Breeding in bamboo: a novel anuran reproductive strategy discovered in Rhacophorid frogs of the Western Ghats, India

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Amphibians exhibit extraordinarily diverse sets of reproductive strategies among vertebrates. Understanding life history strategies in an evolutionary framework is lacking for many amphibian species in the tropics. Here, we report a novel reproductive mode where adult frogs enter hollow internodes of bamboo via a small opening, deposit direct developing eggs, and provide parental care. This behaviour is observed in two species of the frog genus Raorchestes. The first description of this unique life history and details of nest site characteristics and embryo development are provided along with ecological comparisons. Evolution of novel reproductive modes and parental care are discussed in context of natural selection. Dearth of natural history information on amphibians in the Western Ghats and much of the South-East Asian region is highlighted with suggestions for further studies. © 2014 The Linnean Society of London, Biological Journal of the Linnean Society, 2014, ••–••. ADDITIONAL KEYWORDS: amphibian ecology – direct development – evolutionary ecology – natural history – parental care – reproductive strategies.

INTRODUCTION
Reproduction is an important aspect of life history and amphibians exhibit a remarkable diversity of reproductive strategies (Crump, 2010). Anurans in particular, exhibit 40 different reproductive modes (Gururaja, 2010), highest among all vertebrates (Pough, Janis & Heiser, 2009). Clustering the diversity of amphibian reproduction into ‘reproductive modes’ is difficult and often arbitrary (Lehtinen & Nussbaum, 2003); reproductive modes are classified based on egg deposition sites, egg type, and patterns of embryonic/larval development (Wells, 2007). Of the 40 modes, evolutionary significance of direct developing embryos stands out as it depicts an astonishing variety of adaptations and mechanisms in amphibian reproduction. While most frogs have offspring that undergo larval development via a free living aquatic tadpole, live-bearing amphibians and those undergoing direct development are not uncommon (Stuart et al., 2008). In direct developing anurans, dependence on water is completely severed and, instead, embryos develop within eggs from which froglets hatch directly (Crump, 1996), bypassing the free-swimming tadpole stage. Such an adaptation is known from over 1400 species of anurans (Stuart et al., 2008) and has evolved in parallel in unrelated families across different continents (Duellman & Trueb, 1994). Recent investigations have revealed a deep phylogenetic history as terrestrial egg deposition has evolved 48 times with direct development evolving at least 11 times from terrestrial eggs and eight times from aquatic eggs (Gomez-Mestre, Pyron & Wiens, 2012).

In addition to increased terrestriality, several species of anurans have enhanced offspring survival by providing care to eggs and offspring (see review in

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Crump, 1996). For example, *Eleutherodactylus coqui* from Puerto Rico (Taigen, Pough & Stewart, 1984; Townsend, 1986); Microhylid frogs in Papua New Guinea (Bickford, 2002; Bickford, 2004); *Aromobatid* frogs from Peru (Brown, Morales & Summers, 2008; Schulte & Lötters, 2013); French Guiana (Ursprung et al., 2011); *Hyalinobatrachium valerioi* from Costa Rica (Vockenhuber, Hödl & Amézquita, 2009); *Chiromantis hansenae* from Thailand (Poo & Bickford, 2013). Among anurans, parental care is classified into eight distinct types, egg attendance; egg transport; egg brooding; tadpole attendance; tadpole transport; tadpole brooding; tadpole feeding and froglet transport (Wells, 2007). Parental care in frogs is uncommon but widespread, currently reported from 22 of 55 families and roughly 5% of all species (Crump, 1995; Wells, 2007; Frost, 2014).

Costs and benefits of parental care as a reproductive strategy have received increasing attention in the study of amphibian evolutionary ecology (Townsend, Stewart & Pough, 1984; Bee, Schwartz & Summers, 2013). Parental care, like direct development, is uncommon but phylogenetically widespread as revealed by recent studies (Lehtinen & Nussbaum, 2003). Wilson (1975) attributed four drivers for evolution of parental care among anurans, viz.,able, stable and structured habitats; unusually stressful environments; scarce or specialized food resources; and predation pressures. Parental care is known to increase offspring survivorship and these four attributes, individually or as a combination, impose constraints on life history traits of organisms (Crump, 1995; Lehtinen & Nussbaum, 2003). Such constraints affect reproductive fitness and thereby result in adaptations by means of natural selection (Gadgil & Bossert, 1970; Stearns, 2000).

The Western Ghats biodiversity hotspot of India has, in the recent years, become increasingly important in understanding amphibian diversity, evolution, and biogeography (Bossuyt et al., 2004). Whilst species diversity increases from new descriptions (Dinesh et al., 2013), frontiers of knowledge in ecology and evolutionary history are being expanded by discovery of novel reproductive modes and life history traits. For example, nest building in *Nyctibatrachus kumbara* Gururaja, Dinesh, Priti and Ravikanth (Gururaja et al., 2014) and *Rhacophorus lateralis* Boulenger (Biju, 2009) and foot-flagging behaviour in *Micrixalus aff. saxicola* Jerdon (Gururaja, 2010; Preininger et al., 2013a, b) are some of the most recent discoveries in anurans.

Geological history and habitat diversity have propelled amphibian diversity in several families and the Western Ghats is considered a centre of endemism and adaptive radiation (Bossuyt et al., 2006; Roelants et al., 2007; Bocxaer et al., 2010). Of over 180 anurans described from Western Ghats, members of the family Rhacophoridae form a significant component, with four genera (*Pseudophiulatus, Raorchestes, Polyedates, and Rhacophorus*) and 54 species endemic to the Western Ghats-Sri Lanka hotspot (Dinesh et al., 2013). Diversity of reproductive modes among amphibians of the Western Ghats is high with over 15 of 40 known from the region. Direct developing eggs are reported in four species and restricted to two genera (*Pseudophiulatus* and *Raorchestes*) of Rhacophoridae (Gururaja & Ramachandra, 2006; Biju et al., 2010). Other members of these genera presumably undergo direct development (e.g., Seshadri, Gururaja & Aravind, 2012). Further, there are no confirmed reports of anurans with parental care for eggs or offspring apart from an aquatic frog *Nyctibatrachus kumbara* (Gururaja et al., 2014). It is only suspected that egg attendance exists in the bush frog *Raorchestes ochlandrae* (Gururaja et al., 2007). Here, we describe a novel reproductive mode in an arboreal frog, *Raorchestes chalazodes* from remote forests of Western Ghats. We also compare and contrast with reproductive mode of *R. ochlandrae* and provide insights on possible factors leading to the evolution of such novelties in the South Asian region.

*Raorchestes chalazodes* was presumed to be extinct until rediscovered recently from wet evergreen forests of Kalakad Mundanthurai Tiger Reserve (Ganesan, Seshadri & Biju, 2011). The observations we report here are on a species that fits *R. chalazodes* in all known aspects. Our work along with that of several others appears to suggest that this may be a different species or perhaps a cryptic species. *R. ochlandrae* however, is taxonomically stable and all observations made are from Gururaja et al. (2007).

**MATERIAL AND METHODS**

**STUDY AREA**

We made observations on *R. chalazodes* in the Kalakad Mundanthurai Tiger Reserve (KMTR 8.416° N to 8.883° N latitude and 77.166° E to 77.583°, c. 900 sq km, Fig. 1). The region receives high rainfall in two seasons (c. 3000 mm year−1) and harbours rich anuran diversity (Seshadri et al., 2012). Observations were made in stretches of native bamboo *Ochlandra travancorica* (Benth) Gamble found along streams and in primary and secondary forests of Kakachi and Upper Kodayar ranges of the reserve. The frog is also known from a few other locations around the reserve (range c. 400 sq km). *Raorchestes ochlandrae* was observed in Kakkayam, Calicut, in Kerala (see Gururaja et al., 2007).
NEST OBSERVATIONS

Frogs were found calling between 18:00–01:00 h. If the vocalizing male was located inside a bamboo internode, the bamboo was carefully split open. Between years 2009–2012, 20 bamboo internodes were opened for examination irrespective of a male vocalizing. Contents of internodes were photographed and the following measurements were made (measurements in mm; Fig. 2): outer and inner diameter, internode length, number of openings, total length of openings, distance from top of openings to the upward internode and base of openings to the downward internode.

If adult frogs and eggs were found inside bamboo, they were photographed and measured (SVL, length from tip of snout to vent). Number of egg clutches and eggs was counted and, to prevent damage, only a few eggs of each clutch were measured. Adults were placed back inside the bamboo and returned to the same location. Using photographs, eggs were measured using a known object (diameter of the bamboo) as reference in ImageJ® software. No frogs or eggs were euthanized, preserved, or collected for this report. Developmental stages of eggs were categorized by comparing photographs with stages provided by Bahir et al. (2005). Reproductive modes follow Wells (2007). Nest information and characteristics of *R. ochlandrae* were obtained from Gururaja et al. (2007).

A vocalizing male of *R. chalazodes* was videoed twice, once while it was entering an internode via a narrow slit and on subsequent night while it attempted to exit the cavity via the same opening. Video were made using a Nikon D90 SLR camera with a Nikkor 18–105 mm lens with locally sourced light emitting diode video lights.

RESULTS

OVERVIEW OF REPRODUCTIVE MODE IN *R. CHALAZODES*

The reproductive mode of *R. chalazodes* described here is different from all other modes reported from anurans and can be summarized as male parental care for direct developing eggs laid inside a hollow bamboo internode without stagnant water and with a narrow entry/exit opening. Frogs only utilize bamboo with openings. These openings appear to range from <1% up to 50–60% of bamboos in the area. These openings, presumably made by insects or rodents could be a limiting feature of the landscape yet, necessary for frogs to gain access to a reproductive habitat.

Adult males vocalize from in and around the internode of the native bamboo *Ochlandra travancorica* nocturnally (Fig. 2). Adult males (and presumably females) enter and exit the bamboo internode through small narrow openings located towards the base (downward side) of internodes (Fig. 3A–F). Small numbers of eggs (5–8 eggs) are deposited approximately 25 cm above the opening (Fig. 4A). Adult males remain inside and continue vocalizing while providing egg attendance until eggs hatch. Hence, multiple egg clutches can be found within the same internode (Fig. 4B, C). Froglets remain near egg capsules after hatching for c. 24 h (Fig. 4D).

NEST CAVITY

In 10 out of 20 instances, males were either heard vocalizing or seen entering or exiting the internode. Egg clutches were found only in four of these bamboo
internode sections. In all four cases, adult males were always found within the internode. The five of the remaining six cases had no egg clutches, but had vocalizing adult males and in one instance both male and female were found inside bamboo. In 15 focal observations, adult males were observed vocalizing outside internodes six times. One female and one juvenile were observed on bamboo at night. In remaining occasions, males were heard vocalizing inside internodes but were not disturbed. Snout to vent length of males was 23.7 ± 2.66 mm (N = 3, 20.6–25.2) and one female was 25.2 mm long. All egg clutches observed were inside a single species of a Western Ghats endemic bamboo, *Ochlandra travancorica*, which grows extensively along streams and up to 5 m in height. On a few occasions, *R. chalazodes* was also observed on stalks of other bamboo species like *O. scriptoria* which is more common away from streams, but no nest cavities were found in it though it had openings similar to those on *O. travancorica.* *R. ochlandrae* has however been observed in internodes of many *Ochlandra* spp. Stalks of *O. travancorica* had a narrow opening through which frogs entered and exited the hollow internode. All bamboo where egg clutches were observed had openings at the lower ends of internodes (up to almost mid-point) with eggs laid above openings. Characteristics of bamboo stems having egg clutches (N = 2) and having froglets (N = 1) were (mean ± SD in mm with range in parenthesis): outer diameter of stems = 26.5 ± 6.6 mm (range: 22–34.2 mm); inner diameter = 16.4 ± 5.02 mm (range: 13–22.2 mm); length of opening = 39.0 ± 32.88 (range: 20–77 mm); width of opening = 3.4 ± 2.77 mm (range: 0.5–6.0 mm); internode length = 546.3 ± 127.16 mm (range: 400–630 mm) and upper end of opening to nearest egg in each egg clutch = 277.0 ± 187.96 mm (range: 77–450 mm). The bamboo is naturally present in clumps of 13–86 individual bamboo stems/clump (mean = 36.5 ± 34 stems/clump).

![Figure 2. Raorchestes chalazodes in natural habitat. A, Ochlandra travancorica bamboo along streams. Height about 5 m. B, Male R. chalazodes on the internode. C, Male R. chalazodes vocalizing outside the internode opening.](image-url)
EGG CLUTCHES AND EMBRYO DEVELOPMENT

Eggs were spherical and transparent with creamy white yolks. They were attached to the inner walls of the bamboo by means of a mucilaginous strand. Multiple clutches were separated by only a few millimetres (Fig. 4B) and averaged $1.5 \pm 1$ clutches per internode ($N = 6$). Clutch size was $6.7 \pm 1.2$ egg/clutch ($N = 4$) and eggs were $5.73 \pm 0.66$ mm in diameter ($N = 28$ from five clutches). The ratio of egg yolk to the outer jelly was rather small (Fig. 5A). Four focal-observation clutches were covered with debris (Fig. 5A–D) and were in different stages of development (Table 1).

COMPARISONS OF R. CHALAZODES AND R. OCHLANDRAE

Both species, though geographically separated by a physical barrier ‘Palghat Gap’ (Robin, Sinha & Ramakrishnan, 2010) are comparable in reproductive modes (Table 2). Geographic ranges of these species do not overlap and nesting occurs inside different species of bamboo. However, morphology and nest characteristics are similar (Fig. 6). In both species, eggs are found on upward end of internode and openings are near the downward end of internodes. Adult frogs are found inside internodes with egg

Figure 3. Snapshots of male R. chalazodes entering the nest cavity inside a bamboo internode. A, male entering by inserting head; B, mid dorsum and forearms inserted; C, forearms used to haul body in; D, forelimbs almost completely inserted; E, anterior portion of body almost entirely inserted, legs remain outside and; F, legs being pulled inside, one-by-one. Entry sequence lasted almost 30 s. Measurements of frog and internode provided in text. A video grab of this sequence is available at: http://amphibiaweb.org/species/4399.
clutches, indicating parental care. Thus, we consider a single reproductive mode to characterize both R. chalazodes and R. ochlandrae.

**DISCUSSION**

Studies attempting to understand anuran behaviour in an evolutionary framework are rather sparse, largely owing to inadequate life history data (Wells, 1977; Crump, 1995; Bee et al., 2013). Adaptation to constraints towards increasing reproductive fitness drives the general trajectory of diverse life history strategies (Gadgil & Bossert, 1970; Stearns, 1992; Wells, 2007). Reproductive strategies in amphibians, and anurans in particular, have evolved multiple times from aquatic eggs, resulting in direct developing terrestrial eggs lacking dependence on free-standing water (Wells, 2007; Gomez-Mestre et al., 2012; da Silva, Candeira & de Cerqueira Rossa-Feres, 2012; Poo & Bickford, 2013). There exist 16 aquatic reproductive modes compared to 23 non-aquatic (terrestrial) modes when egg deposition site alone is considered (Wells, 2007). Direct development is
reported for 13 unrelated anuran families and in 80 genera, indicating it to be a derived character (Wells, 2007; Gomez-Mestre et al., 2012; Frost, 2014). Such trends in increasing terrestriality are characterized by frogs occurring in wet and warm climates, with life history trade-offs like smaller sized adults depositing fewer but larger eggs, and presence of parental care (Wells, 2007; Gomez-Mestre et al., 2012).

The reproductive mode described here, with direct developing eggs deposited inside a hollow bamboo internode, resembles Wells’ mode 26 (Wells, 2007) in terms of eggs deposited inside hollow bamboo where they hatch out into aquatic free living larvae (e.g., genus: Nyctixalus, Chirixalus). However, it differs drastically since both Raorchestes chalazodes and Raorchestes ochlandrae enter hollow bamboo internodes via small openings and deposit eggs that undergo direct development without water. Also, adults of Raorchestes chalazodes enter hollow bamboo through a narrow opening that offers considerable resistance (Fig. 3; http://amphibiaweb.org/species/4399). This behaviour and the absence of egg clutches outside bamboo indicate that deposition of eggs inside bamboo internodes is a non-random event. Some anurans are also known to actively track breeding resources, exhibit pronounced nesting site fidelity, and breed in leks (Wells, 1977; Ursprung et al., 2011). The Hemiphractid frog Fritziana ohausi from Brazil is known to carry eggs on dorsal pouch and deposit tadpoles in water filled bamboo cavities and has been ascribed to mode 36 (Duellman & Gray, 1983; Wells, 2007). Such dependence on limited resources appears to be critical in several reproductive modes and numerous interesting questions on habitat usage and social interactions among anurans could be asked.

In this report, males appear to track internodes with openings and vocalize to attract females. Systematic searches in the non-breeding season (December–January) have yielded neither adult nor juveniles from within internodes (~40 h of searching).

Table 1. Developmental stages of embryos of R. chalazodes. Stages are in comparison to Pseudophilautus viridis from Sri Lanka (Bahir et al., 2005)

<table>
<thead>
<tr>
<th>Clutch number</th>
<th>Clutch size</th>
<th>Average egg diameter ± SD (mm)</th>
<th>Developmental stage</th>
<th>Characters</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>8</td>
<td>5.09 ± 0.32</td>
<td>5a–6a</td>
<td>Limb differentiation initiated, appears as short stubs. Eyes rather large and pigmented with black. Tail fully developed with prominent venation.</td>
</tr>
<tr>
<td>2</td>
<td>7</td>
<td>6.24 ± 0.55</td>
<td>7a–8a</td>
<td>Head formed. Eyes black. Forelimb as emerging stubs. Toe differentiation in hind limbs initiated. Tail fully emerged.</td>
</tr>
<tr>
<td>3</td>
<td>7</td>
<td>6.29 ± 0.30</td>
<td>6–7a</td>
<td>Hind limb nearing completion. Tail fully developed with prominent venation.</td>
</tr>
<tr>
<td>4</td>
<td>5</td>
<td>5.35 ± 0.34</td>
<td>1</td>
<td>Un-pigmented eggs. Neural fold formation initiated.</td>
</tr>
</tbody>
</table>

Note: Figure 4B, C depicts clutch 2 (B, only four eggs visible); clutch 3 (B, seven eggs); clutch 1 (C, eight eggs at a later stage). Figure 5A–C depicts later stages (~96 h since first observation) of clutch 4 (A, two eggs visible); clutch 3 (B, two eggs visible) and clutch 4 (C, one egg visible).

Table 2. Comparisons of R. chalazodes and R. ochlandrae. Mean ± SD in mm (range) are provided

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Characteristics</th>
<th>Raorchestes chalazodes</th>
<th>Raorchestes ochlandrae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anuran</td>
<td>Elevation</td>
<td>&gt; 1000 m amsl</td>
<td>−600–1000 m amsl</td>
</tr>
<tr>
<td></td>
<td>Clutch size</td>
<td>6.7 ± 1.2 (5–8; N = 4)</td>
<td>6 (N = 1)</td>
</tr>
<tr>
<td></td>
<td>Egg diameter</td>
<td>5.73 ± 0.6 (4.7–6.7; N = 28)</td>
<td>4.94 ± 0.06 (4.87–5.01; N = 6)</td>
</tr>
<tr>
<td></td>
<td>Snout to vent length</td>
<td>23.75 ± 2.6 (20.6–25.5)</td>
<td>24.0 ± 1.38 (22.1–25.6)</td>
</tr>
<tr>
<td>Bamboo</td>
<td>Outer diameter of stems</td>
<td>26.5 ± 6.6 (22–34.2)</td>
<td>81.5 ± 9.3 (70–90)</td>
</tr>
<tr>
<td></td>
<td>Length of opening</td>
<td>39.0 ± 32.8 (20–77)</td>
<td>−27 (NA)</td>
</tr>
<tr>
<td></td>
<td>Width of opening</td>
<td>3.4 ± 2.7 (0.5–6.0)</td>
<td>−5 (NA)</td>
</tr>
<tr>
<td></td>
<td>Species of bamboo</td>
<td>Ochlandra travancorica</td>
<td>Ochlandra setigera</td>
</tr>
</tbody>
</table>

reported for 13 unrelated anuran families and in 80 genera, indicating it to be a derived character (Wells, 2007; Gomez-Mestre et al., 2012; Frost, 2014). Such trends in increasing terrestriality are characterized by frogs occurring in wet and warm climates, with life history trade-offs like smaller sized adults depositing fewer but larger eggs, and presence of parental care (Wells, 2007; Gomez-Mestre et al., 2012).
Females are presumably polyandrous and move from one internode to the next. Amplexus, if present, must occur inside the internode. Our findings suggest that frogs occupy bamboo only if the opening is at the base of the internode. An internode with an opening on top would result in collection of water inside, possibly flooding the eggs or drowning the froglets.

In terms of larval development, the mode we describe resembles modes 23, 27, and 37 (Wells, 2007) where eggs undergo direct development. However, R. chalazodes and R. ochlandrae differ from modes 23 and 27, where eggs are deposited in a terrestrial and arboreal nest respectively (e.g., Eleutherodactylus and Platymantis for both modes). Our report also differs from mode 37 where direct developing eggs are carried on the dorsum of the female (e.g., Stefania). The new mode is different from all three aforementioned modes since the species involved do not build an arboreal or terrestrial nest nor does it carry eggs on dorsum.

The reproductive mode in R. ochlandrae was ascribed (Gururaja et al., 2007) to Wells’ mode 27 (Wells, 2007) but our study shows that, it is the same as that of R. chalazodes. This similarity of reproductive mode between the two species suggests that it is either the result of parallel evolution, or is ancestral in the lineage; however, a phylogeny of this clade is not currently available to understand the evolution of this trait. The northern part of Palghat Gap forms the southern limits for R. ochlandrae and the southern part of Shencotah forms the northern limits of R. chalazodes (Gururaja, 2012). The bamboo species (O. travancorica and O. setigera) are also endemic to the Western Ghats but commonly found along streams in higher elevations irrespective of the barriers (c. 700–1800 amsl; Gopakumar & Motwani, 2013).

**Factors Leading to Parental Care**

Parental care of developing larvae/embryo enhances reproductive success (Crump, 1996; Wells, 2007; Gomez-Mestre et al., 2012). There appears to be common trajectories in behaviour and nest characteristics of anurans having parental care of direct developing eggs. Some of these include smaller clutch sizes, larger eggs, and egg attendance. Multiple egg clutches are also seen at a particular egg deposition site, indicating that males might defend territories (Crump, 1996). Parental care is strongly interdependent on life history traits and has commonly been found in species undergoing direct development, having fewer but larger eggs, and living in lotic environments or areas with seasonal small water bodies (Poo & Bickford, 2013). Multiple causes and consequences of parental care have been discussed (McDiarmid, 1994; Crump, 1996; Wells, 2007). Only a few recent studies have been able to examine costs, benefits, and fitness effects of such parental care behaviour (Cheng et al., 2013; Poo & Bickford, 2013). However, there has been a strong emphasis on the dearth of detailed observations and baseline information to fully understand the evolutionary significance of parental care (Wells, 1977; Crump, 1996; Sterns, 2000; Lehtinen & Nussbaum, 2003; Bee et al., 2013).

**Threats from Habitat Loss**

Among bamboo nesting frogs, only R. chalazodes is critically endangered with small populations occurring in fewer than five localities. However, bamboo nesting frogs are threatened by overharvest of bamboo outside of protected areas for paper and pulp. Often, harvesting coincides with the breeding season of these frogs and viable populations can be decimated (Abraham, 2011). Since the frog only breeds in bamboo internodes, unregulated overharvest of bamboo might destroy breeding habitats and negatively impact long-term viability of populations. It is imperative that further studies be initiated for developing frog-friendly harvest techniques involving companies and managers for conserving these unique frogs.

**Future Directions**

Though South and South-East Asia harbours a rich diversity of amphibians, there is large gap in knowledge as life history accounts exist for only a few species (e.g., Summers, McKeon & Heying, 2006;
costs and benefits leading to the evolution of novel resource availability will also be necessary to discern removal experiments and experiments restricting uncover such behaviour and this report will encourage Rhacophoridae exist. Intensive work will be needed to other parts of South-East Asia where other species of Asia is limited. The novel reproductive mode reported here could be more common and found to occur across other parts of South-East Asia where other species of Rhacophoridae exist. Intensive work will be needed to uncover such behaviour and this report will encourage further research on amphibian diversity in the South-East Asian region. Carefully designed adult removal experiments and experiments restricting resource availability will also be necessary to discern costs and benefits leading to the evolution of novel reproductive mode reported here.

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