Who Cares? The Evolution of Parental Care in Squamate Reptiles

Ben Halliwell
Geoffrey While, Tobias Uller
Parental Care

– any instance of parental investment that increases the fitness of offspring
Parental Care

- Majority of research on mammals and birds
- Care is ubiquitous in mammals and birds
- Constrains our ability to:
  - ask questions about the origins of care
  - Understand the role of parental care in the evolution of social complexity.
- Need alternative systems
Parental Care in Reptiles

- Most sophisticated care behaviour found in Crocodilians
- All species provide parental care
- Provisioning of offspring and care after nutritional dependence
Parental Care in Squamates

Lizards and Snakes

- Establishing and maintaining nests, burrows and territories
- Care of fertilised eggs
- Provisioning of offspring before hatching or birth
- Care after hatching or birth
- Care after nutritional dependence
Parental Care in Squamates

Lizards and Snakes

- Establishing and maintaining nests, burrows and territories ✓
- Care of fertilised eggs ✓
- Provisioning of offspring before hatching or birth ✓
- Care after hatching or birth ✓
- Care after nutritional dependence
Parental Care in Squamates
Lizards and Snakes

- Establishing and maintaining nests, burrows and territories ✓
- Care of fertilised eggs ✓
- Provisioning of offspring before hatching or birth ✓
- Care after hatching or birth ✓
- Care after nutritional dependence
Aims

1. Elucidate the evolutionary pathways (i.e. most common transitions) that have led to current diversity in reptilian care

2. Identify the divergence in key ecological, life-history or phylogenetic characteristics responsible for transitions between modes of care
   - In particular, parent offspring association

3. Understand the evolutionary constraints prohibiting the emergence of more sophisticated modes of care in non-crocodilian reptiles
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   - In particular, parent offspring association

3. Understand the evolutionary constraints prohibiting the emergence of more sophisticated modes of care in non-crocodilian reptiles
Methods

Searched the literature for all reports of parental care behaviour across all squamate reptile species, recording:

1) All forms of parental care

2) Parity mode (oviparity vs. viviparity)

Mapped the data onto a recently published squamate reptile phylogeny (Pyron et al. 2013)

A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes


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Parental Care in Squamates

Pre-Hatching/Birth Care

- Nest Construction

- Egg Attendance/Brooding

- Egg/Nest Guarding

- Viviparity
Parental Care in Squamates

Post-Hatching/Birth Care

- Parent Offspring association (POA)
## Distribution of Care in the Squamates

### Pre Hatch/Birth Care

<table>
<thead>
<tr>
<th>Type</th>
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<tr>
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<td>842</td>
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<td>Nesting behaviour</td>
<td>229</td>
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<td>Brooding/Egg attendance</td>
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<td>Egg defense</td>
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### Post Hatch/Birth Care

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### No Care Reported/Data Available

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Distribution of Care in the Squamates

Overall, 28% of squamate species exhibit some form of care

- 43% at the family level

30% of fish families

6-15% of anuran species

20% of salamander species
Squamate Tree

Snakes

Lizards
Snakes

Viviparity | Pre | Post

[Diagram of a phylogenetic tree showing different snake families with percentages indicating support values.]
Distribution of Care

Pythons (oviparous)
- Xenopeltis antarctica
- Lycophis bicolor
- Python brongersmae
- Python molurus
- Python sebae
- Python curtus
- Python regius
- Broghammerus timorensis
- Broghammerus reticulatus
- Morelia nepehirinec
- Morelia amithistrina
- Morelia boleleri
- Aspidites melanocephalus
- Aspidites ramsayi
- Lialis olivaceus
- Lialis papuanus
- Lialis fuscus
- Lialis maculatin
- Boiga schulleri
- Boiga doriae
- Morelia carinata
- Morelia bredli
- Morelia citriata
- Antaresia macalosa
- Antaresia perthensis
- Antaresia kühnerti
- Antaresia stenomisi

Boas (viviparous)
- Boa constrictor
- Corallus hortulanus
- Corallus auratus
- Corallus caninus
- Epicrates cenchria
- Bunophis notatus
- Bunophis caurinus
- Epicrates angulifer
- Epicrates imorninus
- Epicrates imornius
- Epicrates subflavus
- Epicrates fordi
- Epicrates chrysogaster
- Epicrates striatus
- Epicrates nasicus
Better do some analyses

– Chi-square shows significance  
  \( P < 2.2 \times 10^{-16} \)
Better do some analyses

- Chi-square shows significance \( P < 2.2\text{e-16} \)
- Need analytical technique that can separate transitions between states from speciation/radiation once a state has evolved
- MuSSE models
  - Extention of BiSSE

<table>
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<tr>
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Better do some analyses

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– MuSSE models
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<table>
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<tr>
<th>BLUE</th>
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A few snags...

For the 3952 spp. included in the Pyron et al. squamate phylogeny:
- Care data available for only 390 spp. Of those, POA reported in only 79.

Restrict analyses to a monophyletic group with decent amount of data available – Scincidae!
Scincidae

- Monophyletic group
- POA found in 29 spp.
Distribution of Care

Plestiodon (primarily oviparous)

V

Egernia (viviprous)

Corucia_zebrata
Egernia_saxatilis
Bellatorias_major
Egernia_depressa
Bellatorias_korthi
Egernia_kingii
Egernia_napoleonis
Egernia_richardi
Egernia_luctuosa
Egernia_hosmeri
Egernia_stokesii
Cyclodomorphus_casuarinae
Cyclodomorphus_michaeli
Cyclodomorphus_branchialis
Tiliqua_rugosa
Tiliqua_ardida
Tiliqua_occipitalis
Tiliqua_nigrolinea
Tiliqua_scincoides
Tiliqua_gigas
Egernia_margaretae
Egernia_modesta
Egernia_whitii
Egernia_montana
Egernia_gulthia
Egernia_inomata
Egernia_striata
Egernia_multiscutata
Egernia_pulchra
Egernia_kintorei
Tree of Scincidae
**Approaches**

Run Models with:

1. Whole data set (including NA’s for care)

2. Reduced data set, including only those species for which care data are available

3. Dummy data sets in which NA’s were replaced with randomly assigned care values based on a given probability of care occurring (0.02)

Ran all of these:

1. Constrained and unconstrained speciation and extinction rates
## Results

### Speciation and Extinction Constrained

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Speciation and Extinction allowed to vary

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### Results

**Randomized Data Sets**

**Speciation and Extinction Constrained**

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Where to from here?

- Conduct more thorough analyses to get at the apparent association between viviparity and POA
  - Extend to whole tree

- Look into multi-trait analysis to see if the current distribution of care modes can be explained by some logical sequence of transitions

  e.g. N → B → ED → POA

  V ← POA
What predicts transitions to parental Care in Squamates?

For care to have evolved from an ancestral state of no care, both ecological and life history traits must favour the transition – these include:

1) Ecological Factors
   - Resource availability
   - Climate (viviparity)

2) Life History Factors
   - Egg size / Investment in offspring
   - Longevity / Age at maturity

3) Association: Care is more likely to evolve when parents regularly encounter their offspring
   - Territoriality
   - Viviparity
Summary

1. Parental care in squamates is more sophisticated than often assumed.

2. Care is taxonomically widespread and represents multiple evolutionary transitions.

3. These patterns are equivalent to those seen in fish, amphibians and invertebrates – all of which are assumed to have more sophisticated care behaviour compared to reptiles.

4. Both life history traits and ecology are likely to be important – specifically, viviparity appears to be an important (but not essential) precursor to parent-offspring association.

7% of viviparous species in the squamate phylogeny exhibit post-hatching care but only 1% of oviparous.
Broader Evolutionary Implications of Parental Care

<table>
<thead>
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<th>Species</th>
<th>Parity</th>
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Questions and Suggestions?