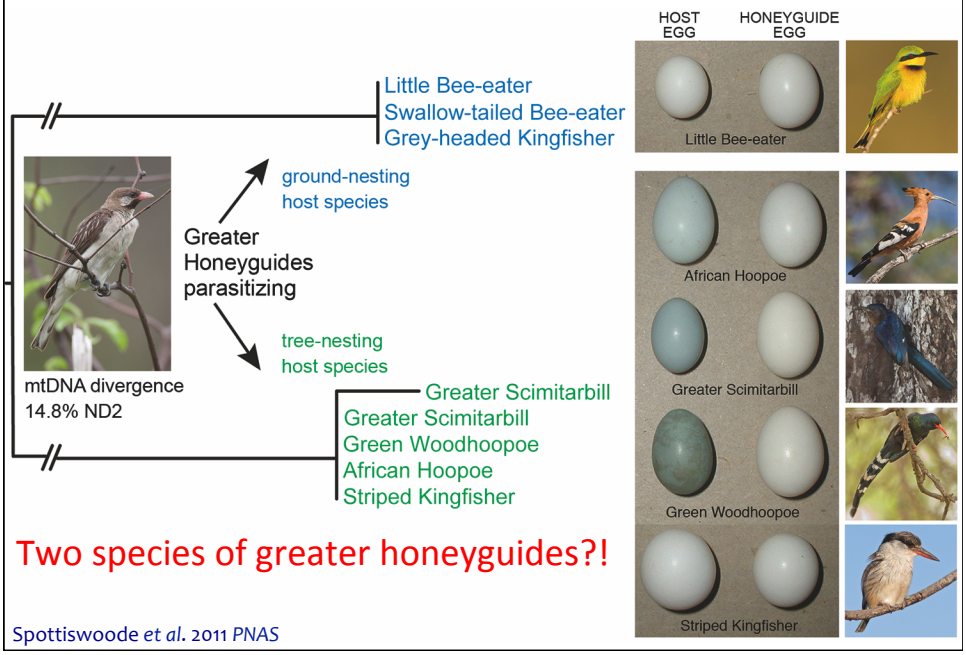
Figure 1. (*a*) Hatching lesser honeyguide, showing fully developed bill hooks; (*b*) greater honeyguide chick with three recently killed little bee-eater hatchlings; (*c*) biting human hand; (*d*) biting unhatched swallow-tailed bee-eater egg; (*e*) aged about 8 days. All photos are from different nests.



Significant host-specific variation in greater honeyguide eggs

Spottiswoode *et al.* 2011 *PNAS*

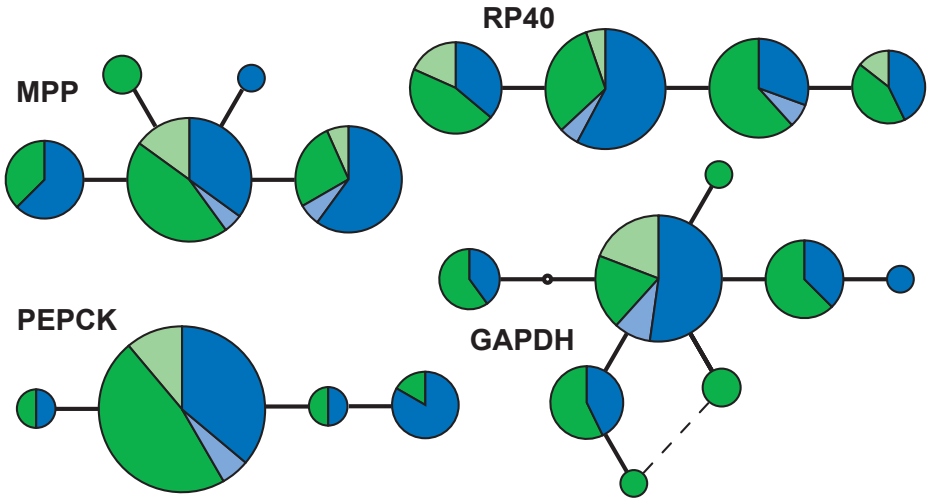
Greater Honeyguide (Indicator indicator) mtDNA phylogeny



Two species of greater honeyguides?!

Spottiswoode *et al*. 2011 *PNAS*

No evidence of differentiation at nuclear loci!



Haplotype networks for greater honeyguides colored by host species. **Blue** = Little Bee-Eater; **green** = African Hoopoe, Common Scimitarbill, Green Wood Hoopoe, or Striped Kingfisher; lighter blue and green from Ghana in West Africa

Spottiswoode *et al*. 2011 *PNAS*

Honeyguide Conclusions

- taken at face value, our data suggest:
  - greater honeyguide matrilines have remained faithful to ground- and tree-nesting hosts, respectively, over the course of **millions** of years
  - mating of male and female greater honeyguides is **not** assortative with respect to host species
  - the small eggs of "bee-eater" honeyguides may be maternally inherited

Cuckoo finch
Anomalospiza imberbis

Tawny-flanked Prinia Cuckoo Finch

Spottiswoode & Stevens, *PNAS* 2010

Eggs of cuckoo finches and two common hosts in Zambia

Host Parasite

Red-faced Cisticola

Tawny-flanked Prinia

Divergent mtDNA lineages in cuckoo finch!

**Data for cuckoo finch eggs/chicks in nests of different host species

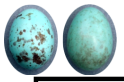
Prinia subflava
(*n* = 21 chicks from 14 nests)

Prinia subflava
(*n* = 8 chicks from 6 nests)

Prinia subflava
(*n* = 1 chick from 1 nest)

Prinia subflava
(*n* = 3 chicks from 3 nests)

9 % ND2 sequence divergence



Cisticola erythrops
(*n* = 10 chicks from 7 nests)

Cisticola erythrops
(*n* = 7 chicks from 4 nests)

Cisticola natalensis
(*n* = 2 chicks from 2 nests)

Cuckoo finches belonging to different mtDNA lineages (matrilines) lay eggs of different color

"red"
(Prinia subflava)

"blue"
(Prinia subflava)

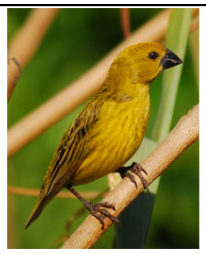
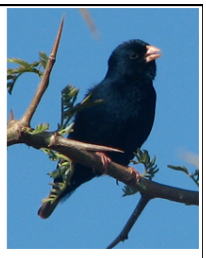
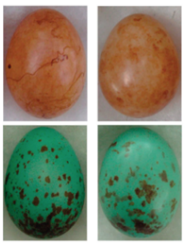
9 % ND2 sequence divergence

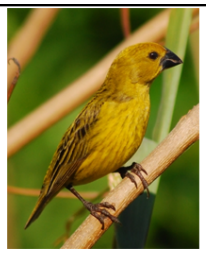
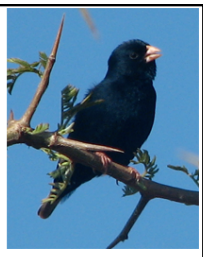
"bright"
(Cisticola erythrops)

"dull"
(Cisticola erythrops)

(Cisticola juncidus)

Cisticola natalensis

				
	Common Cuckoo	**Greater Honeyguide**	**Cuckoo Finch**	**Indigobirds**
	Cuculus canorus	***Indicator indicator***	***Anamalospiza imberbis***	***Vidua* spp.**
host-specific adaptation	egg color and pattern	egg size and shape	egg color and pattern	nestling mouth markings
				

				
	Common Cuckoo	**Greater Honeyguide**	**Cuckoo Finch**	**Indigobirds**
	Cuculus canorus	***Indicator indicator***	***Anamalospiza imberbis***	***Vidua* spp.**
host-specific adaptation	egg color and pattern	egg size and shape	egg color and pattern	nestling mouth markings
mechanism of host-specificity	host/habitat imprinting?			imprinting on host song
mechanism of assortative mating	none?			song mimicry
mtDNA/nuclear differentiation	deeply divergent lineages / little or none			significant / variable but significant
genetics of adaptation	maternal inheritance (W-chromosome) (?)			divergence w/ gene flow

What's different about indigobirds?

- in contrast to common cuckoos, greater honeyguides and cuckoo finches, host switches lead to speciation in indigobirds because **both** females and males imprint on their hosts
- maternal inheritance of egg mimicry "works" because only females lay eggs, but mouth markings are expressed in both male and female chicks, and so must be bi-parentally inherited