Animal Behaviour Lecture: Proximate mechanisms

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Proximate mechanisms: structure of lecture

- Definition and note of caution
- Proximate mechanisms can go wrong
- Brain evolution in vertebrates and social decision making network
- Hormonal governing of behaviour: vasopressin and prolactin
- Input: how to read a scientific paper in 5 min?
- Genes and variation in behaviour: mating, migration and bird song
- Variation in dispersal timing
- Cuckoos and other cheats
- Summary

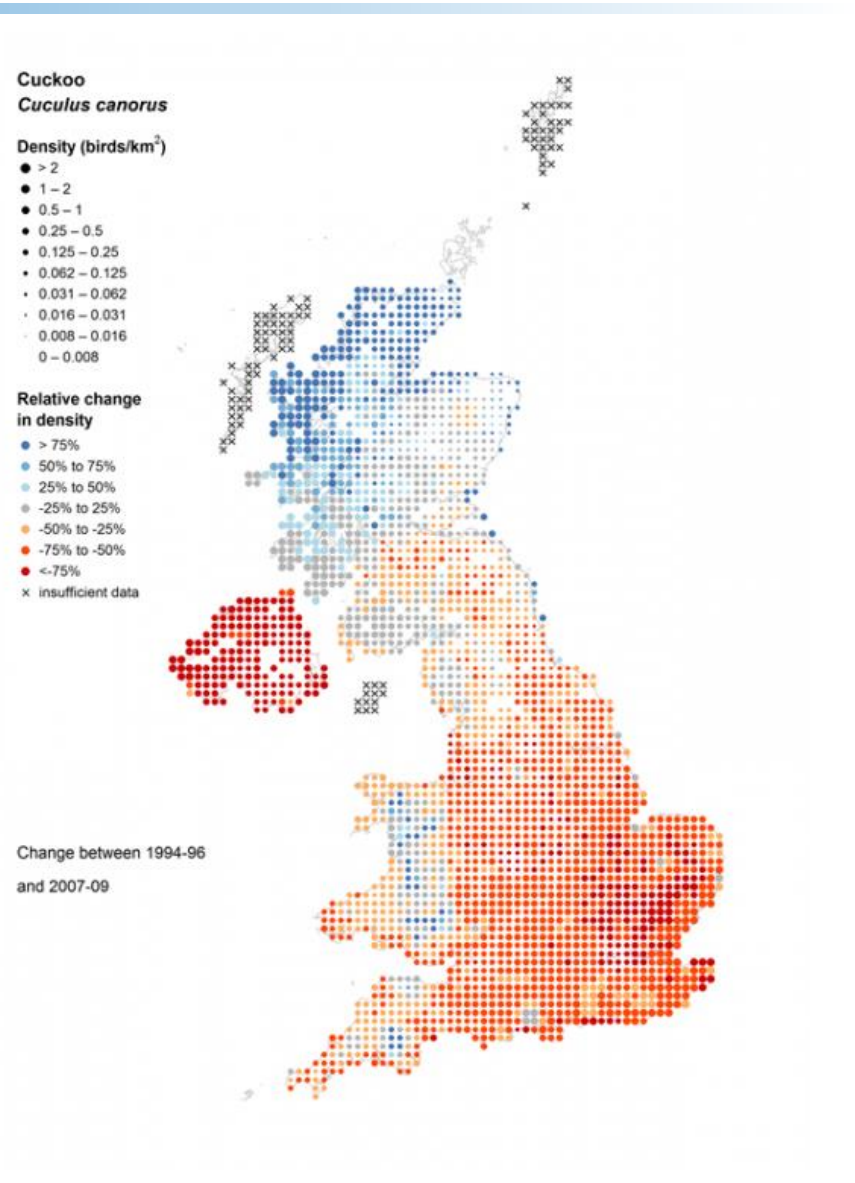
Definition of proximate

- Proximate = causal mechanism underlying behaviours
- Brain: central engine
- Hormones: govern behaviours, linking neural activity to rest of the system
- Pheromones: secreted/excreted chemical that affects behaviours of others

- Keep in mind, I am not a endocrinologist or neurobiologist

Proximate mechanisms: useful, but can go wrong

Proximate mechanisms: useful, but can go wrong



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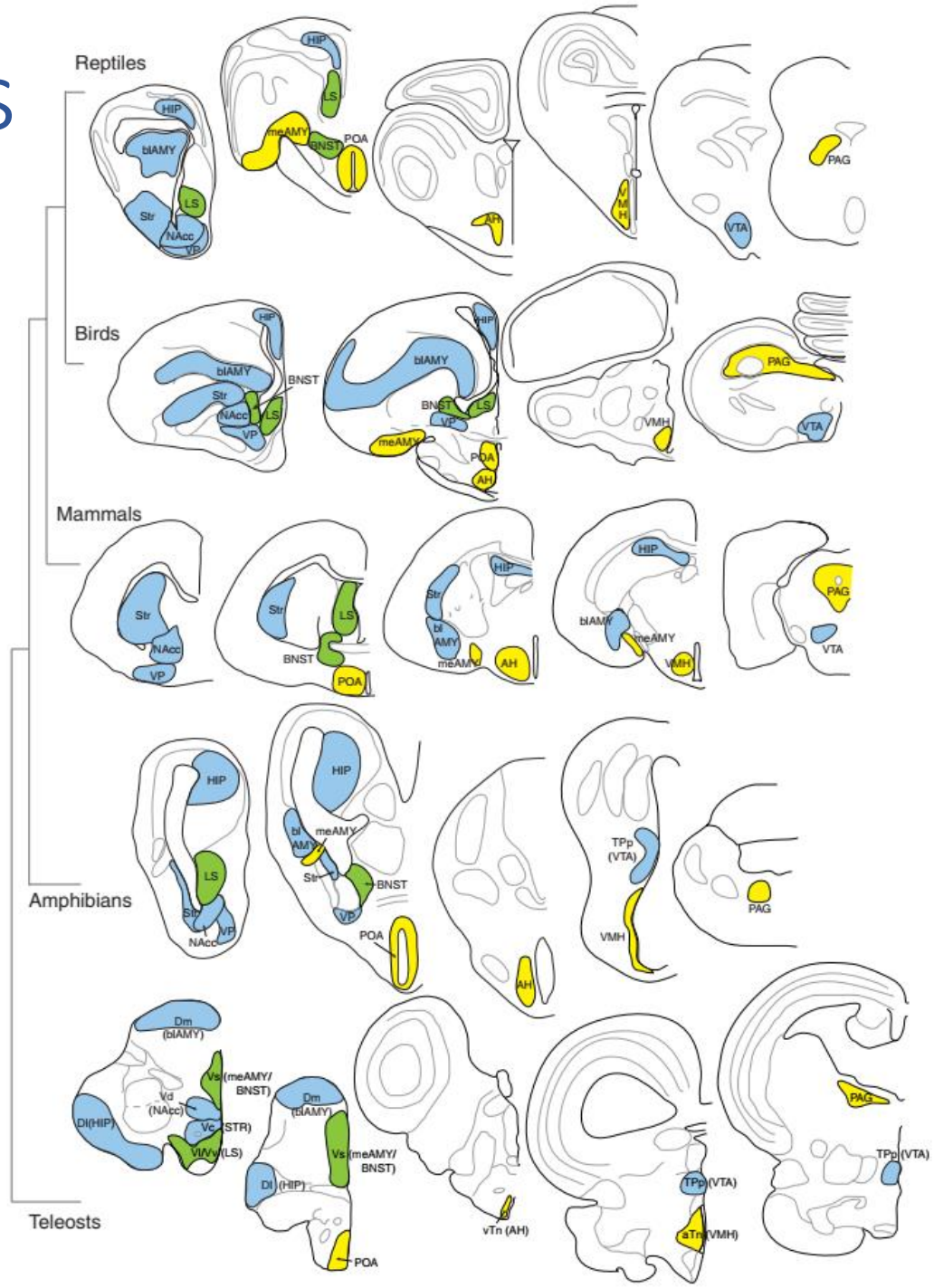
Phylogeny of key brain elements

- Neural basis of behavioural diversity
- Blue: mesolimbic reward system
- Yellow: social behaviour network
- These systems have the same roots in vertebrates
- Structural and functional similarities, including the hormones



O'Connell and Hofman 2012

Phylogeny of key hormones

- Given the shared social behaviour network, animals share the same/similar set of hormones that have similar, but at times different functions

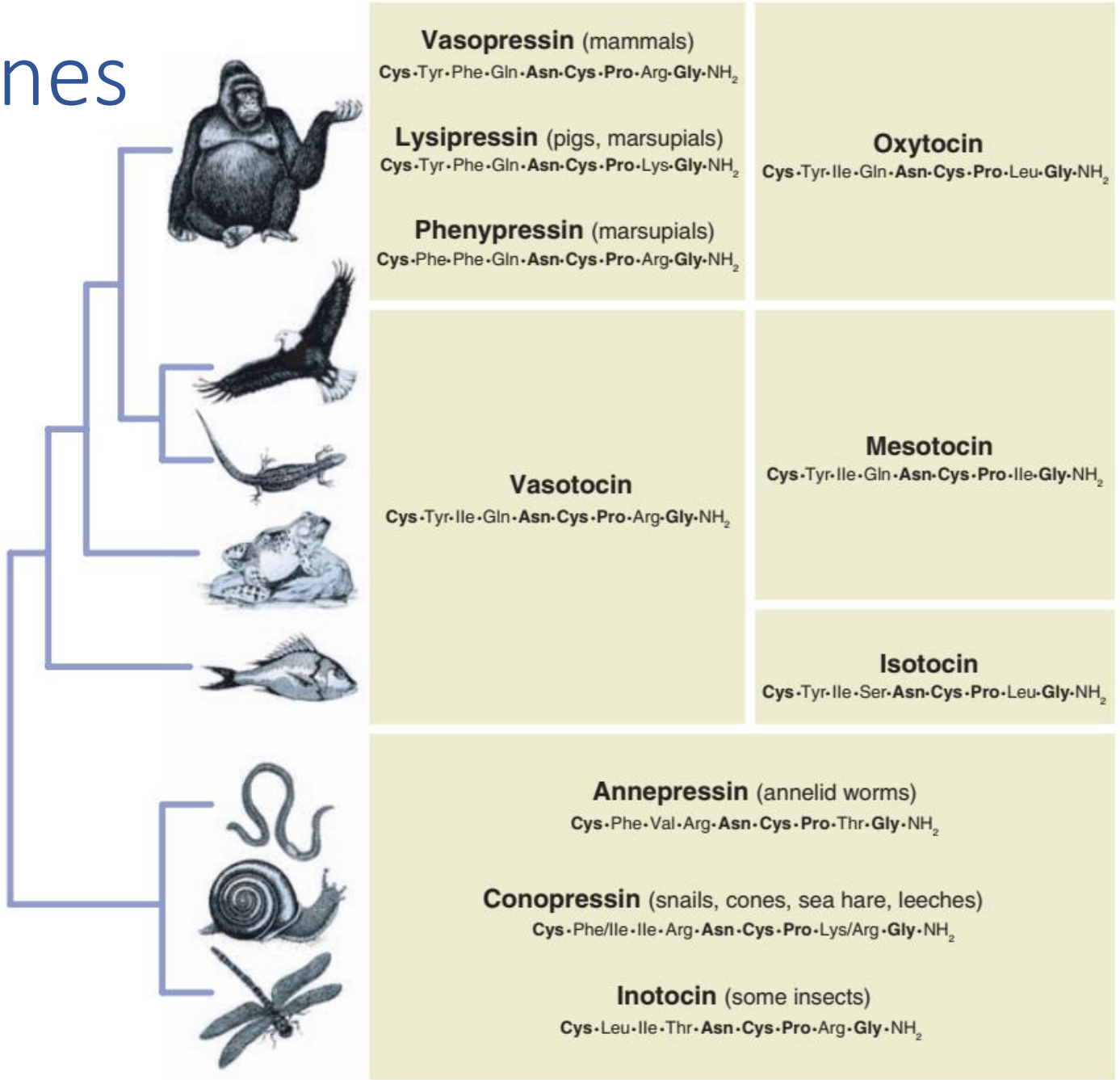
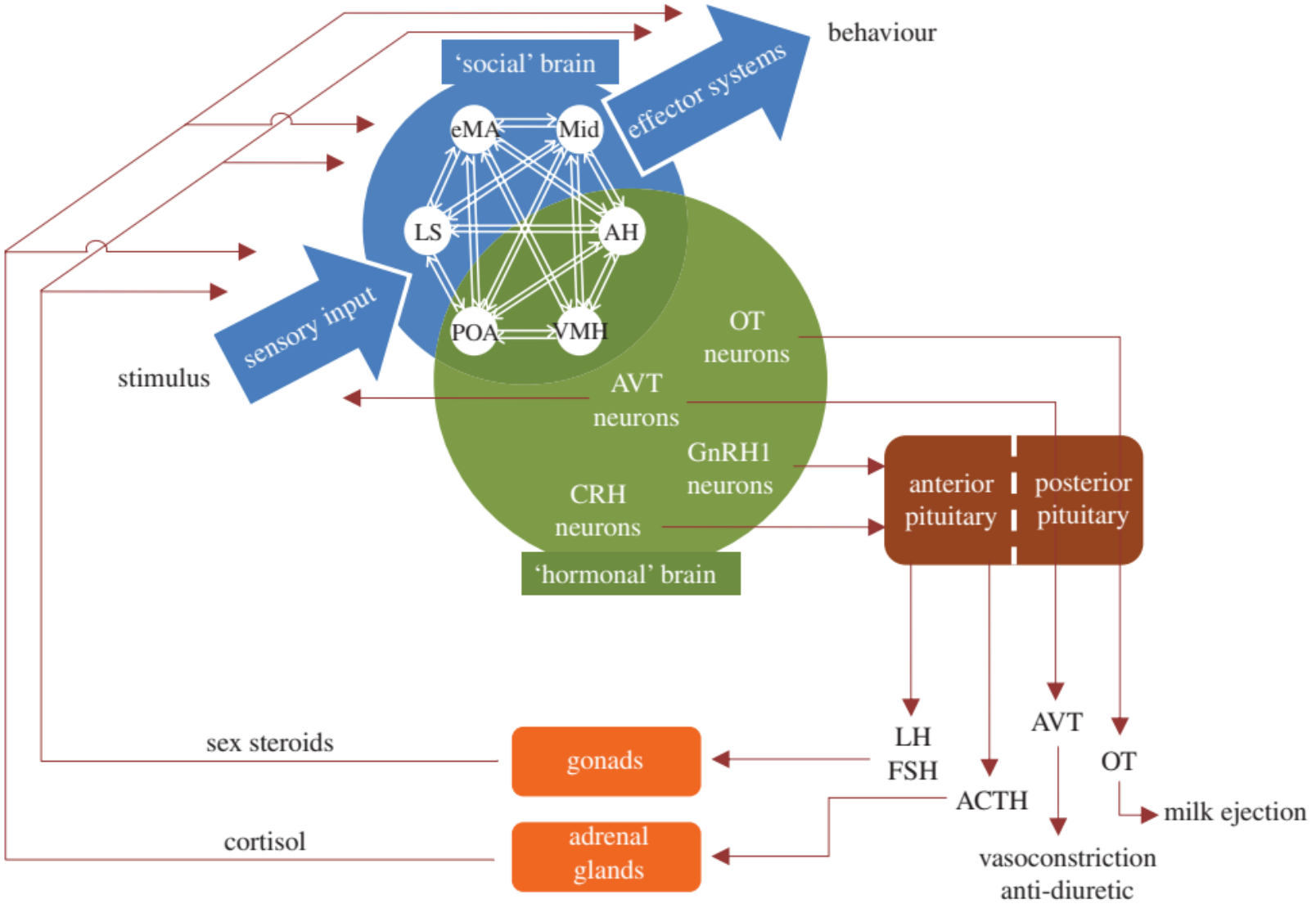


Fig. 1. Oxytocin and vasopressin homologs.

Donaldson and Young 2008

Social behaviour network is critical for behaviour

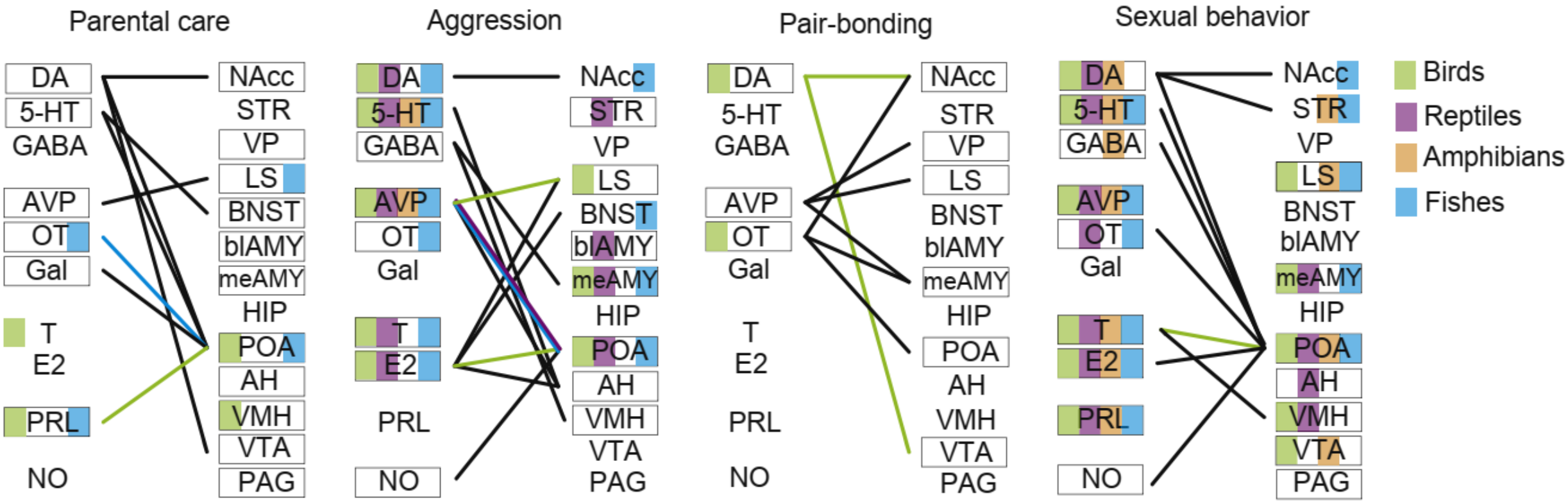
- Social behaviour networks (blue) links to hormonal brain (green) takes different states, depending on the behaviour
- Neurohormones (AVT: vasotocin; OT oxytocin) modulate other hormones and thereby the expressed behaviour



Soares et al 2010

Social behaviour network is critical for behaviour

Neural patterns of key behaviours, showing relationship between neurochemicals and brain regions in different lineages



Weitekamp and Hofmann 2017

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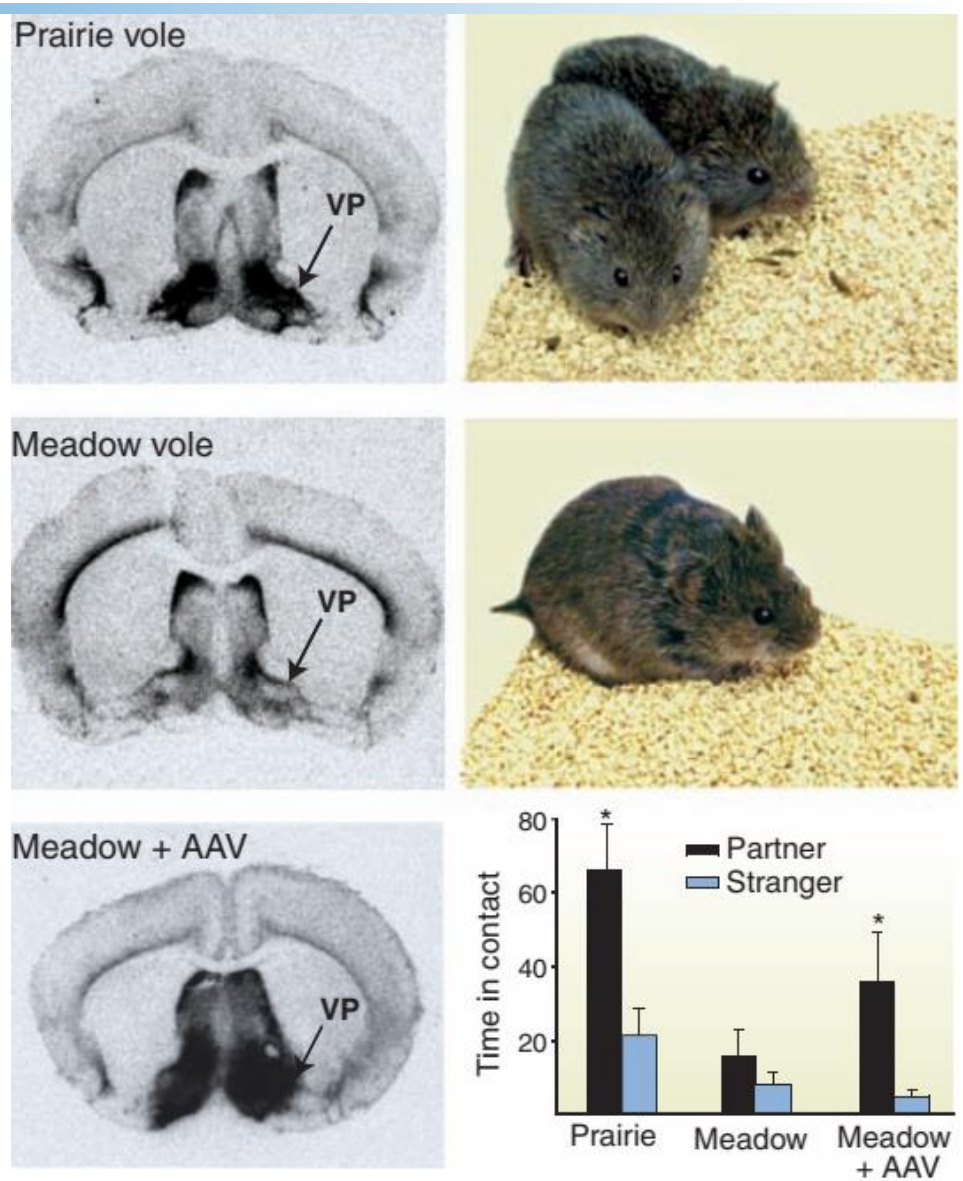
Vasopressin receptor matters for social behaviour

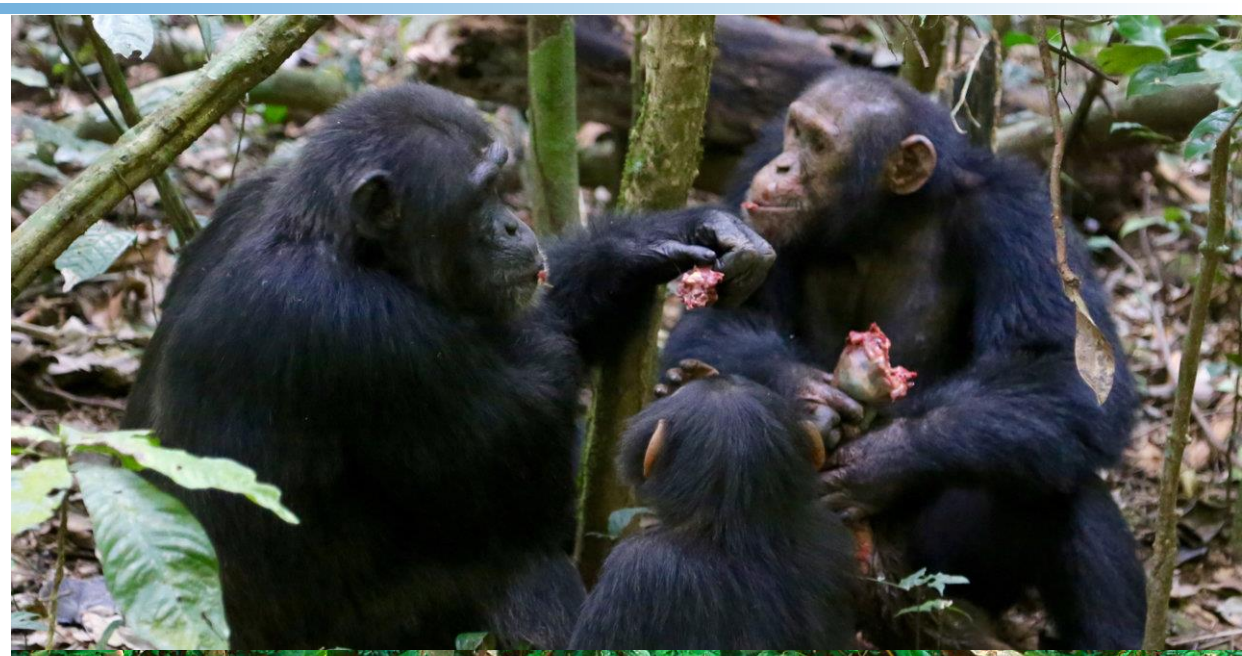
- Close related north American voles differ in their mating system
- Prairie voles are monogamous
- Meadow voles are polygamous
- Species differ in vasopressin receptor density
- Increasing the numbers of VP receptor in meadow voles make them to behave like prairie voles



Donaldson and Young 2008

Vasopressin receptor matters for social behaviour

- Chimps vary in a gene promotor region of the vasopressin gene
- DupB +/+ alleles lead to increased levels of vasopressin receptors
- Chimps with DupB +/+ are more sociable, especially males
- The more sociable bonobo has only the DupB +/+ phenotype

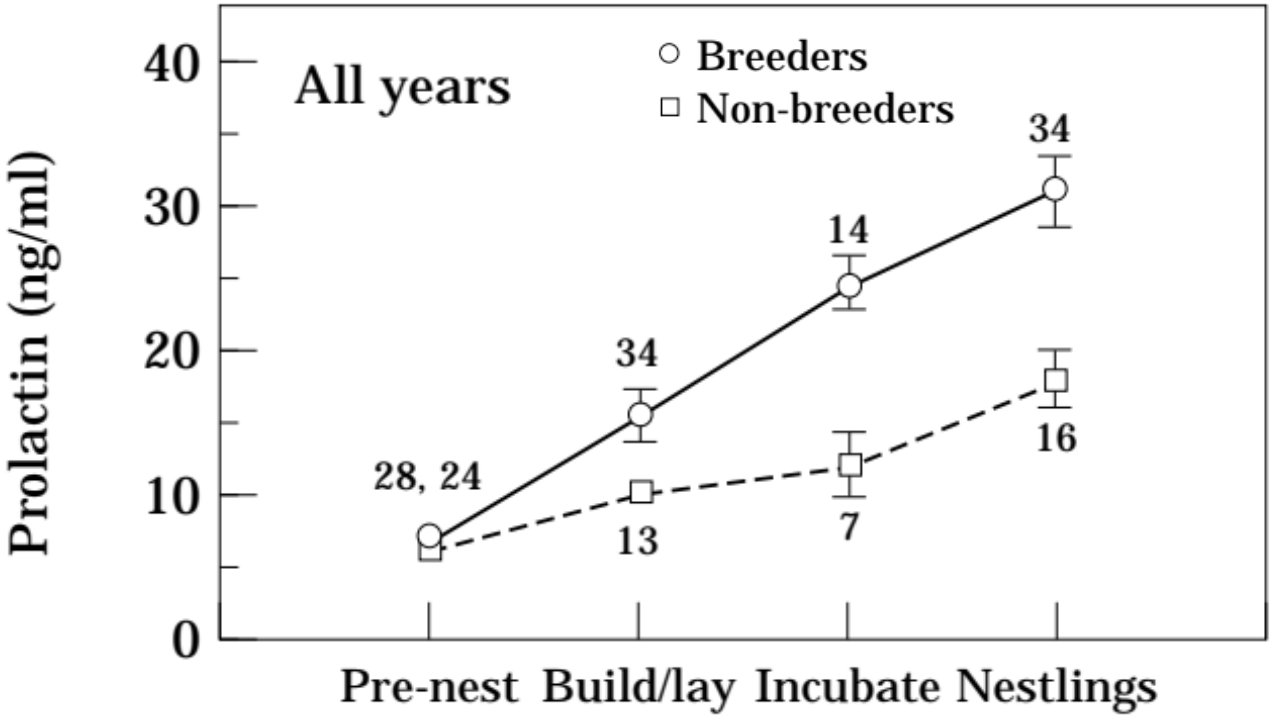


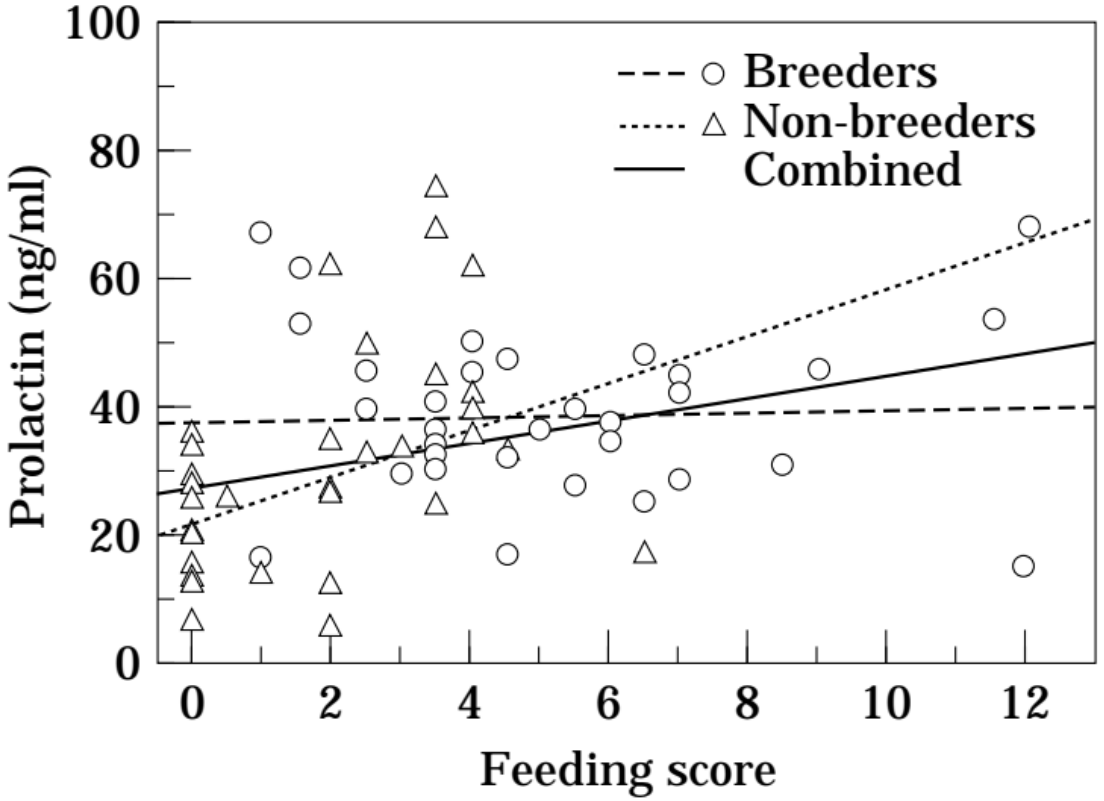
Prolactin, a parenting hormone

- Florida scrub jays are cooperative breeders where offspring remain with the parents and help raising younger siblings
- Which mechanism underlies cooperative breeding?

Prolactin, a parenting hormone

Prolactin increases during breeding season, and is associated with feeding, also in non-parents





Schoech et al 1996

Prolactin, a parenting hormone

- Meerkats are one of the few cooperative-ely breeding mammals
- Alfa females suppress reproduction of other group members
- Other group members help with offspring care, e.g. babysitting or feeding them

Input: how to read a paper in 5min?

- Scientific papers are a key means to communicate findings
- They have a very specific format
- Understanding this structure allows you do get quickly informed
- Key elements are:
  - Title
  - Abstract
  - Figure and tables

Input: how to read a paper in 5min?

Elevated prolactin levels immediately precede decisions to babysit by male meerkat helpers

Carlson et al 2006 Hormones and Behavior

Recent studies suggest that decisions to care for the offspring of others in societies of cooperative vertebrates may have a hormonal basis. The crucial question of whether changes in hormone levels immediately precede or merely follow bouts of offspring care, however, remains largely unanswered. Here, we show that in wild groups of cooperatively breeding meerkats, male helpers that decided to babysit for the day had significantly higher levels of prolactin, coupled with lower levels of cortisol, before initiating a babysitting session compared with similarly aged individuals that decided to forage. In addition, these hormonal differences disappeared over the course of the day, suggesting that hormone levels changed in a fundamentally different way in meerkats that babysat versus those that foraged. In contrast, long-term contributions to babysitting were not significantly associated with plasma levels of prolactin, cortisol, or testosterone in individual male helpers. Our results show, for the first time, that elevated levels of prolactin may immediately precede bouts of helping behavior but differ from recent findings on the same study population in which plasma levels of cortisol, but not prolactin, were significantly and positively associated with rates of pup feeding by male helpers. Together, these results lend significant weight to the idea that decisions to help in cooperative vertebrates have a hormonal basis, although different hormones appear to be associated with different types of care.

Input: how to read a paper in 5min?

Elevated prolactin levels immediately precede decisions to babysit by male meerkat helpers

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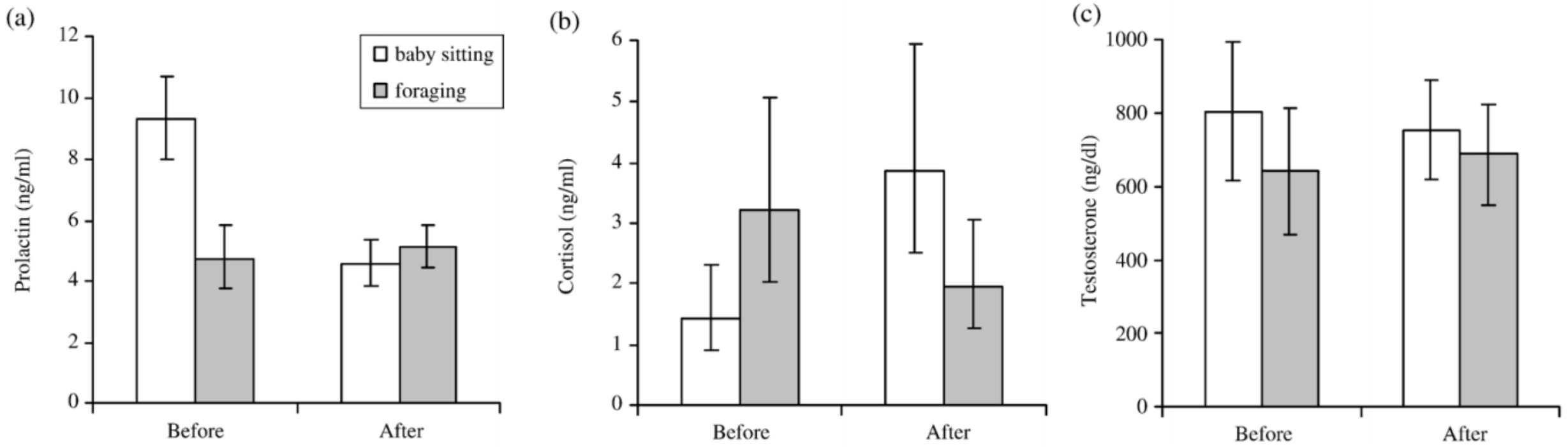
Prolactin, a parenting hormone

- Increased prolactin levels are associated with baby sitting, not foraging
- Baby sitting is stressful, increasing stress hormone levels



Before / After engaging in behaviour

Carlson et al 2006

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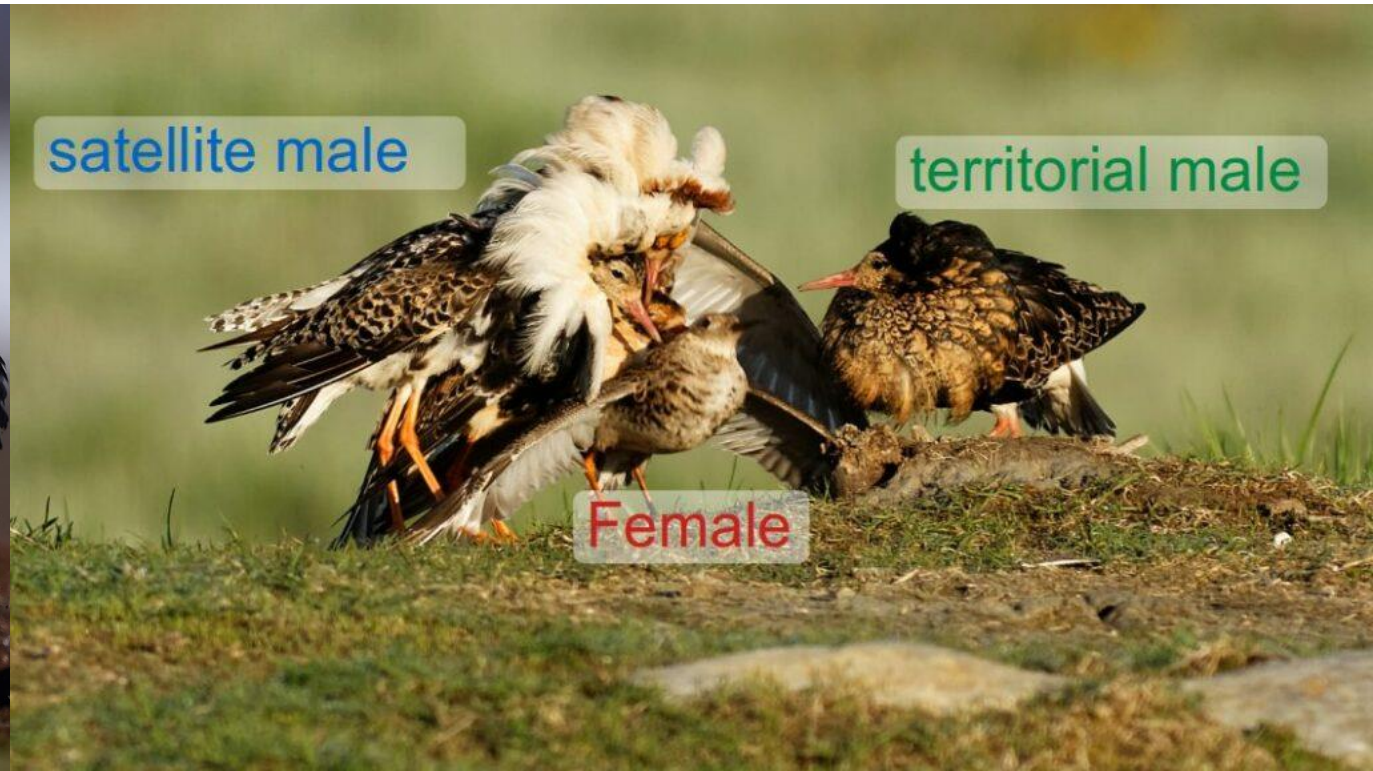
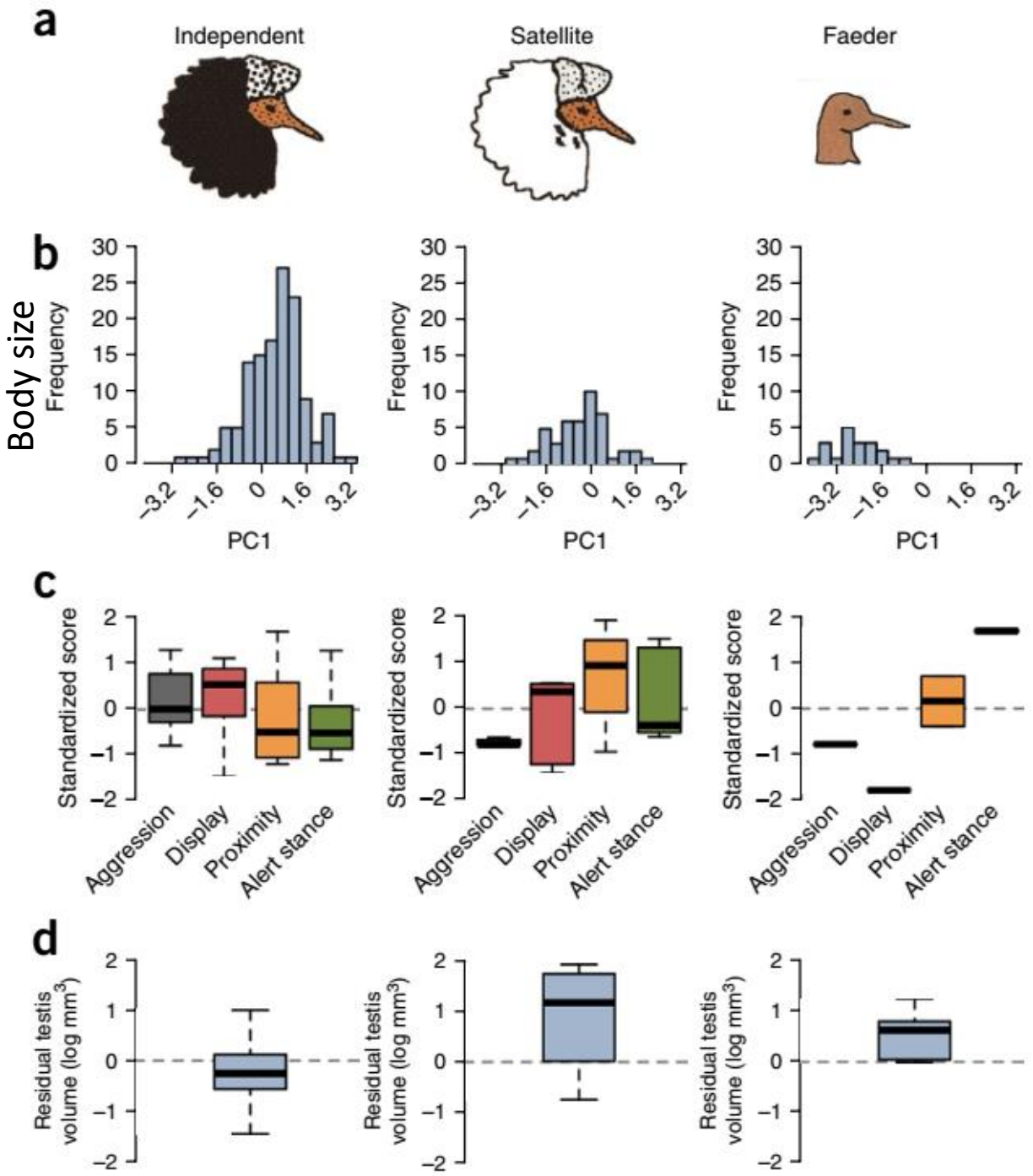
Ruff males differ in their mating strategy and plumage

- Ruffs are waders that form leks (males display together) to attract females
- Ruff males vary in their plumage colouration and mating strategy



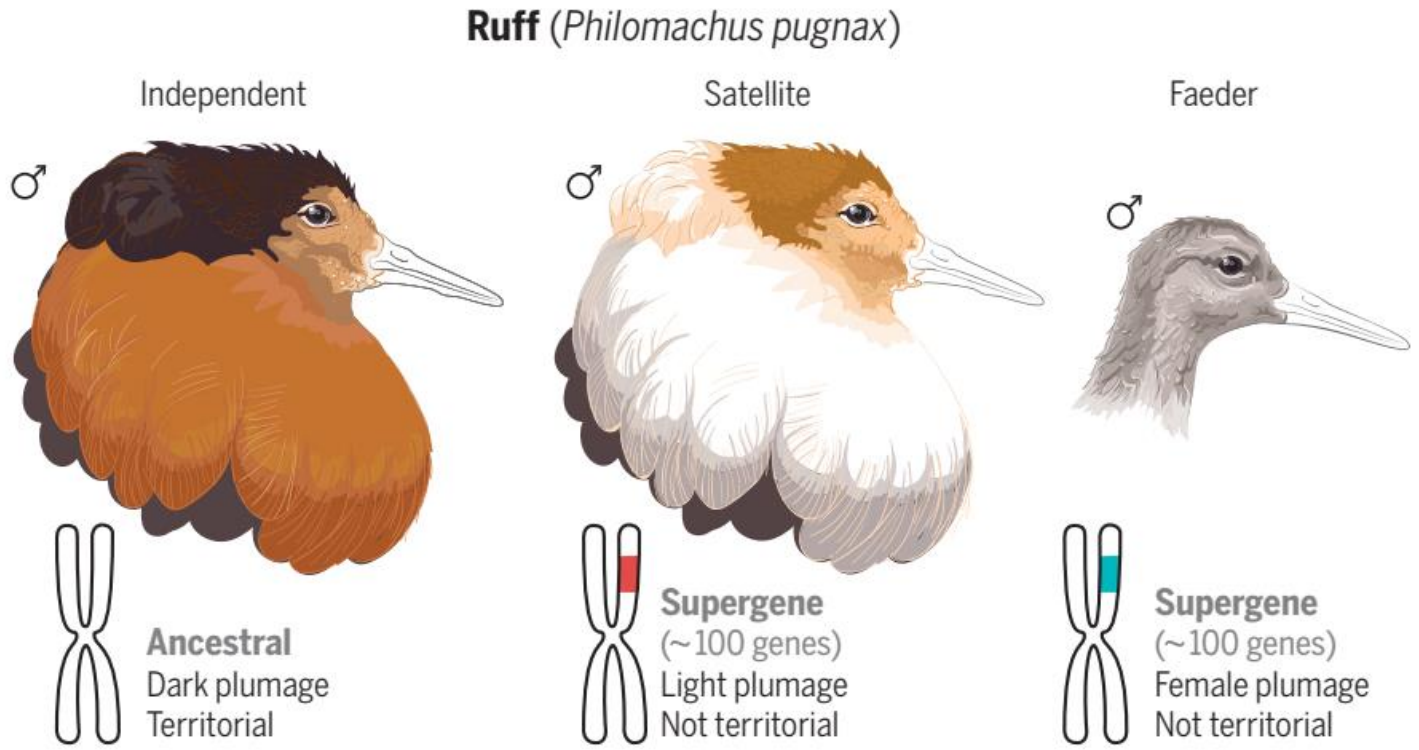
- Ruff males come in 3 phenotypes
- Black headed males are dominant
- White headed males are subordinate
- Faeder males look like females, and sneak in to copulate



Küpper et al 2016

Ruff males differ in their mating strategy and plumage

- Difference among males is encoded in 100 genes merged in a supergene (an inversion) on chromosome 11
- The faeder gene is ca 4my old, the satellite one is a rare recombination between the independent gene and the faeder supergene ca 0.5my ago

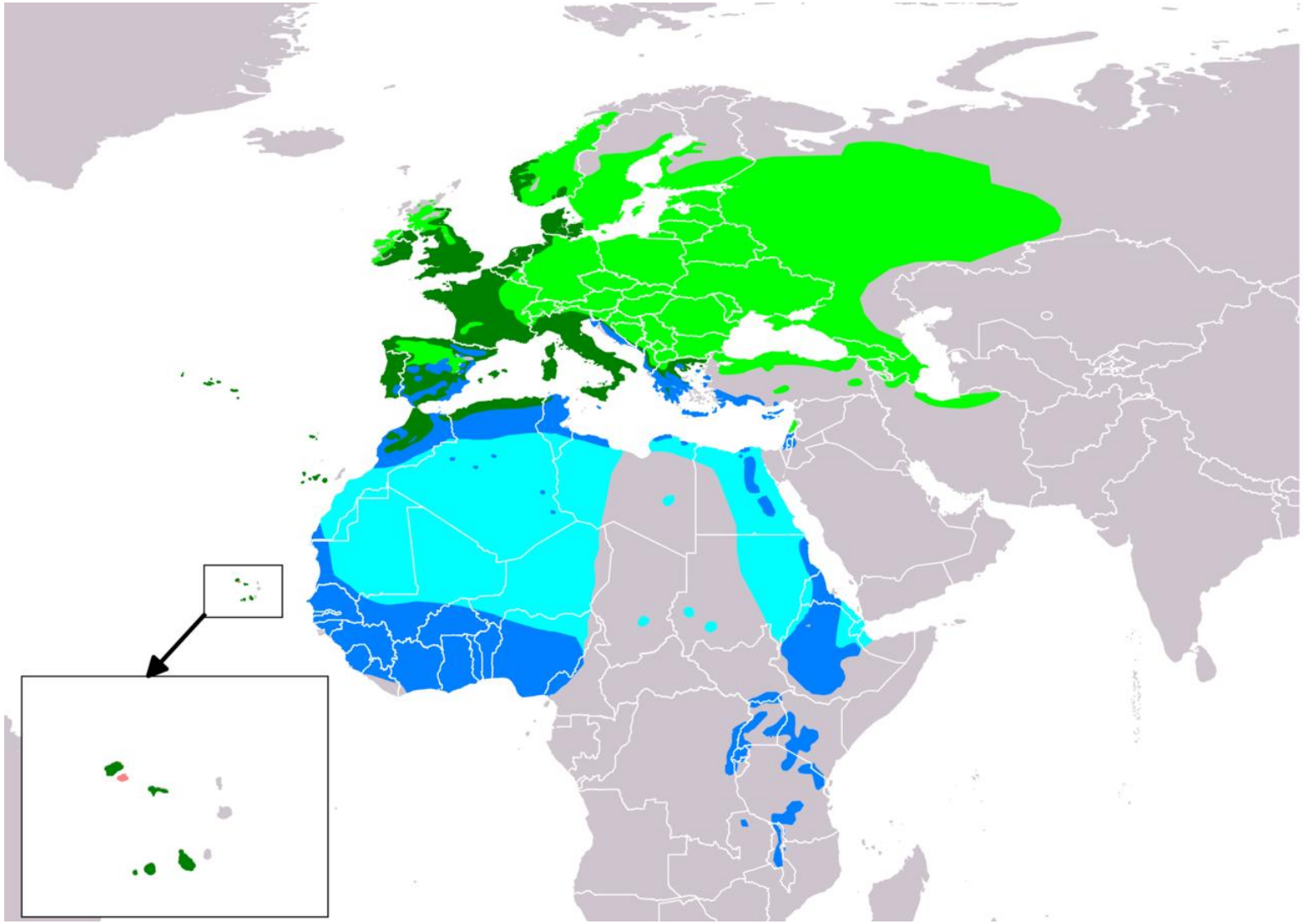


Küpper et al 2016

Blackcaps vary in their migratory behaviour

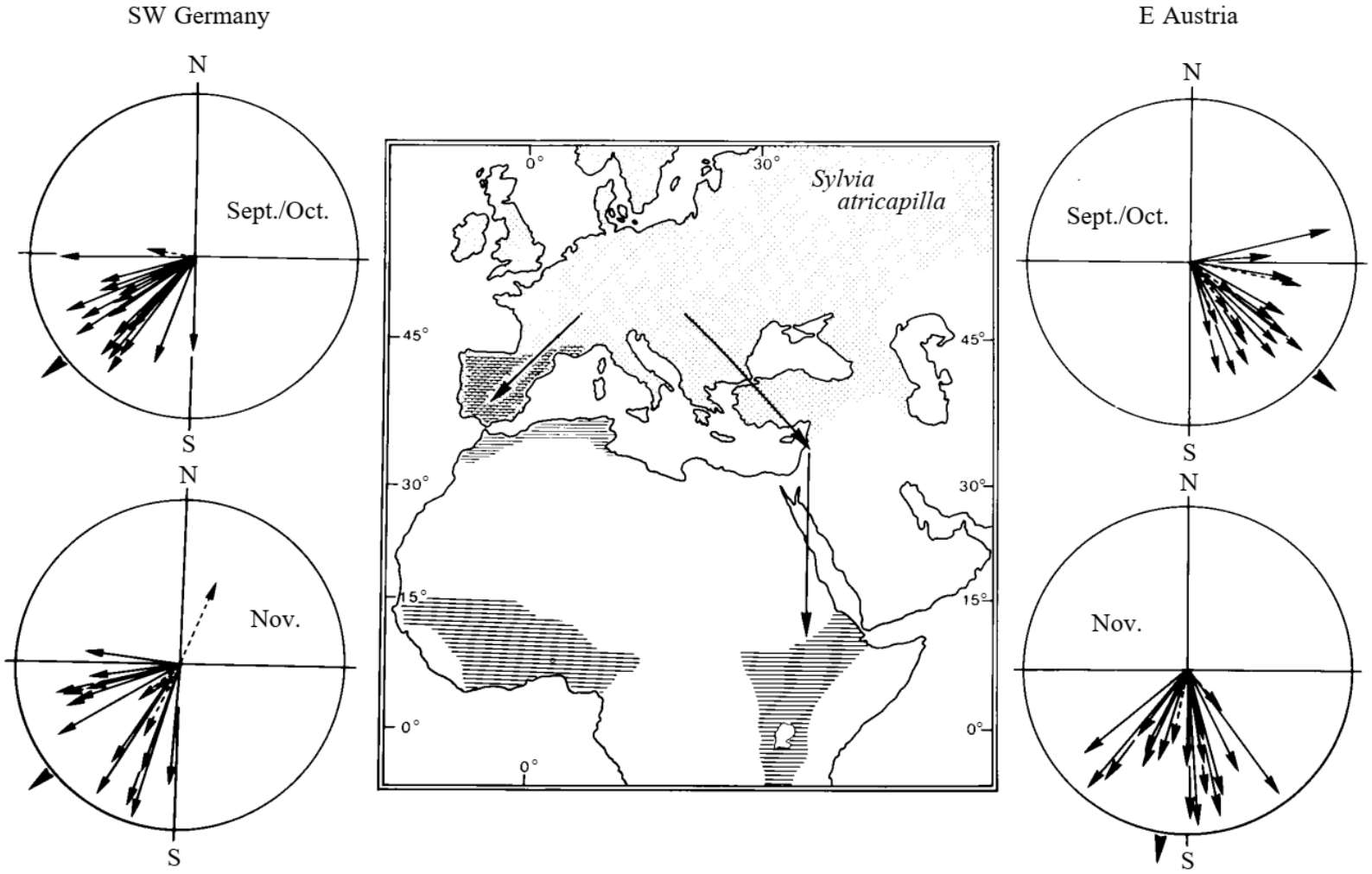
Blackcaps vary in their migratory behaviour

- Different populations different patterns
- Sedentary populations
- 2 migratory routes



Blackcaps vary in their migratory behaviour

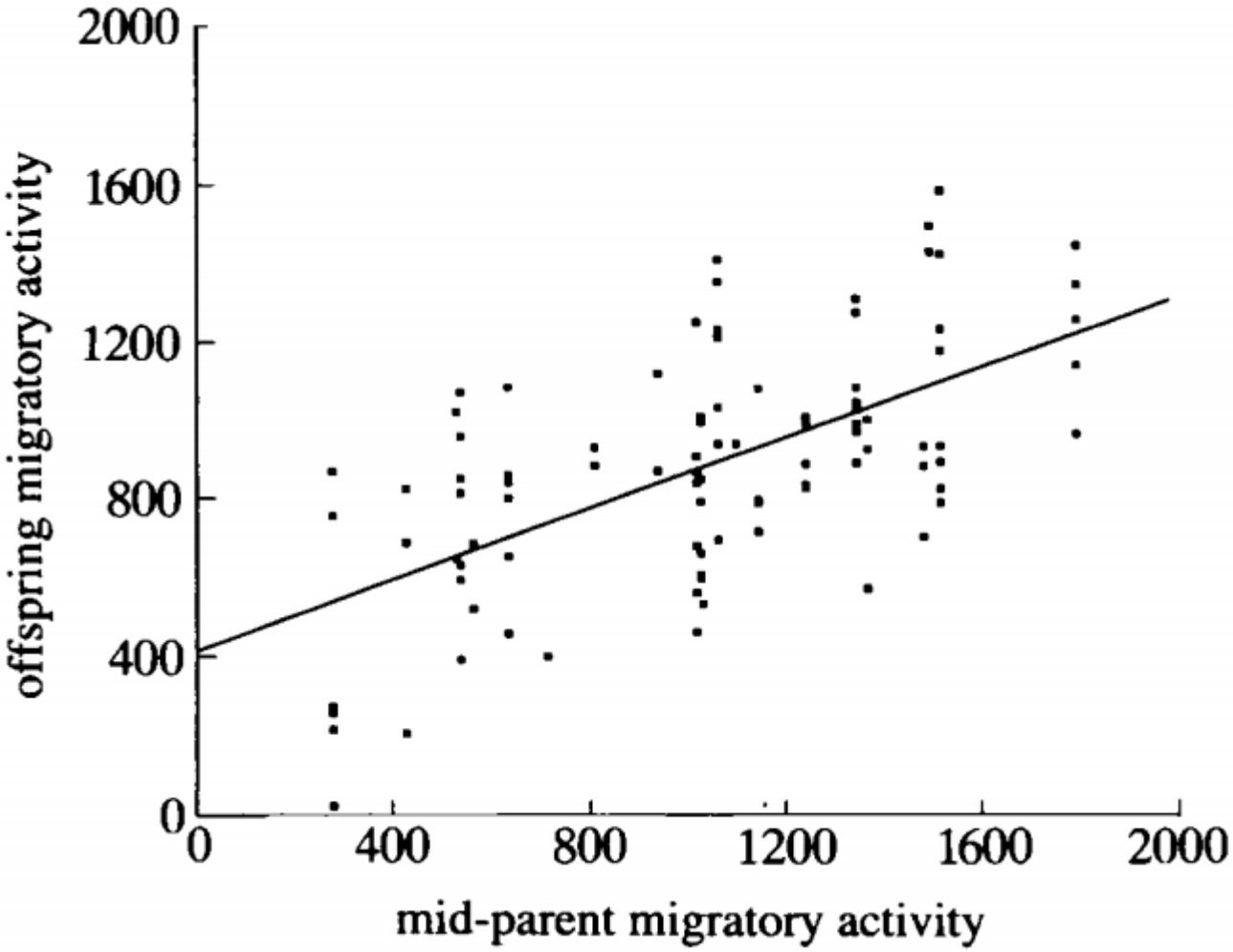
- Blackcap populations differ in their migratory behaviour
- Western ones move SW
- Eastern ones move SE



Helbig 1996

Blackcaps vary in their migratory behaviour

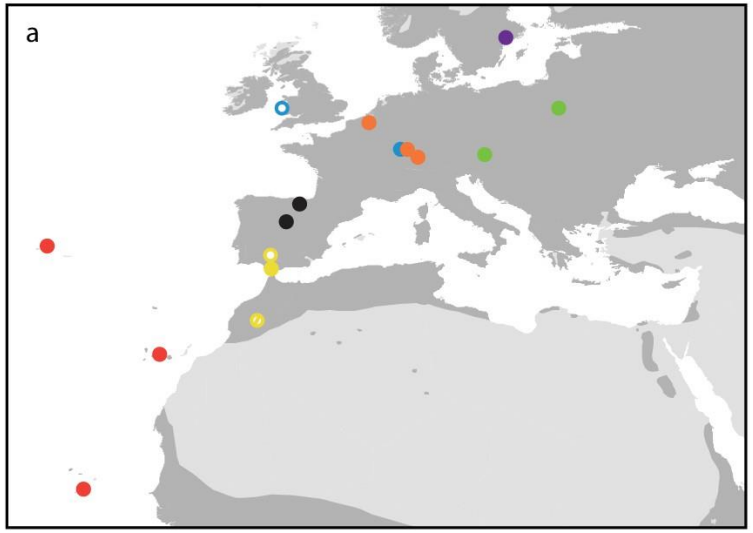
- Blackcap migratory behaviour is inherited
- Patterns of migratory restlessness between parent and offspring correlate

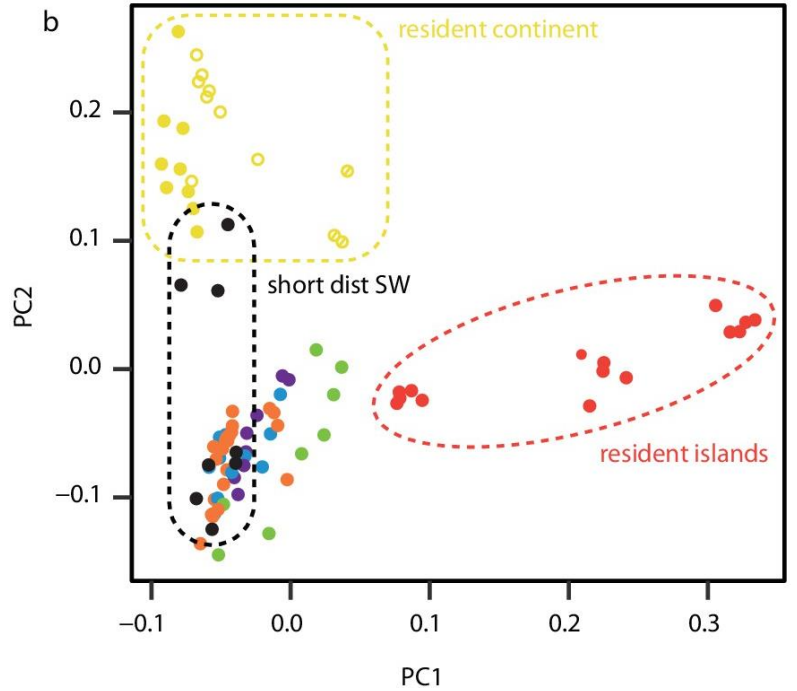


Berthold and Pullido 1994

Blackcaps vary in their migratory behaviour

- Genetic similarity among different blackcap populations
- Resident continental, migratory, and resident island populations cluster based on genetic similarity
- North Iberian population is a mix of resident and migratory populations, occurring ca 5000 years ago

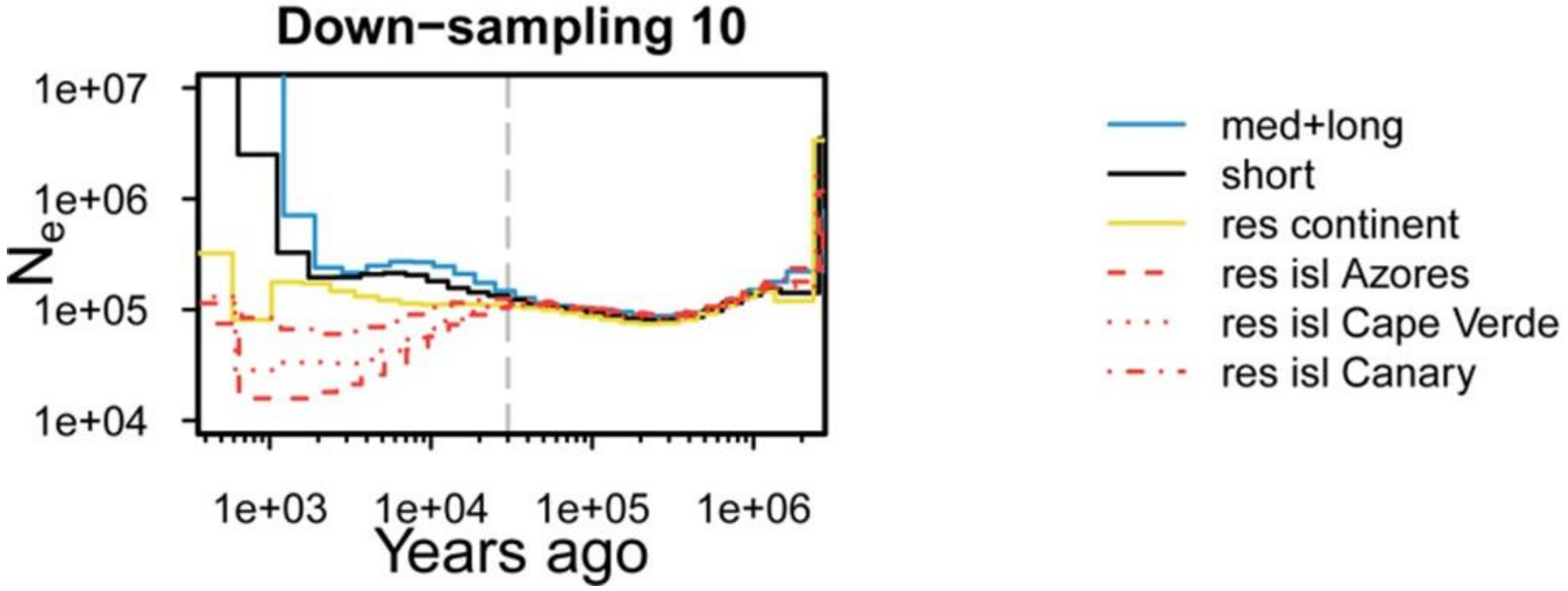




Delmore et al 2020

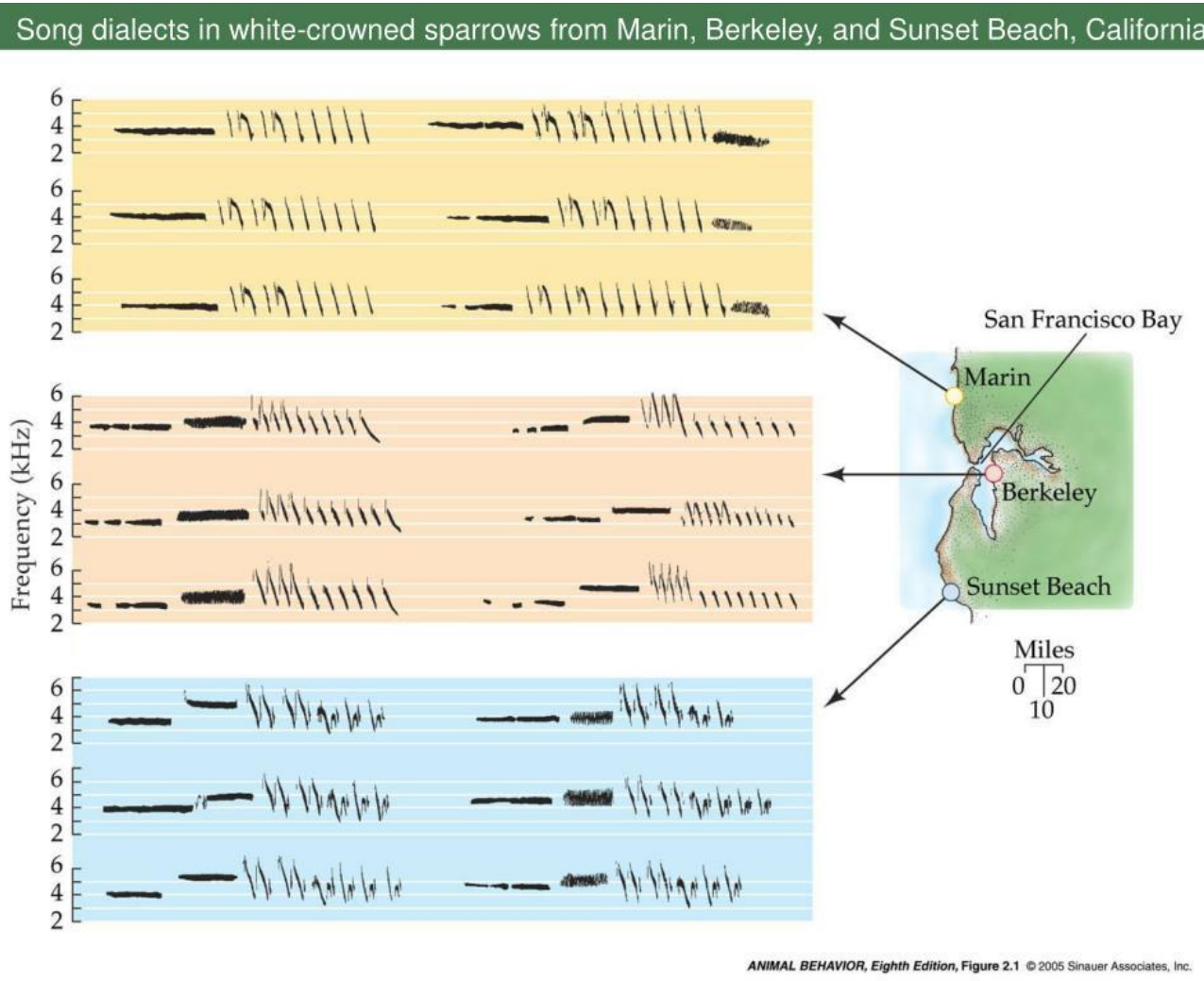
Blackcaps vary in their migratory behaviour

- Genetic variation in migratory behaviour evolved 30’000 years ago, at the end of last glaciation
- Reflected in estimated population sizes in different populations



Delmore et al 2020

Song dialects in white-crowned sparrows

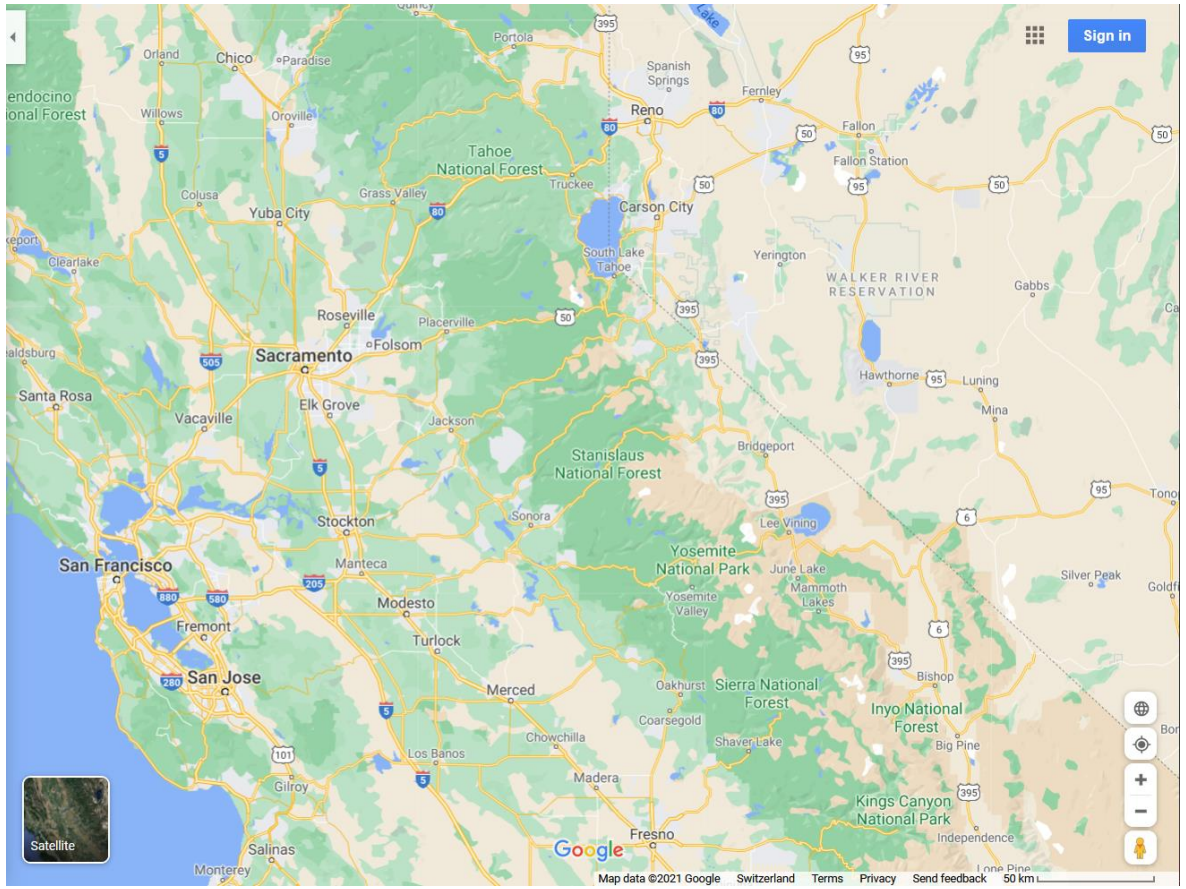


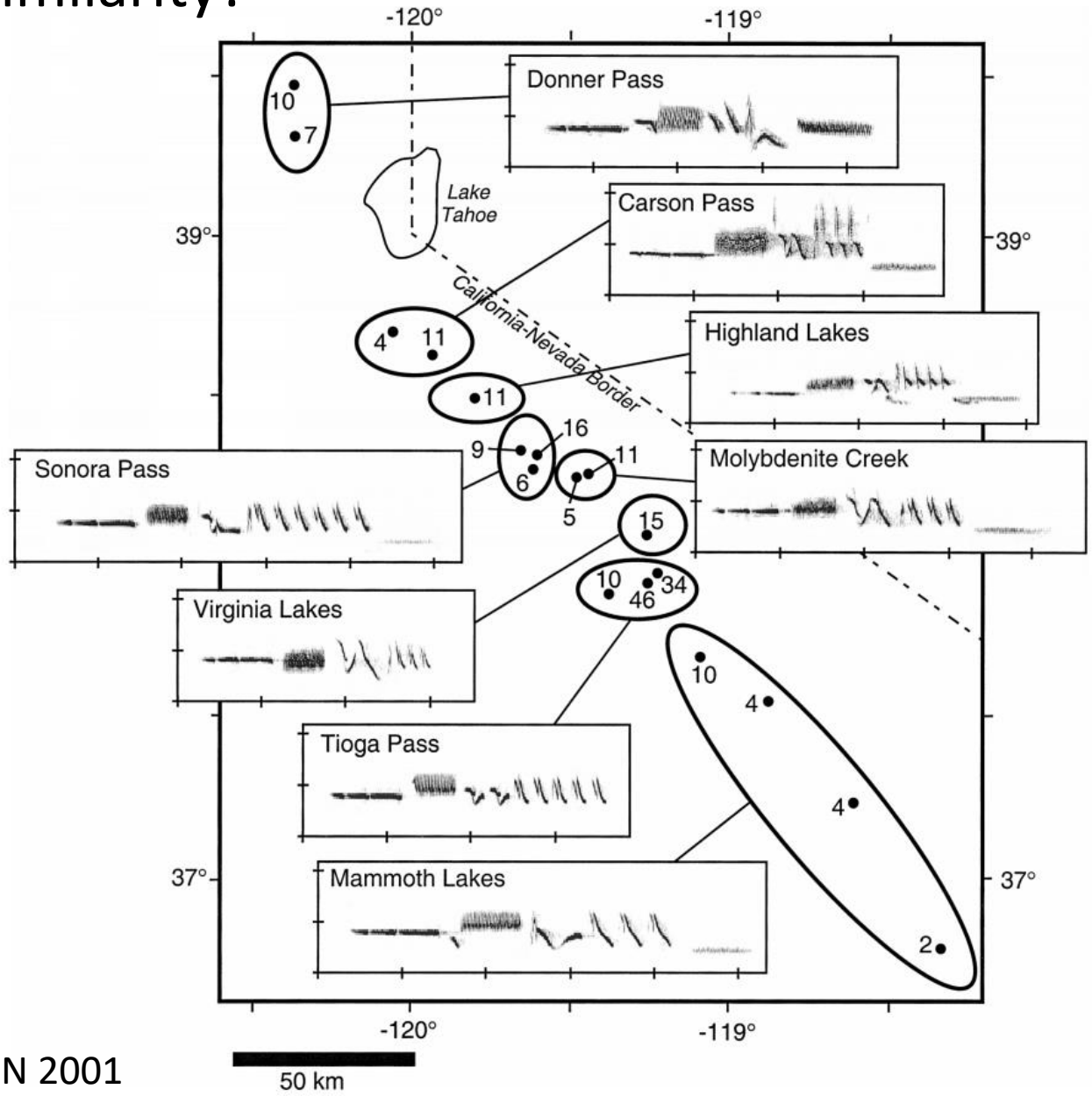
Marler and Tamura 1962

Song dialects in white-crowned sparrows

- Species with vocal learning can have different dialects
- Dialect = local differences in vocalisations
- How come?
  - Too much variation may hamper understanding the signal
  - Probably culturally transmitted trait (learned locally)

- Is song similarity reflecting genetic similarity?



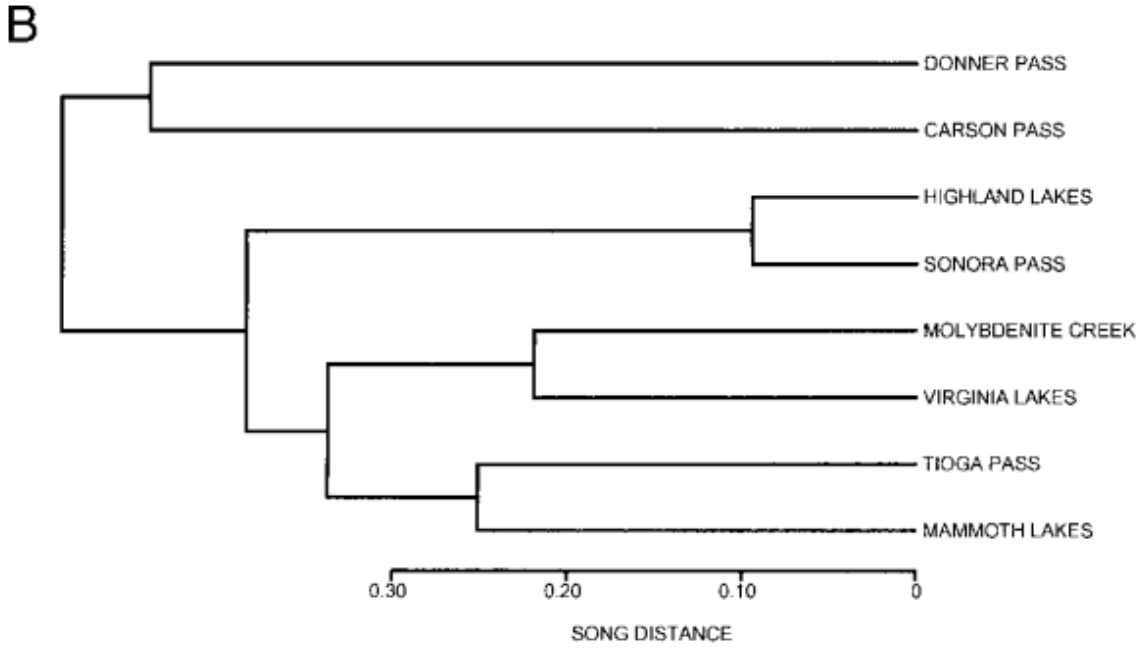


MACDOUGALL-SHACKLETON & MACDOUGALL-SHACKLETON 2001

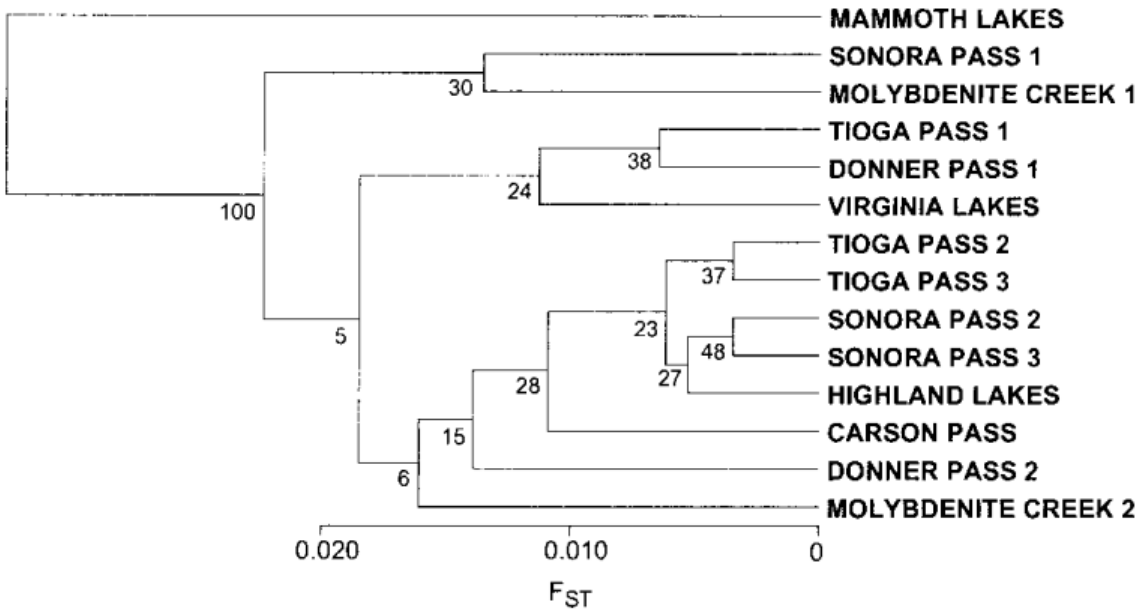
Song dialects in white-crowned sparrows

- Song tree and genetic tree to not match up
- Songs are not encoded genetically, but learned locally
- What is then the benefit of “dialects”?

Song similarity



Genetic similarity



MACDOUGALL-SHACKLETON & MACDOUGALL-SHACKLETON 2001

What’s the advantage of dialects?

Background

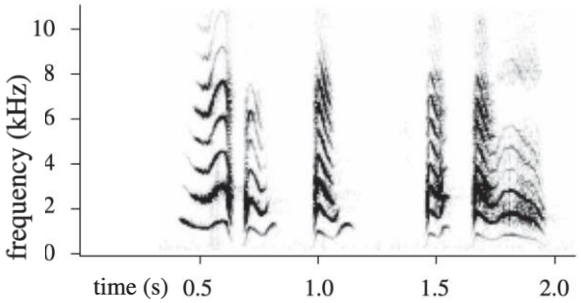
Experimental setup

Outcomes

Siberian jay group members cooperate in various contexts, e.g., during foraging and predator mobbing.

Exp. I: Playback of mobbing calls of former cooperation partners.

Hawk mobbing call of Siberian jays



Breeders trust hawk mobbing calls of cooperation partners, escaping immediately to safety.

Some jays emit hawk mobbing calls in the absence of hawks to access food on neighboring territories.

Exp. II: Playback of mobbing calls of neighbours.

Breeders distrust hawk mobbing calls of neighbors, delaying departure from a feeding device.

Cunha and Griesser 2021

What’s the advantage of dialects?

- Juvenile jays learn mobbing calls from breeders
- Local dialects that differs between territories
- Humans trust speakers of own dialect
- Universal proximate signal of being local, trustworthy?

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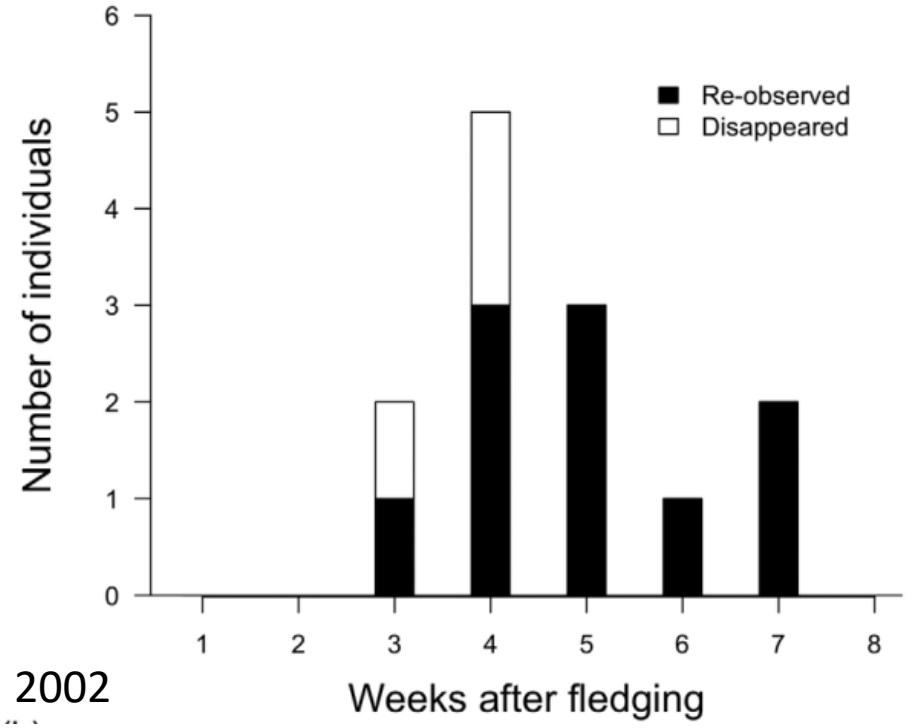
Variation in dispersal in Siberian jays

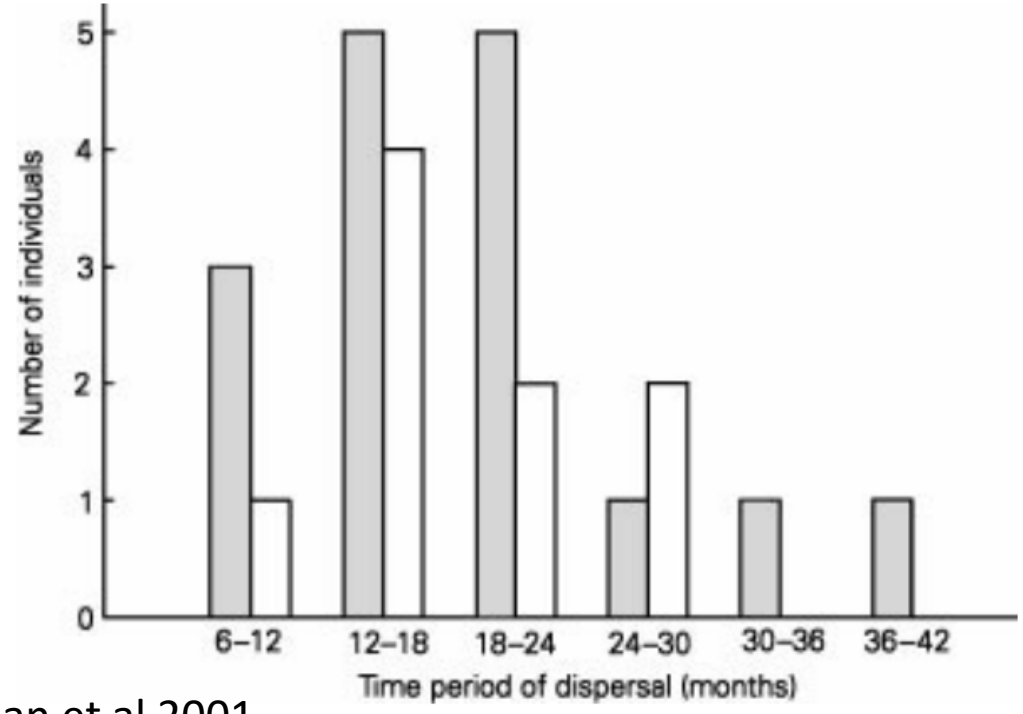
- How come Siberian jay groups can include both own offspring and offspring of others?
- Remaining with the parents is beneficial, so why leave some offspring?

Variation in dispersal in Siberian jays

- Some offspring leave soon after fledging
- They do not leave voluntarily
- Socially dominant siblings force them to disperse
- Dominant siblings stay up to 4 years with their parents



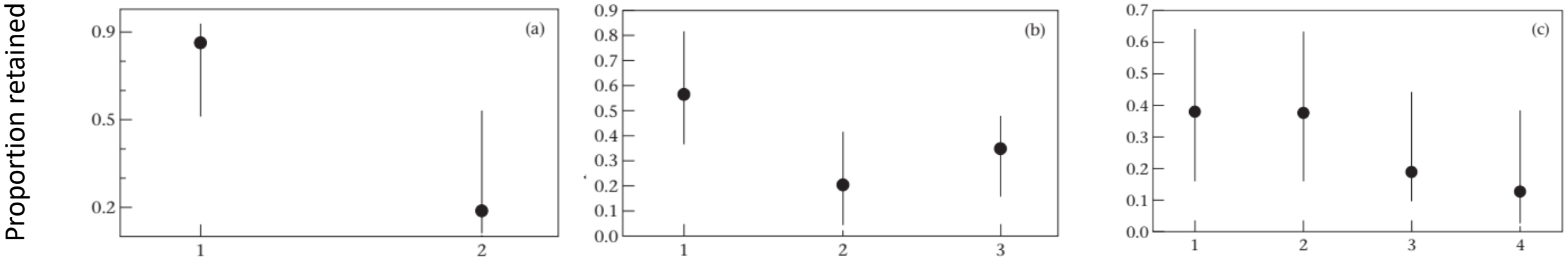
Ekman et al 2002



Ekman et al 2001

Variation in dispersal in Siberian jays

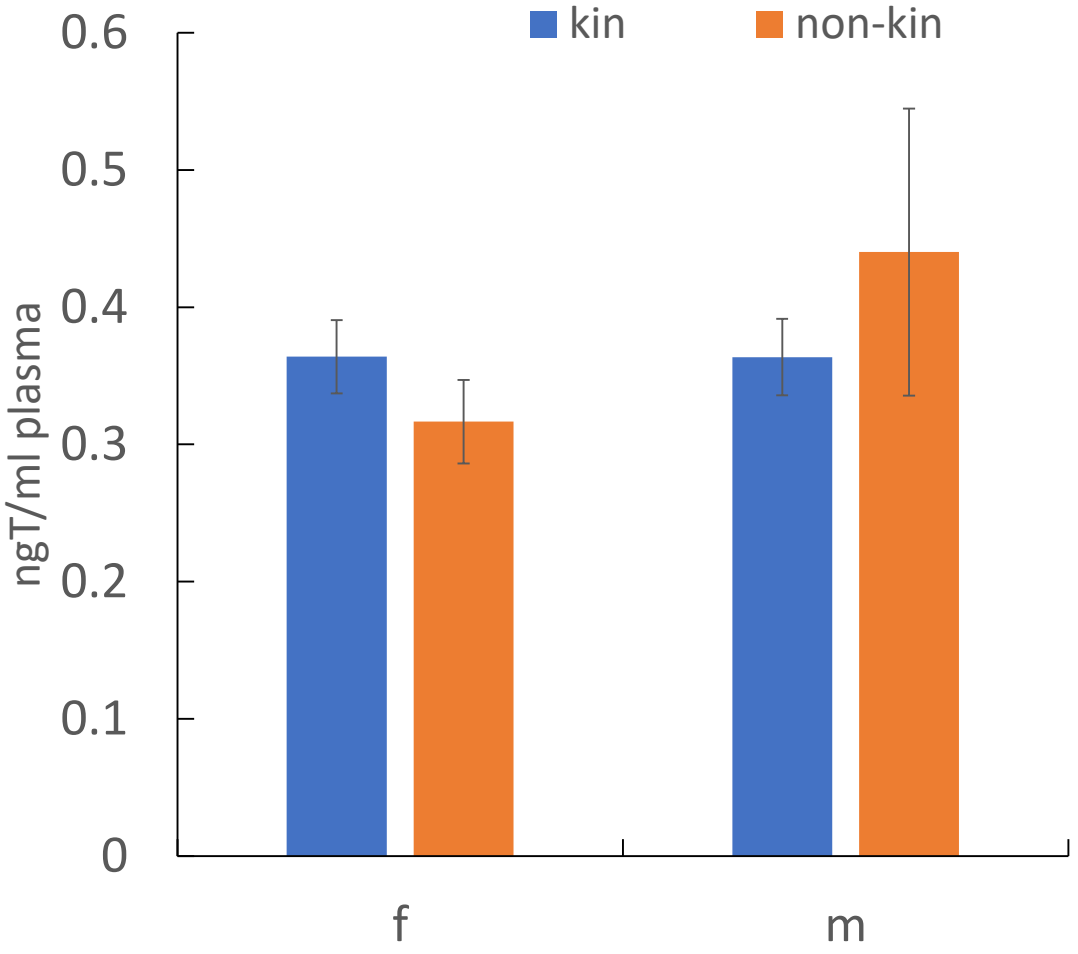
- Females incubate eggs from the first egg onwards (it can be -30C!)
- Later laid eggs hatch later
- Later hatched offspring are subordinate and forced to disperse



Ekman et al 2002

Variation in dispersal in Siberian jays

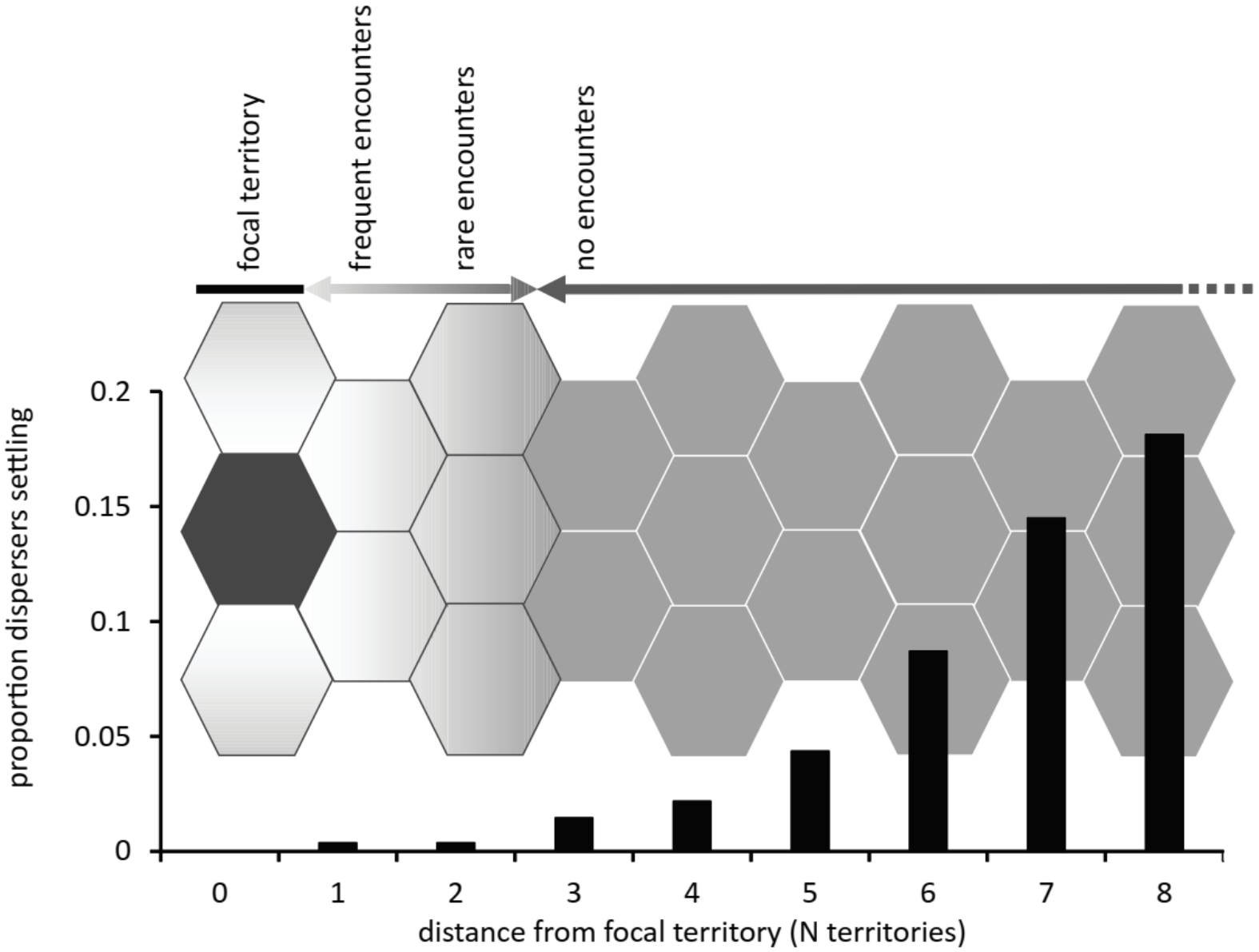
- Dispersal is not driven by testosterone differences
- If anything dispersing offspring (non-kin) males have somewhat higher levels than non-dispersing kin
- Measured at the wrong time?
- Other mechanism?



Griesser et al unpublished

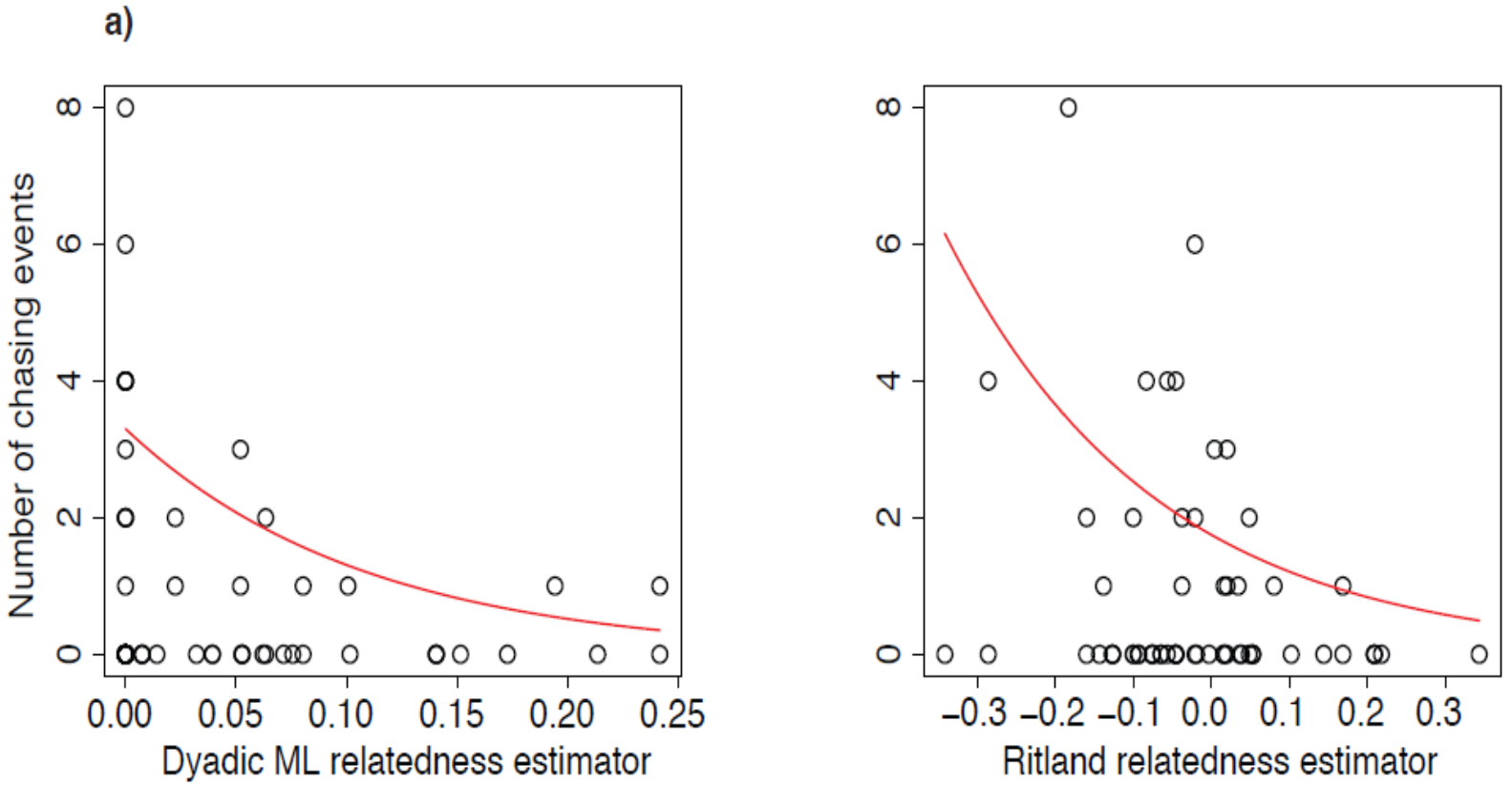
Variation in dispersal in Siberian jays

- Dispersers move in average 6-8 territories
- Beyond the range where they know individuals
- However, breeders vary in their aggression towards non-breeders depending on the genetic relatedness



Variation in dispersal in Siberian jays

- Siberian jay breeders seem capable to assess the degree of genetic similarity of unknown individuals



Griesser et al 2015

Kin recognition vs cuckoos

- Despite that Siberian jays can discriminate kinship based on an external cue, parents treat swapped offspring as own
- Rule: offspring in my nest = my offspring is stronger
- What has this to do with cuckoos?

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Kin recognition vs cuckoos

- How come that cuckoos can trick other species to feed their offspring?
- Why not use kin recognition mechanisms?

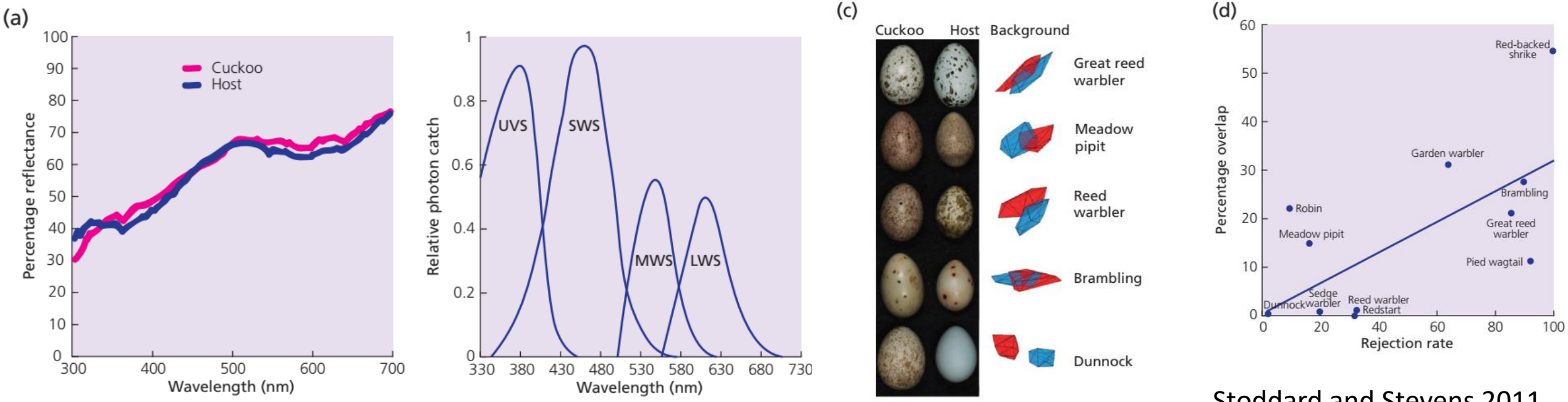
Cuckoo egg coloration mimicry

- Cuckolding others evolved repeatedly
- Within species: egg dumping, e.g. American coot → see parental care lecture
- Across species: cuckoos, cowbirds and others
- European cuckoo has different genotypes
- Matching in egg size and colouration between host species (left) and cuckoo (right)

Brook and Davies 1988

Cuckoo egg coloration mimicry: cuckoo tricks

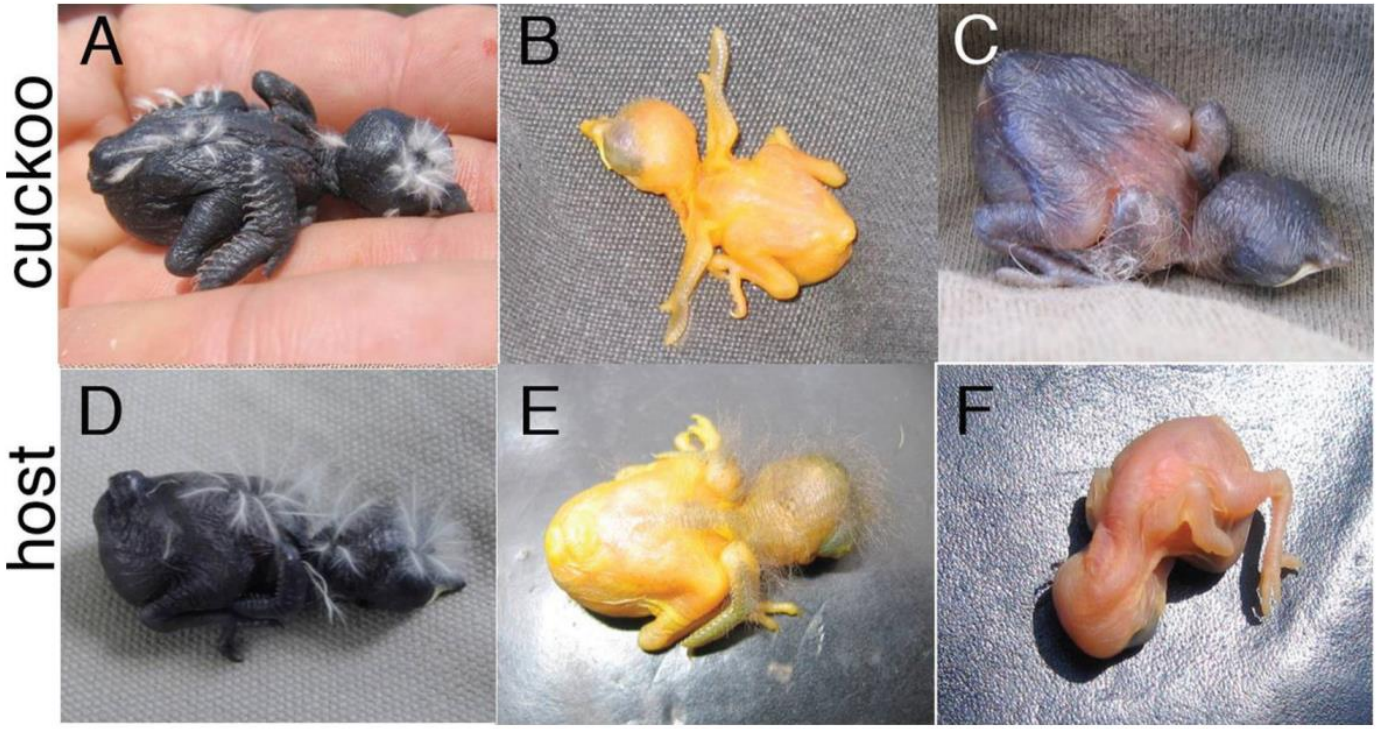
- Eggs need to be laid without being seen, remove an egg
- Cuckoos eggs need to match host eggs, else they are rejected
- Bird colour vision is better than ours, so matching is critical



Stoddard and Stevens 2011

Cuckoo egg coloration mimicry: cuckoo tricks

- Australian bronze cuckoo species have different host species
- Nestlings of each species match the colouration of the host!



Langmore et al 2011

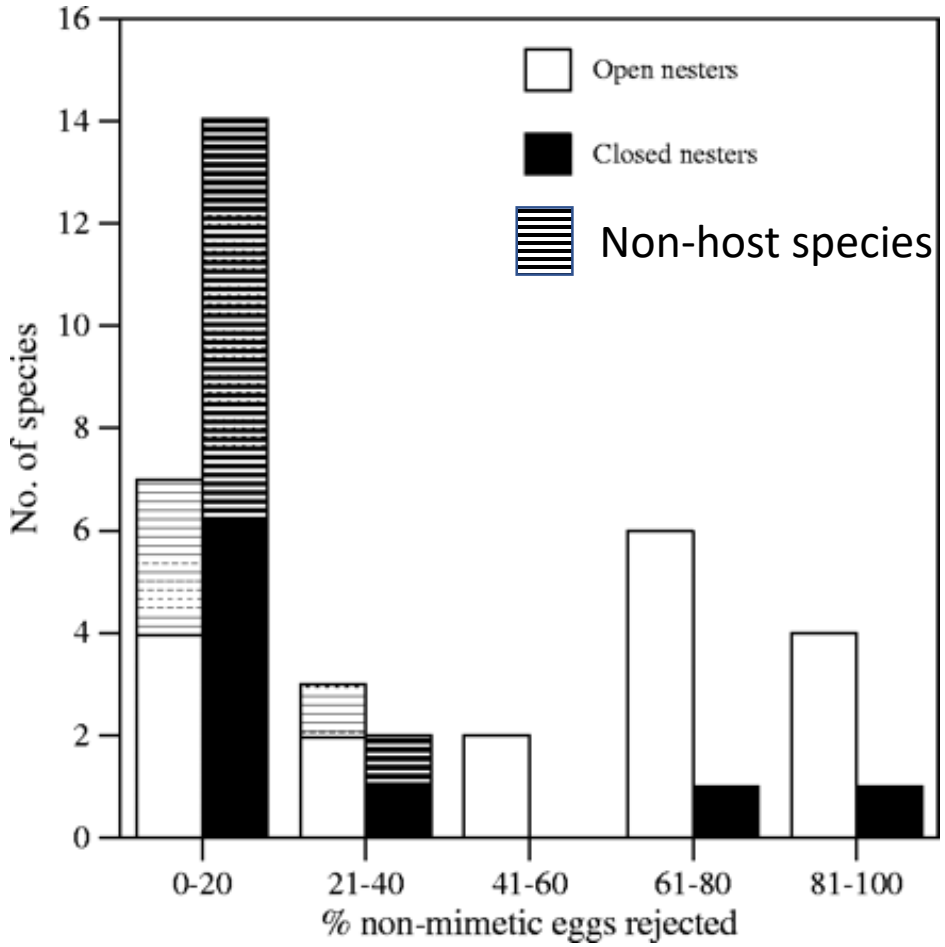
Cuckoo egg coloration mimicry: host tricks

- Tawny flanked prinia eggs are highly variable across females (outer circle)
- Cuckoos are forced to mimic this variation, and select the right phenotype of egg colour patterns (inner circle)
- Arms race between host and parasite!

Spottiswoode and Stevens 2012

Cuckoo egg coloration mimicry: host tricks

- Arms race between cuckoos and hosts
- Hosts become more sensitive over time
- Cuckoos need to switch hosts
- European cuckoos may run out of options, accelerating their decline
- Resets arms race over time



Langmore et al 2005

Proximate mechanisms: structure of lecture

- Definition and note of caution
- Proximate mechanisms can go wrong
- Brain evolution in vertebrates and social decision making network
- Hormonal governing of behaviour: vasopressin and prolactin
- Input: how to read a scientific paper in 5 min?
- Genes and variation in behaviour: mating, migration and bird song
- Variation in dispersal timing
- Cuckoos and other cheats
- Summary

Proximate mechanisms: summary

- Proximate mechanisms govern behaviour
- Critical elements: brain (engine) and hormones (messengers)
- Hormones have rather conserved functions across species
- Differences in their expression patterns make quite a difference!
- Differences in behaviour are more and more linked to specific (super)genes
- Social inheritance ≠ genetic inheritance→ critical to assess the mechanisms
- Natural history constraints can shape fundamental behaviours, e.g. dispersal
- Proximate mechanisms can override others (kin vs offspring recognition)
- Fitness benefits matter for this: what's in my nest = my offspring
- This can be exploited by others, e.g. cuckoos