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Developments in Amphibian Parental Care Research: History, Present Advances, and Future Perspectives

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Abstract: Despite rising interest among scientists for over two centuries, parental care behavior has not been as thoroughly studied in amphibians as it has in other taxa. The first reports of amphibian parental care date from the early 18th century, when Maria Sibylla Merian went on a field expedition in Suriname and reported frog metamorphs emerging from their mother's dorsal skin. Reports of this and other parental behaviors in amphibians remained descriptive for decades, often as side notes during expeditions with another purpose. However, since the 1980s, experimental approaches have proliferated, providing detailed knowledge about the adaptive value of observed behaviors. Today, we recognize more than 30 types of parental care in amphibians, but most studies focus on just a few families and have favored anurans over urodeles and caecilians. Here, we provide a synthesis of the last three centuries of parental care research in the three orders comprising the amphibians. We draw attention to the progress from the very first descriptions to the most recent experimental studies, and highlight the importance of natural history observations as a source of new hypotheses and necessary context to interpret experimental findings. We encourage amphibian parental care researchers to diversify their study systems to allow for a more comprehensive perspective of the behaviors that amphibians exhibit. Finally, we uncover knowledge gaps and suggest new avenues of research using a variety of disciplines and approaches that will allow us to better understand the function and evolution of parental care behaviors in this diverse group of animals.

Key words: Anurans; Behavior; Caecilians; Ecology; Evolution; Hormones; Urodeles

The development of a scientific field (or subfield) is an intricate process involving detours, failures, and unexpected flukes. It usually starts with random observations noted in the margins during an unrelated study. Something peculiar catches the eye, awakens interest, and opens doors to a whole new field of research. This process is often sluggish and punctuated; for example, the outstanding importance of DNA was not realized until 75 yr after Miescher first discovered it (Dahm 2008).

In the biological sciences, new subfields generally start with purely descriptive work, which builds an essential foundation of knowledge: new species, morphological structures, histological features, or unique behaviors. These descriptions start to draw pictures of potential function and significance, forming hypotheses to be tested, which thereupon lead to new questions, hypotheses, and discoveries that ultimately create new scientific subfields. For example, the field contemporarily known as "evo-devo" was catalyzed in the 1980s when parallel observations in fields such as evolutionary genetics, molecular biology, and embryology were first transformed into "how" questions about the integrative mechanisms underlying the significance and function of evolutionary development (Love 2015).

Within the field of animal behavior, numerous subfields have emerged in the last few decades. Many started because a particular organism exhibited extraordinary characteristics. Over time, similar behaviors were found in other species, and the classification of the behavior shifted from a unique anomaly to a widespread pattern. For example, initial observations of recently hatched chicks following a hen (Spalding 1873) propagated subfields focused on imprinting and animal learning (e.g., Moore 2004; Dukas 2013; Martinho and Kacelnik 2016). Anecdotal observations are also the origin of the study of parental care behavior (e.g., Lottinger 1776; Jiménez de la Espada 1872; Lydekker 1895), which has since been broadly investigated with diverse approaches including genetic, neurological, ecological, and hormonal studies.

Despite their widespread occurrence across the animal kingdom, parental behaviors have been investigated in detail mostly in mammals (e.g., Gubernick and Klopfer 1981; Rilling and Young 2014; Wu et al. 2014) and birds (see Stahlschmidt 2011). Many other vertebrate and invertebrate groups demonstrate unique and incredibly diverse parental care behaviors (e.g., insects, Fetherston et al. 1990; Gilbert and Manica 2010; crustaceans, Dick et al. 1998; Thiel 2007; arachnids, Simpson 1995; Yip and Rayor 2014; fish, Goodwin et al. 1998; Steinhart et al. 2008; Buckley et al. 2010; amphibians, Crump 1996, 2015; Gomes et al. 2012; Kupfer et al. 2016; reptiles, O'Connor and Shine 2004; Vergne et al. 2009), but these groups have received much less attention in the animal behavior literature. However, many recent advances in parental care have emerged from research in these lesser studied groups. For example, a deeper understanding of the roles of hormones, neurobiology, experience, and social impact in parental care mechanisms and strategies has emerged from work with insects and fish (O'Connell et al. 2012; Wong et al. 2013; Samuk et al. 2014; Santangelo 2015; Schrader et al. 2015).

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As part of the reproductive cycle, parental care is often an essential component of an individual's fitness (Gross 2005), and parents need to balance their investments between current offspring, further mating opportunities (Székely and Cuthill 2000), future offspring (e.g., parent–offspring conflict; Trivers 1974), and predation risk. For this reason, the strategies utilized among—and sometimes within—different species vary substantially, and selective pressures for alternative parental care strategies among taxa can shape other traits, such as habitat choice, morphological structures, or cognitive abilities.

In this review, we chronicle the development of parental care research in a group that has been identified as one of the most neglected (see Stahlschmidt 2011 for comparison among different animal groups): the amphibians. This group—comprised of gymnophionans (caecilians), urodeles (newts and salamanders), and anurans (frogs and toads)—in fact exhibits one of the most diverse assemblages of parental-care behaviors known to date (Crump 1996). As explained by Crump (1996), parental care is sometimes defined as a behavior that increases survivorship of young (Clutton-Brock and Vincent 1991), but more generally refers to nongametic investments in offspring that incur a cost to the parent. Here, we consider presumably costly behaviors that parents perform for the benefit of offspring both prior to hatching, oviposition, or birth (e.g., nest construction, intrauterine feeding) and after (e.g., egg attendance or brooding, tadpole transport) as parental care, but we do not include reproductive modes (e.g., viviparous, oviparous). Although in many taxa the true nature of parental costs remains to be defined or quantified, we have included cases for which future research seems likely to reveal that parents incur costs.

A series of review papers have strived to classify parental behaviors into types, expanding the list when new forms of care have been discovered and merging similar forms when obvious coincidences are identified (e.g., Wunder 1932; McDiarmid 1978; Wells 1981; Crump 1996; Lehtinen and Nussbaum 2003; Haddad and Prado 2005). Because of new discoveries, the percentage of species recognized as providing parental care steadily rises; up to 10% of anuran and 20% of urodelian species care for their offspring after fertilization (Balshine 2012; Crump 2015). It is assumed that most caecilians provide some form of parental care, but information about the reproductive behavior of this group is relatively scarce. Among the review papers, some offer generalized overviews (e.g., Crump 1996, 2015), whereas others pursue specific research questions, such as relationships between parental care and egg size (Nussbaum and Schultz 1989; Summers and McKeon 2006), phylogenetics (Lehtinen and Nussbaum 2003), and fetal or larval morphology (Altig and Johnston 1989; Wake 2015). Although some reviews list parental-care modes of all amphibians (Salthe and Mecham 1974; Crump 1996), several focus purely on anurans (Lamotte and Lescure 1977; Duellman 1992; Beck 1998; Crump 2015). Only a few works review urodelian parental care (Ryan 1977; Nussbaum 1985, 1987; Kupfer et al. 2016), and—to the best of our knowledge—only one review touches on parental care in caecilians (Gomes et al. 2012).

Here, we try to draw a comprehensive picture of parental care in amphibians, including all three orders across centuries of research. Our review not only summarizes the known parental-care modes, but also recounts the progress of amphibian parental care research since it was first reported in the late 17th century. We recap the full ontogeny, from early natural history descriptions, to the hypothesis-based knowledge that budded out from those descriptions, and finally to modern synthetic approaches that are bound to trigger a metamorphosis in our understanding of the function and evolution of amphibian parental care.

Materials and Methods

This review aims to provide a comprehensive resource and synthesize research papers and books describing or studying parental-care behaviors in amphibians. We conducted a thorough literature search on Web of Science in 2017, using the search terms "anura*, frog*, toad*, tadpole*, froglet*, salamander*, newt*, urodela*, caudata*, caecilia*, gymnophiona*, or amphibia*" in combination with "parental care, guard*, attend*, paternal*, maternal*, egg-feed*, oophagous, begg* or provision." We also combined the first five search terms with "transportation." We carefully checked all search results, and cross-referenced them with previous reviews (see introduction). To search for very old records (given that this review covers over 300 yr of research), we examined old reports and searched the Biodiversity Heritage Library as well as archive.org.

Results and Discussion

Our search revealed a total of 685 studies. All references were used for data analyses, but only a subset could be cited in the text of this review. We identified over 30 parental care modes, some of which overlap between the three orders. We defined a total of four caecilian, eight urodelian, and 28 anuran parental care modes, and for each of those we tried to seek the first description, which ranged from 1705 to 2017 (see Table 1 and corresponding examples in the text). To allow for comparisons among groups, we further condensed these behaviors into the following nine parental care modes: (1) foam/bubble nest construction, (2) nest construction (digging, wrapping, or covering eggs), (3) egg attendance (defending, cleaning, hydrating), (4) larvae/tadpole/froglet guarding, (5) egg transport/brooding on body or in skin, (6) offspring transport/brooding in vocal sac/stomach, (7) tadpole/froglet transportation on body, (8) feeding of free-living larvae/tadpoles, and (9) feeding of larvae/tadpoles inside the parent (in uterus or skin pouches). By mapping these modes onto a modified cladogram of currently accepted amphibian families, we found that parental-care behavior is known in 56 of 76 families (see Fig. 1). Of those, 44 families show some form of egg attendance, making it the most phylogenetically widespread parental care mode in amphibians. Twenty-nine families show one or more other parental care mode(s) besides egg attendance. One parental-care mode, feeding of free-living larvae/tadpoles, is known from 10 families, 9 of which also display egg attendance.

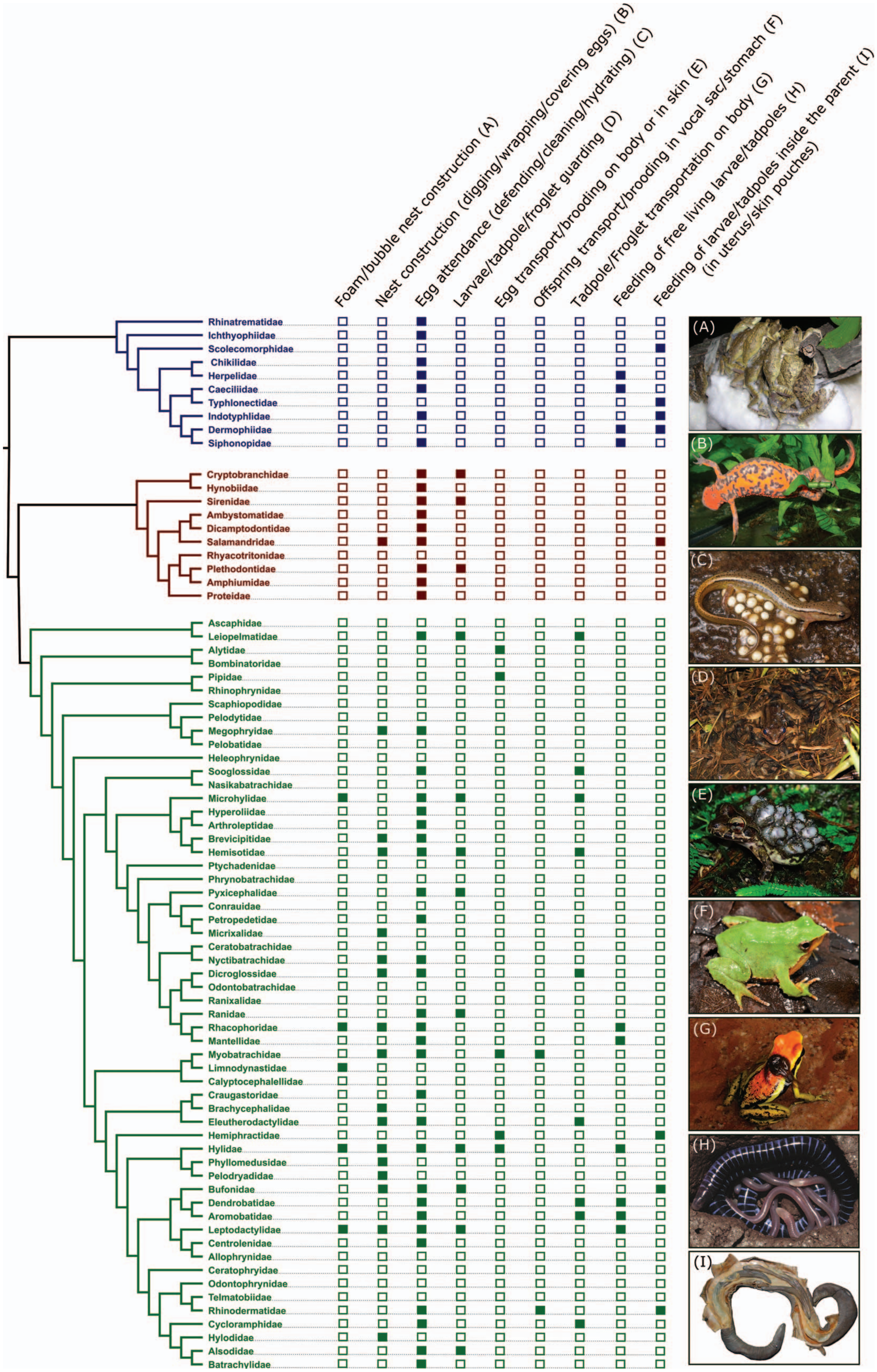
Most of the parental care modes defined in Table 1 are only found in one of the three amphibian orders. For example, offspring transportation is only known in anurans, and some forms of transport are only found in single families or genera within a family. The same is true for foam- or bubble-nest building (only in anurans) or aquatic egg-rolling

Table 1.—Parental care modes in Amphibians and (one of) their first mention(s) in the literature. The different modes are numbered by amphibian order (Caecilia = C1–4, Urodela = U1–8, Amphibia = A1–28).

Order	Number	Parental care mode	Species	First mention
Caecilia	C1	Guarding of terrestrial eggs (female)	*Ichthyophis glutinosus*	Sarasin and Sarasin (1887)
	C2	Intrauterine feeding (female)	*Schistometopum* sp.	Parker (1956)
	C3	Dermatotrophic offspring feeding (and simultaneous guarding of larvae; female)	*Geotrypetes seraphini*	O'Reilly et al. (1998)
	C4	Alloparental dermatotrophic feeding (female)	*Boulengerula taitana*	Kupfer et al. (2008)
Urodela	U1	Egg rolling/wrapping in aquatic leaves (female)	*Notophthalmus viridescens* (as *Diemyctylus*)	Gage (1891)
	U2	Guarding of terrestrial eggs (female)	*Amphiuma tridactylum*	Hay (1888)
	U3	Guarding of terrestrial eggs (male)	*Andrias japonicus* (as *Megalobatrachus maximusi*	Kerbert (1904)
	U4	Guarding of aquatic eggs while on land (until pond fills; female)	*Ambystoma opacum*	Noble (1931)
	U5	Alloparental guarding of terrestrial eggs (attendance by a nonparental adult)	*Hemidactylium scutatum*	Blanchard (1934)
	U6	Guarding of terrestrial eggs and juveniles (female)	*Speleomantes strinatii*	Oneto et al. (2010)
	U7	Guarding of aquatic eggs and juveniles (male) [*sex initially unknown*]	*Siren intermedia*	Hubbs (1962)[a]
	U8	Intrauterine feeding (female)[b]	*Salamandra atra*	Czermak (1843)
Anura	A1	Construction of foam nests (for protection, nutrition, etc.)	*Leptodactylus mystaceus* (as *Cystignathus*)	Hensel (1867)
	A2	Construction of hollows/caves for nests (for protection)	*Leptodactylus* sp. (as *Cystignathus ocellatus*)	Hensel (1867)
	A3	Construction of leave-pouch nests (for protection)	*Phyllomedusa iheringii*	von Ihering (1886)
	A4	Construction of bubble nest (biparental)	*Chiasmocleis leucosticta*	Haddad and Hödl (1997)
	A5	Usage of interspecific nests (i.e., heterospecific brood parasitism)	*Allobates sumtuosus*	Kok and Ernst (2007)
	A6	Covering the eggs with dirt (camouflage; female)	*Brachycephalus ephippium*	Pombal et al. (1994)
	A7	Guarding of terrestrial eggs (male; originally described as females)]	*Eleutherodactylus coqui* (as "co-qui" *Hylides*)	Bello (1871)
	A8	Guarding of terrestrial eggs (female)	*Leptodactylus* sp. (as *L. ocellatus*)	Fernández and Fernández (1921)
	A9	Guarding of tadpoles (female)	*Leptodactylus* sp. (as *L. ocellatus*)	Fernández and Fernández (1921)
	A10	Guarding of froglets	*Cophixalus parkeri*	Simon (1983)
	A11	Transportation of tadpoles (male)	*Ameerega trivittata* (as *Hylodes lineatus*)	Wyman (1857)
	A12	Transportation of tadpoles (female)	*Colosthetus inguinalis*	Wells (1977)
	A13	Transportation of freshly hatched (direct-developed) froglets (females)	*Eleutherodactylus cundalli*	Diesel et al. (1995)
	A14	Transportation of freshly hatched (direct-developed) froglets (males)	*Sphenophryne cornuta*; *S. schlaginhaufeni*	Bickford (2002)
	A15	Brooding of eggs on legs; released as tadpoles (male)	*Alytes obstetricans* (not named yet in 1741)	Demours (1741)
	A16	Brooding of eggs on in dorsal pouches/basins; released as tadpoles (female)	*Fritziana goeldii* (as *Hyla*)	Göldi (1895)
	A17	Brooding of eggs in dorsal pouches; released as froglets (female)	*Gastrotheca ovifera* (as *Notodelphys*)	Weinland (1854)
	A18	Brooding of eggs embedded in dorsum of aquatic species; released as froglets (female)	*Pipa pipa* (not named yet in 1705)	Merian (1705)
	A19	Brooding of eggs in dorsum depressions, froglets attached to back with special gills (female)	*Hemiphractus bubalus* (as *Cerathyla*)	Boulenger (1903)
	A20	Brooding of eggs exposed on the dorsum; released as froglets (female)	*Stefania evansi* (as *Hyla*)	Boulenger (1904)
	A21	Brooding of eggs in stomach; released as froglets (female)	*Rheobatrachus silus*	Corben et al. (1974)
	A22	Brooding of eggs (in late developmental stage) and tadpoles in the vocal sac; released as froglets (male)	*Rhinoderma darwinii*	Jiménez De La Espada (1872)
	A23	Brooding of freshly hatched tadpoles on the dorsum; released as froglets (female)	*Cycloramphus stejnegeri* (as *Craspedoglossa*)	Heyer and Crombie (1979)
	A24	Brooding of freshly hatched tadpoles on the dorsum; released as froglets (male)	*Anomaloglossus degranvillei* (as *Colostethus*)	Lescure (1984)
	A25	Brooding of freshly hatched tadpoles in inguinal pouches; released as froglets (males)	*Assa darlingtoni* (as *Crinia*)	Straughan and Main (1966)
	A26	Intrauterine feeding (female)	*Nimbaphrynoides occidentalis* (as *Nectophrynoides*)	Vilter and Lugand (1959)
	A27	Feeding of tadpoles with eggs (female)	*Oophaga pumilio* (as *Dendrobates*)	Graeff and Schulte (1980)
	A28	Feeding of tadpoles with eggs (biparental)	*Ranitomeya imitator* (as *Dendrobates reticulatus*)	Kneller (1982)

[a] Aquatic egg guarding (but not juvenile guarding) was already described in *Andrius japonicas* by Kerbert (1904).

[b] Suggested nutritive uptake from thickened uterine walls with gills instead of teeth.



	Foam/bubble nest construction (A)	Nest construction (digging/wrapping/covering eggs) (B)	Egg attendance (defending/cleaning/hydrating) (C)	Larvae/tadpole/froglet guarding (D)	Egg transport/brooding on body or in skin (E)	Offspring transport/brooding in vocal sac/stomach (F)	Tadpole/Froglet transportation on body (G)	Feeding of free living larvae/tadpoles (H)	Feeding of larvae/tadpoles inside the parent (I) (in uterus/skin pouches)
Rhinatrematidae	□	□	■	□	□	□	□	□	□
Ichthyophiidae	□	□	■	□	□	□	□	□	□
Scolecomorphidae	□	□	□	□	□	□	□	□	■
Chikilidae	□	□	■	□	□	□	□	□	□
Herpelidae	□	□	■	□	□	□	□	■	□
Caeciliidae	□	□	■	□	□	□	□	■	□
Typhlonectidae	□	□	□	□	□	□	□	□	■
Indotyphlidae	□	□	■	□	□	□	□	□	■
Dermophiidae	□	□	□	□	□	□	□	■	■
Siphonopidae	□	□	■	□	□	□	□	■	□
Cryptobranchidae	□	□	■	■	□	□	□	□	□
Hynobiidae	□	□	■	□	□	□	□	□	□
Sirenidae	□	□	■	■	□	□	□	□	□
Ambystomatidae	□	□	■	□	□	□	□	□	□
Dicamptodontidae	□	□	■	□	□	□	□	□	□
Salamandridae	□	■	■	□	□	□	□	□	■
Rhyacotritonidae	□	□	□	□	□	□	□	□	□
Plethodontidae	□	□	■	■	□	□	□	□	□
Amphiumidae	□	□	■	□	□	□	□	□	□
Proteidae	□	□	■	□	□	□	□	□	□
Ascaphidae	□	□	□	□	□	□	□	□	□
Leiopelmatidae	□	□	■	■	□	□	■	□	□
Alytidae	□	□	□	□	■	□	□	□	□
Bombinatoridae	□	□	□	□	□	□	□	□	□
Pipidae	□	□	□	□	■	□	□	□	□
Rhinophrynidae	□	□	□	□	□	□	□	□	□
Scaphiopodidae	□	□	□	□	□	□	□	□	□
Pelodytidae	□	□	□	□	□	□	□	□	□
Megophryidae	□	■	■	□	□	□	□	□	□
Pelobatidae	□	□	□	□	□	□	□	□	□
Heleophrynidae	□	□	□	□	□	□	□	□	□
Sooglossidae	□	□	■	□	□	□	■	□	□
Nasikabatrachidae	□	□	□	□	□	□	□	□	□
Microhylidae	■	□	■	■	□	□	■	□	□
Hyperoliidae	□	□	■	□	□	□	□	□	□
Arthroleptidae	□	□	■	□	□	□	□	□	□
Brevicipitidae	□	■	■	□	□	□	□	□	□
Hemisotidae	□	■	■	■	□	□	■	□	□
Ptychadenidae	□	□	□	□	□	□	□	□	□
Phrynobatrachidae	□	□	□	□	□	□	□	□	□
Pyxicephalidae	□	□	■	■	□	□	□	□	□
Conrauidae	□	□	□	□	□	□	□	□	□
Petropedetidae	□	□	■	□	□	□	□	□	□
Micrixalidae	□	■	□	□	□	□	□	□	□
Ceratobatrachidae	□	□	□	□	□	□	□	□	□
Nyctibatrachidae	□	■	■	□	□	□	□	□	□
Dicroglossidae	□	■	■	□	□	□	■	□	□
Odontobatrachidae	□	□	□	□	□	□	□	□	□
Ranixalidae	□	□	□	□	□	□	□	□	□
Ranidae	□	□	■	■	□	□	□	□	□
Rhacophoridae	■	■	■	□	□	□	□	■	□
Mantellidae	□	□	■	□	□	□	□	■	□
Myobatrachidae	□	■	■	□	■	■	□	□	□
Limnodynastidae	■	□	□	□	□	□	□	□	□
Calyptocephalellidae	□	□	□	□	□	□	□	□	□
Craugastoridae	□	□	■	□	□	□	□	□	□
Brachycephalidae	□	■	□	□	□	□	□	□	□
Eleutherodactylidae	□	■	■	□	□	□	■	□	□
Hemiphractidae	□	□	□	□	■	□	□	□	■
Hylidae	■	■	■	■	■	□	□	■	□
Phyllomedusidae	□	■	□	□	□	□	□	□	□
Pelodryadidae	□	■	□	□	□	□	□	□	□
Bufonidae	□	■	■	■	□	□	□	□	■
Dendrobatidae	□	□	■	□	□	□	■	■	□
Aromobatidae	□	□	■	□	□	□	■	■	□
Leptodactylidae	■	■	■	■	□	□	□	■	□
Centrolenidae	□	□	■	□	□	□	□	□	□
Allophrynidae	□	□	□	□	□	□	□	□	□
Ceratophryidae	□	□	□	□	□	□	□	□	□
Odontophrynidae	□	□	□	□	□	□	□	□	□
Telmatobiidae	□	□	□	□	□	□	□	□	□
Rhinodermatidae	□	□	■	□	□	■	□	□	■
Cycloramphidae	□	□	■	□	□	□	■	□	□
Hylodidae	□	■	□	□	□	□	□	□	□
Alsodidae	□	□	■	■	□	□	□	□	□
Batrachylidae	□	□	■	□	□	□	□	□	□

FIG. 1.—Cladogram of amphibian families (modified after Pyron and Wiens 2011, with data from Frost 2019) with a simplified list of known parental care behaviors. (A) *Chiromantis xerampelina* (Rhacophoridae) building foam nests (photo: P. Byrne); (B) female *Cynops pyrrhogaster* (Salamandridae) wrapping eggs in leaves (photo: M. Sparreboom); (C) *Eurycea cirrigera* (Plethodontidae) during egg attendance (photo: B.D. Todd); (D) *Leptodactylus insularum* (Leptodactylidae) female guarding tadpoles (photo: K. Hurme); (E) *Cryptobatrachus boulengeri* (Hemiphractidae) female brooding directly developing eggs on her back (photo: L.A. Rueda); (F) *Rhinoderma darwinii* (Rhinodermatidae), a species with tadpole development inside the male's vocal sac (photo: H. Werning); (G) *Ameerega bassleri* (Dendrobatidae) transporting tadpoles (Photo: E. Twomey); (H) *Boulengerula taitanus* (Herpelidae) feeding larvae with skin (photo: A. Kupfer); (I) *Typhlonectes natans* (Typhlonectidae) female with offspring, dissected during intrauterine feeding (photo: A. Kupfer). A color version of this figure is available online.

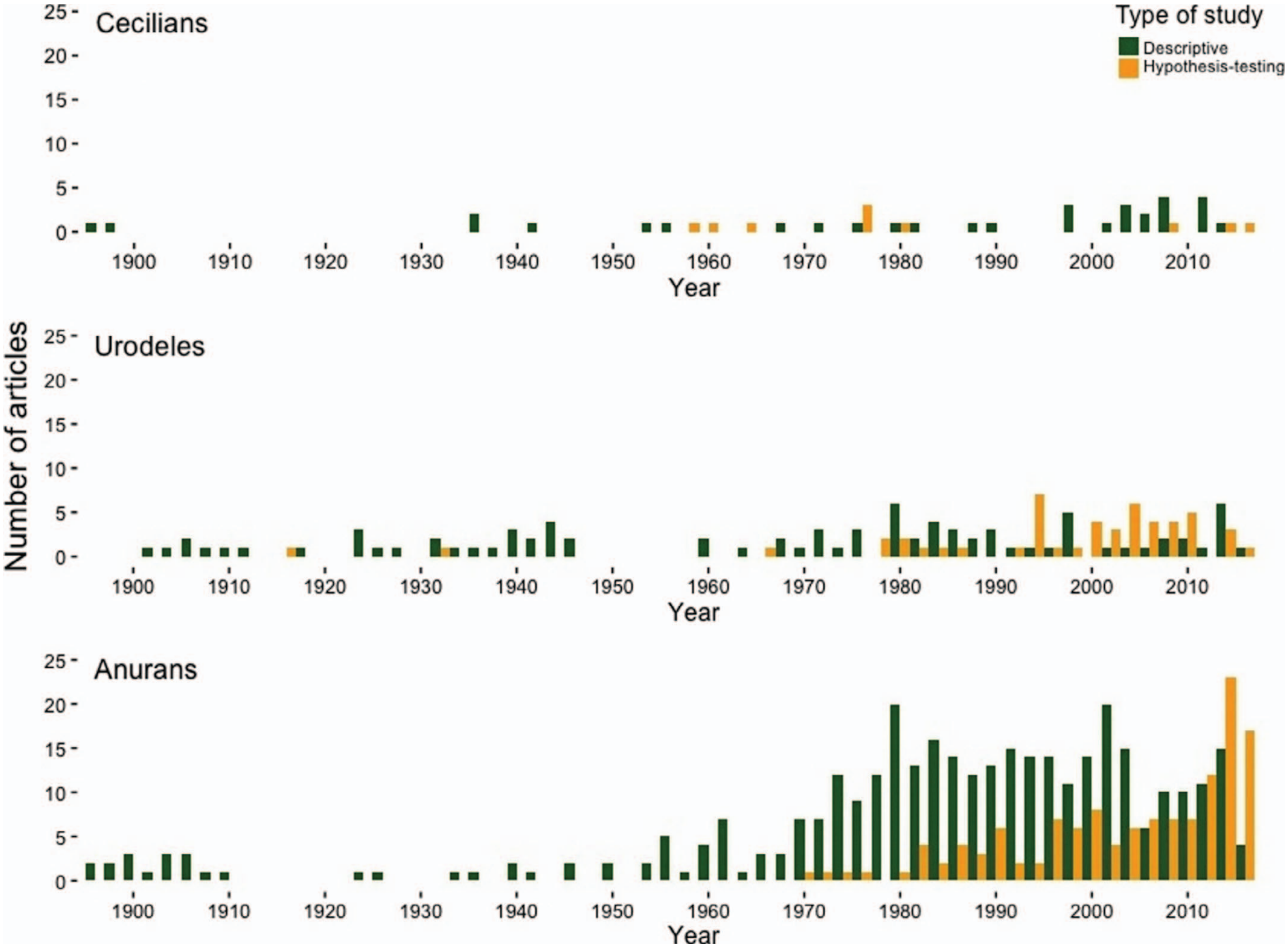


Fig. 2.—Number of studies about parental care behaviors in caecilians, urodeles, and anurans after 1900 that were identified in our literature review. A color version of this figure is available online.

(only in urodelians), as well as egg-feeding (only in anurans) or dermatotrophic feeding (only in caecilians; Table 1). On the other hand, some parental-care modes are found across several families within all three amphibian orders. It has been suggested that the most common behavior, female terrestrial egg guarding (Table 1), has evolved convergently across different families and orders (Crump 1996). Intrauterine feeding also appears to have evolved multiple times in unrelated species (Wake 1993). Ideally, patterns that emerge in the cladogram (Fig. 1) will stimulate future research on the evolution of parental care modes across amphibians.

This literature review aims to go beyond depicting the currently described forms of parental care (Table 1; Fig. 1), and also focuses on the discovery and approaches to understanding these behaviors over the history of research. Therefore, it is structured chronologically: starting with observations from the early past (1705–1950), followed by hypothesis- and experiment-based approaches of the recent past and present (since 1951), and finishing with future perspectives that emphasize multidisciplinary approaches and applications of parental care studies in times of habitat destruction and climate change.

The Early Past: (1705–1950): First Observations and Anecdotal Reports

The first descriptions of parental care in amphibians appeared in the 18th century, with a subsequent exponential increase in publication rate over the last 275 yr (Fig. 2). Prior to 1950, most of the amphibian literature consisted of either descriptive natural history notes—oftentimes as anecdotal side notes within travel reports—or studies focused on taxonomy, morphology, or anatomy. Some of these observations about parental care became important later, sparking more profound studies, and others still represent the only information available about the parental behavior of a given species. Such limited knowledge is concerning, given recent worldwide declines of amphibian populations, including the presumed extinction of species with very special parental behaviors such as *Rheobatrachus silus*, *Rhinoderma rufum*, *Gastrotheca coeruleomaculatus*, and *Nectophrynoides poyntoni* (see below).

Caecilians

Because of their hidden and often subterranean lifestyle, caecilians are the least understood of the three amphibian orders, which is reflected in the relatively low amount of parental care research in this group (Fig. 2). However, caecilian parental behavior was first mentioned as far back as the late 19th century, when Sarasin and Sarasin (1887) described female *Ichthyophis glutinosus* coiling around eggs. The authors were already proposing hypotheses about adaptive benefits of this behavior via protection from desiccation and predation. They observed that females lost and embryos gained weight, and speculated that females may give nutrients in form of skin secretions to their young.

Brauer (1897) disagreed with the idea that females could provision nutrients to offspring while describing the maternal behavior of oviparous *Hypogeophis rostratus* and *Grandisonia alternans*. An anecdotal description of maternal care in the direct developing *Siphonops annulatus* was given by Göldi (1899), reporting a female coiled around her eggs. More than 30 yr later, Parker (1936) and Sanderson (1937) described female *Idiocranium russeli* coiling around direct developing eggs. Sanderson (1937) furthermore observed that females spit at intruders (although this could not be confirmed in later studies; Gower et al. 2015). He also gave the first report of parental care by a viviparous caecilian, *Geotrypetes seraphini*, describing a female "wrapped around a bundle of smaller replicates of herself" (Sanderson 1937:222).

Only one of four caecilian parental care modes was reported in these early observations: female guarding of terrestrial eggs (caecilian parental care mode C1; Table 1). Another mode—maternal dermatotrophic offspring feeding (mode C3; see below)—was foreshadowed in *I. glutinosus* (Sarasin and Sarasin 1887), although this species does not exhibit this behavior. Dermatotrophic feeding is exhibited by *Geotrypetes seraphini*, but was described as guarding behavior in early studies of this species (Sanderson 1937), and was not officially reported until much later (O'Reilly et al. 1998).

Urodeles

Even though urodeles are much easier to find than caecilians, parental care in this group was barely mentioned before the 20th century. Hay (1888:315), for example, described a female "congo snake" (*Amphiuma tridactylum*) coiled around her eggs. He wondered how hatchlings reach the water from a terrestrial nest, proposing female transport "as a dog carries a bone"—a speculative and unconfirmed theory. Following this report, parental behavior in the family Amphiumidae went unexplored for half a century (Parker 1937; Weber 1944; Baker 1945).

In the early 20th century, egg guarding was reported in both aquatically and terrestrially breeding urodele families. In the Cryptobranchidae, male *Cryptobranchus alleganiensis* and *Andrias japonicus* were observed defending eggs against potential predators and even against mothers (Kerbert 1904; Smith 1907; Stejneger 1907). In the Plethodontidae, female (or biparental) terrestrial egg guarding was reported in several species (Ritter 1903; Strecker 1908; Piersol 1910; Wilder 1913, 1917; Bishop 1919).

A few studies in plethodontids went further than just describing behavioral observations. For example, Piersol (1910) noticed that fewer eggs became moldy when attended by female *Plethodon cinereus*, and suggested that parental skin has antifungal or antibacterial properties. Wilder (1913) noted that female *Desmognathus fuscus* found their way back to their eggs, even if their surroundings were changed. She proposed testing for offspring recognition by switching clutches between females, possibly being the first scientist to suggest hypothesis-based experiments in amphibian parental care behavior. Two years later, she conducted similar experiments, demonstrating that female *D. fuscus* will care for a foster clutch after exchange (Wilder 1917). With the exception of one other study in this same species (Noble and Evans 1932), an experimental approach like that of Wilder (1917) was (to the best of our knowledge) not further developed in the following decades.

In 1920–1950, additional descriptions (and sometimes speculations) dominated the literature, mainly regarding terrestrial egg guarding and moistening by females (e.g., Storer 1925; Bishop 1926; Blanchard 1934; Henry and Twitty 1940; Kessel and Kessel 1942; Miller 1944; Baker 1945; Storm 1947), and some males (Tago 1929; Bishop 1941). The first observations of alloparental egg guarding (attendance by a nonparental adult; Blanchard 1934) and terrestrial guarding of aquatic eggs (Noble 1931) were published. But experimental work with urodeles was lacking.

In sum, six of eight urodelian parental care modes were described before 1950: four variations on egg guarding (U2–U5 in Table 1), egg-wrapping behavior in aquatic newts (Gage 1891; U1, see below), and intrauterine feeding (U8). Czermak (1843) was the first to suggest that *Salamandra atra* offspring receive nutrition from thickened uterine walls (via the gills rather than the teeth). Several other authors supported this possibility (Schwalbe 1896; Hirzel 1909; Wunderer 1910), but the nutritive mechanism and maternal tissue was identified only recently (Guex and Chen 1986; Guex and Greven 1994; see below).

Anurans

Among the amphibian orders, parental behavior has always been best documented in anurans. To our knowledge, the first report of parental behavior in any amphibian was of a frog in the early 18th century. After a journey to Suriname in 1699, German naturalist and artist Maria Sibylla Merian (1705) published her famous book *Metamorphosis insectorum Surinamensium*. Although primarily filled with outstanding drawings of insects, this book also offered the first illustration and description of metamorphic *Pipa pipa* crawling out of a female's dorsal skin (Merian 1705; Fig. 3). Given both the remoteness of Suriname at the time and the elusive aquatic habits of *P. pipa*, it is surprising that this was the first-ever description of amphibian parental care. Aside from depicting ovaries along the female's back, Merian's description and drawing are accurate, and were confirmed more than 50 yr later by the Swedish and Dutch naturalists von Linné (1758) and Fermin (1765), who noted that female *P. pipa* hatches its young by laying them on its back. Thirty years after Merian's observations, the egg-carrying behavior of the European Midwife Toad, *Alytes obstetricans*, was described by Demours (1741, 1778). But his reports were met with disbelief, and he did not receive credit until a century later when de l'Isle du Dréneuf (1876) described the same behavior in these frogs.

In the 19th century, Boulenger (1886) gave the first review of parental behavior in anurans, listing seven species that transport their offspring. The list included the mouth-brooding frog, *Rhinoderma darwinii*, which was thought to

FIG. 3.—(A) Maria Sibylla Merian (1647–1717), first scientist to describe parental behavior in an amphibian, *Pipa pipa*. It is noteworthy that the discovery was made by a woman, especially at that time. (B) Illustration from Merian's book, *Metamorphosis insectorum Surinamensium,* showing adult female *P. pipa* with metamorphic offspring on its back and young juvenile behind her in the water. A color version of this figure is available online.

be viviparous until Jiménez de la Espada (1872) recognized that males actually incubate offspring in the vocal sac (Howes 1888; Weltner 1896; Wiedersheim 1900; Janvier 1935). The list also included *Gastrotheca ovifera*, first reported to carry eggs in dorsal pouches by Weinland (1854). Although not yet included in Boulenger's list, other species had been seen carrying eggs on their backs without pouches, such as an unknown bromeliad-dwelling species discovered by Müller (Darwin 1879) and *Fritziana goeldi*, described in the same year by Göldi (1895) and Boulenger (1895).

Boulenger (1895) also noted tadpole transport in dendrobatid poison frogs. This behavior was first described by Wyman (Wyman 1857, 1859; Boulenger 1888a), who had heard about this unusual parental care mode from a colleague (Mr. G. O. Wacker) before observing it in Suriname. Early observations of tadpole carrying in poison frogs were also made by Kappler (also in Suriname; Kappler 1885; Boulenger 1888b) and Smith (1887), who was informed about this behavior by native hunters in western Brazil. In an early review, Sampson (1900) summarized tadpole transport behavior of several dendrobatid species. Deposition of poison frog tadpoles into tree holes was first described by Eaton (1941). Brauer (1899) also reported tadpole transport behavior in male Seychellen frogs, *Sooglossus sechellensis*. He further observed these frogs guarding their eggs before transportation.

Early on, some authors hypothesized that frogs staying close to their eggs might be protecting them (Peters 1876). Von Ihering (1886) observed *Phyllomedusa iheringii* building nests by gluing leaves together, which was supported by similar observations in other species of the same genus (Mole and Urich 1894; Budgett 1899; Bles 1905; Agar 1909). Hensel (1867) observed leptodactylids digging nest sites outside of large water bodies and constructing foam nests, suggesting they might protect larvae from fish predators—a theory that reappears much later in the anuran parental care literature (see below). Some reports unintentionally describe egg guarding, such as when von Ihering (1886:462) stated, "The adult animal is a stupid creature, and will let itself be taken without attempting to escape." Most early descriptions of egg guarding assumed that care-giving parents were female (e.g., Bello 1871), but true female egg guarding was not described until the early 20th century in *Leptodactylus* sp. (Fernández and Fernández 1921).

In the first half of the 20th century, descriptions of parental care in anurans became more abundant (e.g., Bürger 1905; Krefft 1911; Noble 1926; Dunn 1941), and in some cases became the main focus of publications (e.g., Andrews 1901; Brandes and Schoebnichen 1901; Deixner 1924). For example, Boulenger (1903, 1904) described egg brooding on or in depressions of the female dorsum. However, some reports remain unconfirmed. For example, ventral egg transport in *Pseudophilautus reticulatus* (Andrews 1901), female mouth-breeding in *Leptopelis brevirostris* (Boulenger 1906), and nest building with aromatic resins in *Trachycephalus resinifictrix* (Göldi 1907) are three parental-care modes that are not known today (Schiesari et al. 2003).

Prior to 1950, 14 of 28 anuran parental care modes were described (Table 1). Wunder (1932) offered a solid review of the known parental-care modes at the time, separating offspring guarding and offspring transport, and further dividing transport into seven brood-care categories (long- and short-term tadpole transport, egg development in body cavities, etc.). These categories have been reorganized several times up to the present day (Table 1; Crump 2015). Wunder (1932) was also the first to link intensive parental care with fewer and larger eggs (see Summers and McKeon 2006) and to note that most parental-care modes are found in the tropics. Lutz (1947) also discussed the tropical biogeography of parental-care modes, and, together with her father, described several new species that conduct parental care (reviewed in Schulte and Rödder 2016). Lutz (1947) posed a key hypothesis about the evolution of brood care in anurans that is still supported today (Brown et al. 2010): that aquatic predator pressure and larval competition promoted the evolution of new breeding modes in smaller water bodies, on land, or directly on parents' bodies, and thus stimulated the evolution of complex parental behavior in anurans.

The Recent Past and Present (Since 1951): Hypothesis- and Experiment-Based Approaches

After 1950, remarkable amphibian parental behaviors migrated from the margin into the spotlight of scientific reports. As in many budding fields, anecdotal descriptions were replaced by hypothesis-testing experiments. Accordingly, the number of publications about parental care in amphibians has increased dramatically over the last seven decades (Fig. 2).

Caecilians

During the second half of the 20th century, accumulating observations of caecilian reproductive behavior led to the hypothesis that most caecilians exhibit some form of parental care (Wake 1992; Gower et al. 2008). Oviparous species with aquatic larvae generally exhibit clutch guarding (Nishikawa et al. 2008; Bei et al. 2012), which is considered the ancestral form of parental care in caecilians (Wilkinson and Nussbaum 1998; C1, Table 1). Some direct-developing species provide postpartitive maternal care, and some viviparous species—those that retain young in the maternal reproductive tract and give birth after metamorphosis—provide intraoviductal (also referred to as "intrauterine"; see Wake 1993) or epithelial nutrition (Wake 1992; Gower et al. 2008; Lodé 2012). In fact, all viviparous and some oviparous caecilian young have specialized, deciduous fetal dentition (e.g., Parker 1936, 1956; Parker and Dunn 1964) used for scraping the thickened oviduct lining and/or skin of the mother (e.g., Wake 1992; Kupfer et al. 2006; C2 and C3). Intrauterine feeding facilitates offspring growth in the oviduct (Parker and Dunn 1964; Wake 1977a, 1980; Welsch et al. 1977) and teeth scraping may stimulate the secretion of nutritive epithelia (Wake 1977b; Gomes et al. 2012). However, young may also be nourished in the oviduct via highly vascularized gill structures functioning as a pseudo-placenta (e.g., *Typhlonectes*, Delsol et al. 1981). In contrast, offspring that use their teeth to scrape off maternal skin or skin secretions after birth are born much smaller than species with intrauterine feeding (O'Reilly et al. 1998). Maternal dermatotrophy has been demonstrated in several distantly related direct-developing oviparous species via ex situ behavioral experiments and histological examinations (Kupfer et al. 2006; Wilkinson et al. 2008, 2013; Kouete et al. 2012). Genetic parenthood analysis further revealed that even though this parental-care strategy is very cost intensive, parents do not discriminate care to their own offspring (i.e., alloparenting; Kupfer et al. 2008; C4).

Reproductive and parental care modes are known for about 25% of the approximately 200 described caecilian species. Recently, San Mauro et al. (2014) integrated life-history traits with modern phylogenetic tools to reconstruct caecilian life-history evolution. Also, Kupfer et al. (2016) conducted a character-state reconstruction to investigate the evolutionary relationships between reproductive modes, parental investment, and offspring size and quality. Together, these studies suggest that the concurrent evolution of direct development and juvenile teeth gave rise to skin-feeding—likely a precursor of oviduct feeding—and thus enabled the independent evolution of viviparity at least four times within Gymnophiona (Lodé 2012). Although caecilians are the least-investigated amphibians, contemporary studies combining natural history and genomics are broadening our understanding of parental-care evolution.

Urodeles

Parental care in urodeles has been described as simple and limited to egg attendance (Salthe and Mecham 1974; Nussbaum 1985; Crump 1996; U2–5 in Table 1). However, egg attendance is difficult to demonstrate, because spatial proximity alone does not ensure either a benefit to offspring or a cost to parents (Crump 1996). The terms "brooding," "attendance," and "guarding" have been used inconsistently across the literature (Crump 1996), further confusing the adaptive significance of the spatial association between adults and their clutches.

Despite its relative simplicity, parental care is abundant in urodeles, appearing in up to 20% of species (Balshine 2012) from eight of nine families (all except Rhyacotritonidae), including in about 80% of plethodontid salamanders. Surprisingly, recent reviews about parental care in vertebrates barely touch on urodeles (cf. Balshine 2012). Information about urodele parental care was reviewed extensively in the 1980s and 1990s (Salthe 1969; Nussbaum 1985; Verrell 1989; Crump 1996).

Salamanders are an ideal group for studying the evolution of parental strategies because of their diverse fertilization mechanisms, lifestyles, mating systems, and habitats, and also because parental care has probably evolved independently many times in this group (Salthe and Mecham 1974; Nussbaum 1985, 2003). Maternal care is generally found in species with internal fertilization whereas paternal care is mainly associated with external fertilization and male territoriality (Gross and Shine 1981; Verrell 1989). Furthermore, both brooding and nonrandom selection of oviposition sites are strongly associated with breeding habitat (Salthe

1969); pond breeders typically deposit many small, exposed eggs in standing water and provide no postoviposition parental care, whereas stream breeders usually deposit few eggs at hidden, protected locations and one or both parents attend the clutch. Terrestrial breeders (e.g., plethodontid salamanders, some newts) generally lay clutches of eggs in hidden locations, have prolonged brooding periods, produce direct developing larvae, and aggressively defend their eggs against predators (Salthe 1969; Crump 1996). Nussbaum (1985, 1987) hypothesized that parental care evolved in stream- rather than pond-breeding species because foraging in stream currents requires larger and stronger larvae, in turn allowing consumption of the larger prey found in lotic ecosystems. For stream-dwelling larvae to grow larger, they must spend more time in the egg (Salthe and Duellman 1973; Salthe and Mecham 1974), and parental egg guarding could have evolved in response to predation risk during the extended egg phase.

Viviparity in urodeles is considered an adaptation to protect vulnerable offspring from water shortages, caused by either harsh high-altitude climates or droughts (Vilter and Vilter 1964; Joly et al. 1994; Lodé 2012; but see Dopazo and Korenblum 2000). Although in general the Fire Salamander (*Salamandra salamandra*) is ovoviviparous (mothers retain eggs in the oviduct until hatching without nutritional exchange, and several weeks of aquatic development are required after birth; Buckley et al. 2007), some subspecies (*Salamandra salamandra fastuos, Salamandra salamandra bernadezi*) are decidedly viviparous and give birth to fully metamorphosed offspring (Dopazo and Alberch 1994; Joly et al. 1994; García-París et al. 2003). The same is the case for the Black Salamander (*Salamandra atra*; Vilter and Vilter 1960). The suggestion that alpine salamanders exhibit intrauterine feeding was made centuries ago (U8). More recently, integrative approaches have identified specialized maternal tissues known as "oviductal epithelium" or "zona trophica," which provides embryos nutrition after yolk depletion (epitheliophagy; Guex and Chen 1986; Guex and Greven 1994).

Newts (salamanders from the subfamily Pleurodelinae) were long considered to lack parental behavior (cf. Crump 1996). However, some terrestrial breeding newts exhibit parental behavior, such as the Himalayan newt (*Tylototriton verrucosus*) in which females coil around their eggs (Kuzmin et al. 1994). Furthermore, numerous aquatic breeding newts such as those in the genera *Triturus* and *Lissotriton* exhibit parental behavior, although it is limited to egg rolling (or also "egg wrapping"; Bell and Lawton 1975; Bell 1977; Díaz-Paniagua 1989; Miaud 1994; U1). This behavior was either not considered true parental behavior or was seen as a primitive form of parental care (Miaud 1993), in part because there is no parental care *after* eggs have been wrapped in a leaf (Bell 1977; Beebee and Griffiths 2000), and was originally described only as a reproductive mode (Mode I: many eggs are laid singly on supports such as aquatic plants; Salthe 1969). However, lab and field experiments tested the protective function of egg wrapping and confirmed its adaptive significance (Ward and Sexton 1981; Miaud 1993, 1994; Orizaola and Brana 2003), as well as time and energy costs to the parent (Díaz-Paniagua 1989; Miaud 1994). In fact, wrapped eggs have a much higher survival rate because they are less visible and accessible to predators (Miaud 1993, 1994; Orizaola and Brana 2003), and suffer from less mechanical destruction (Ward and Sexton 1981), fungal infection, and damaging UV-B radiation (Kiesecker and Blaustein 1995; Green 1999; Marco et al. 2001). Thus, there is considerable support that egg wrapping in newts is in fact a real parental behavior.

Egg-wrapping strategies vary among (and within; Tóth et al. 2011) *Lissotriton* species (Miaud 1995; Orizaola and Brana 2003; Norris and Hosie 2005; Dvořák and Gvoždík 2009; 2010; Kurdíková et al. 2011) such that larger females are more skilled in egg-laying and wrapping than smaller females, and individual female behavior influences offspring survival (Díaz-Paniagua 1989; Tóth et al. 2011). However, a comparative understanding of the behavioral repertoires of individuals and species is lacking. Use of standardized ethograms—such as that created by Norris and Hosie (2005) to compare oviposition behavior in *Lissotriton helveticus* and *Lissotriton vulgaris*—would improve our ability to compare behaviors across taxa.

Oviposition behavior in aquatic breeding newts has received increasing attention in recent decades because of the decline of newt populations globally (Waldmann and Tocher 1998; Marco et al. 2001). Apart from broad stressors such as habitat fragmentation and loss, acidification of water by pollutants such as the fertilizer ammonium nitrate are detrimental to egg development and alter female wrapping behavior (Ortiz-Santaliestra et al. 2007). Changes in water temperature, such as those associated with a shifting climate regime, also negatively affect oviposition performance (Dvořák and Gvoždík 2009, 2010; Kurdíková et al. 2011).

Relative to the newts, only limited and anecdotal reports exist about another aquatic breeding urodele family, Sirenidae. Based on observations of two breeding pairs in captivity, *Siren intermedia* territorial males guard, move, and oxygenate (via fanning) their clutches, and aggressively defend developing and recently hatched larvae against intruders (Reinhard et al. 2013, 2015)—a parental care mode first described by Hubbs (1962; U7). In contrast, parental behavior was not observed in *Pseudobranchus striatus* (Kowalski 2004). Because parental care is otherwise rare in male and aquatic breeding urodeles, Sirenidae represents an important taxon for studying the evolutionary drivers of maternal and paternal care, but more information about the behavior and natural history of this group is needed before selective pressures can be evaluated.

Even though most species in the family Ambystomatidae (represented by a single genus *Ambystoma*) lack parental care, this family is a valuable target for comparative approaches given its diverse range of life-history patterns, ecology, and reproductive modes (Petranka 1990). Brooding has not been documented in most *Ambystoma* species, in contrast to many plethodontids, even though both groups breed terrestrially next to streams (Anderson and Williamson 1976; Petranka and Petranka 1981; Nussbaum 1985). However, adult Marbled Salamanders (*Ambystoma opacum*) migrate to breeding sites and females actively select oviposition sites inside dry pond beds, coiling around their clutches until the ponds fill with rainwater (Noble 1931; Figiel and Semlitsch 1995). Both brooding and active nest site selection improve offspring survival in *A. opacum* (Petranka and Petranka 1981; Jackson et al. 1989; Petranka 1990; Croshaw and Scott 2005). Interestingly, the costs of brooding appear to be low or even absent, as females did not appear to lose weight during the brooding period (Kaplan and Crump 1978). That costs are low is particularly surprising because female marbled salamanders frequently abandon nest sites before pools fill up with rainwater (Kaplan and Crump 1978); the underlying causes of this behavior remain unclear.

Even less is known about parental behavior in Cryptobranchidae, one of the oldest salamander lineages (Pyron and Wiens 2011). Species in this group are fully aquatic, secretive, and have well-hidden nest sites. They are also rapidly declining worldwide. Although historical anecdotes described egg fanning and defense, recent field observations and video monitoring have revealed an extended period of pre- and posthatching parental care in the Japanese giant salamander, *Andrias japonicus* (Okada et al. 2015; Takahashi et al. 2017). Large males ("den-masters") occupy nesting burrows along stream banks, performing tail fanning, agitation, filial hygienic cannibalism, and active predator defense (Okada et al. 2015), both before hatching (1–2 mo) and with juveniles (up to 5 mo; Takahashi et al. 2017). Unfortunately, small sample sizes ($n = 2$) impede inferences about the causes, correlates, and function(s) of these behaviors.

Parental care is particularly widespread in the family Plethodontidae, which includes over 70% of extant urodele species. Life in stressful environments has likely been a major factor in the development of parental strategies in this group (Wilson 1975). Nonetheless, the distribution and diversity of plethodontid parental behaviors is probably underestimated, as the reproductive biology of many species is unknown, and most research is limited to 7 of 476 species in this family (*Plethodon cinereus*; *Desmognathus ochrophaeus*; *Hemidactylium scutatum*; *Speleomantes strinatii*; *Bolitoglossa mexicana*; *Plethodon albagula*; *D. fuscus*; Frost 2019). Egg attendance (or the secondary loss thereof), however, has also been reported in many other species in the group (e.g., *Ensatina eschscholtzi*, Stebbins 1954; *Batrachoseps nigriventis*, Jochusch and Mahoney 1997; *Bolitoglossa rostrata*, Houck 1977; *Aquiloeurycea cafetalera*, Aguilar-López et al. 2017). Plethodontid salamanders have internal fertilization (via retrieval of male spermatophores with female cloacal muscles), terrestrial clutches, and predominantly female parental care (Verrell 1989). Because mothers do not leave the nest to eat and they face higher predation risk, egg brooding and guarding are considered quite costly (Forester 1981; Bachmann 1984; Hom 1988; Harris et al. 1995; Ng and Wilbur 1995; Yurewicz and Wilbur 2004). Egg production and brooding may consume almost half of a female's annual energy budget (Fitzpatrick 1973).

The adaptive benefits of plethodontid maternal behaviors are diverse (Forester 1979). Brooding females provide active and passive defense against conspecific and heterospecific predators (Highton and Savage 1961; Bachmann 1964; but see Carreño and Harris 1998), move and turn their eggs to increase oxygenation and prevent adhesive malformations (Stebbins 1954; Vandel and Bouillon 1959; Durand and Vandel 1968; Salthe and Mecham 1974), and moisten eggs during periods of drought (Forester 1984). Furthermore, mothers ingest infected eggs to prevent the spread of fungal infection (Snyder 1971; Tilley 1972; Salthe and Mecham 1974). Although most fungi develop on nonviable eggs (Villa 1979), some pathogenic fungi infect healthy eggs (Villa 1979; Warkentin et al. 2001). An antimicrobial function of salamander skin was hypothesized long ago (Piersol 1910), but the mechanisms were not experimentally verified until 100 yr later (Lauer et al. 2007; Banning et al. 2008; Brucker et al. 2008). Chemical and molecular analyses have shown that peptides and alkaloids produced in skin glands inhibit fungal growth (Simmaco et al. 1998; Rollins-Smith et al. 2002). In addition, amphibian skin harbors bacteria that produce antibiotic compounds, which could be transferred from mothers to clutches to enhance embryo survival (Lauer et al. 2007, 2008).

Although microbe transmission is generally considered to be a cost of group living in mammals and birds, transmission of antifungal skin bacteria may have favored the evolution of communal nesting in several plethodontids (Banning et al. 2008). For example, in *Hemidactylium scutatum*, a few females deposit clutches in the same nest and one of them remains for nest brooding (Harris and Gill 1980; Harris et al. 1995). Brooding may facilitate the transmission of antifungal bacteria to embryos (Banning et al. 2008), and although joint brooding females exhibit preferential care for their own clutch, their energy expenditure is not considerably higher than females with solitary nests (Carreño and Harris 1998). The adaptive significance and function of communal nesting in plethodontids is barely understood, but it has not been found to be a behavioral response to habitat limitation or high population density (Emlen 1982; Hatchwell and Komdeur 2000), conspecific brood parasitism, or high predation threat requiring group nest defense (cf. Harris et al. 1995).

Cross-fostering experiments in solitary nesting plethodontids have elucidated some adaptive benefits of parental care. Infrared cameras and manipulations of parents and clutches in the Northwest Italian Cave Salamander, *Speleomantes strinatii* revealed that postoviposition care influences offspring size more than preoviposition care, and that mothers attend and guard young for weeks after hatching (Oneto et al. 2010; U6). Although a substantial body of literature has illustrated many aspects of parental care in urodeles and particularly in plethodontids (Forester 1979, 1983; Nussbaum 1987; Verrell 1989; Jaeger and Forester 1993; Crespi and Lessing 2004; Trauth et al. 2006; Banning et al. 2008), we still have minimal knowledge about the diversity and abundance of parental behaviors in many families (Fig. 1). Integrative work that combines observational, experimental, genetic, and modeling approaches is needed to identify the mechanisms underlying the diversity of urodele parental strategies.

Anurans

The study of parental care in anurans has recently come of age, with the number of descriptive natural history and hypothesis-testing reports in our literature search rising since the 1980s (Fig. 2). The number of parental-care modes doubled from 14 to 28 in the last few decades (Table 1). In fact, more than two-thirds (456 of 685) of the papers that we found about parental care in amphibians were published since 1950 and focus on anurans. However, recent experimental work in anuran parental care is heavily biased toward Neotropical taxa, and in particular toward Dendrobatidae (Fig. 4). This family exhibits particularly complex

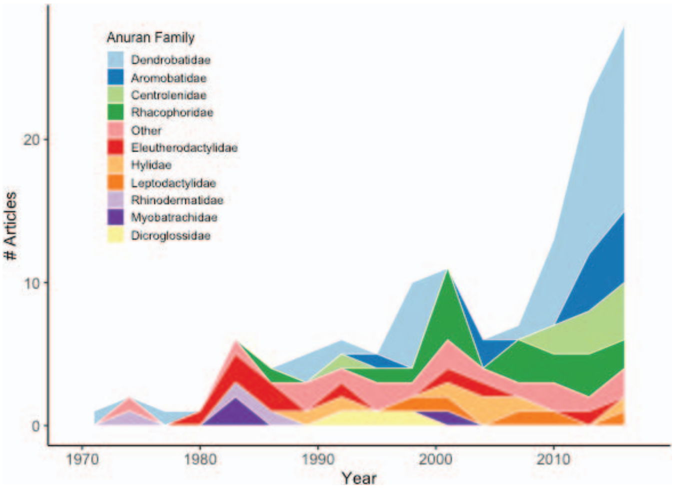


FIG. 4.—Number of hypothesis-testing parental care studies in anurans (that were identified in our literature review) published in the last five decades, colored by family. Note how some families such as Dendrobatidae have received more attention than others. A color version of this figure is available online.

forms of parental care, and significant research effort has strived to cultivate a deep understanding of their functions and origins, in contrast to other anuran families where, in most cases, parental care research is merely scratching the surface. Few other taxa have played a substantial role in anuran parental-care research, including *Allobates femoralis* (Aromobatidae, from the same superfamily as Dendrobatidae), *Kurixalus eiffingeri*, *Alytes obstetricans* (Alytidae), *Eleutherodactylus coqui* (Eleutherodactylidae), *Leptodactylus bolivianus* (Leptodactylidae), and *Kurixalus eiffingeri* and *Feihyla hansenae* (both Rhacophoridae). Additionally, studies using comparative methods among various centrolenid species have revealed new perspectives on the adaptive significance of anuran parental care (Delia et al. 2017). Given the extreme diversity of parental-care modes in anurans (Table 1; Fig. 1), a wider comparative scope in other families would strengthen our understanding of adaptive and mechanistic functions, especially outside of the most commonly studied behaviors: tadpole transport, egg attendance, site choice, and nutritive provisioning.

Research on parental care in anurans after 1950 can be categorized as either "descriptive," revealing fascinating aspects of natural history, or "hypothesis-testing," probing deeper into established natural history. Generally, descriptive studies rely on observational field or lab work, whereas hypothesis-testing studies integrate methods from behavior, phylogenetics, genetics, morphology, neuroendocrinology, and chemistry to assess ultimate and proximate hypotheses.

Observations of diverse parental behaviors.—Recent descriptive studies have revealed new modes of parental care, better knowledge of poorly understood species, and new details about well-studied species. Several types of parental care have been discovered in distinct geographical regions, hinting at striking, yet underexplored, examples of evolutionary convergence. For example, guarding of eggs—that will either develop directly into froglets or hatch into aquatic tadpoles—has been reported in taxa as diverse as the South African Bullfrog (Cook et al. 2001), African hyperolids (Stevens 1971), New Zealand leiopelmids (Bell 1978), Papuan and Australian microhylids and myobatrachids (Pengilley 1971; Roberts 1984; Bickford 2004; Hoskin 2004; Günther 2006), Bornean dicroglossids (Inger and Voris 1988), and many South American species in the families Craugastoridae, Eleutherodactylidae, Centrolenidae, and Dendrobatidae. In some cases, egg guarding is further derived: (1) building of mud, foam, bubble, or leaf-pouch nests (A1–4, Table 1; Gladiator Frog, Kluge 1981; Túngara Frog, Ryan 1985; Gray Foam-Nest Tree Frog, Coe 1974; Santa Catarina Humming Frog, Haddad and Hödl 1997; Reticulate Leaf Frog, de Oliveira 2017); (2) use of heterospecific nests (A5; *Allobates sumtuosus*, Kok and Ernst 2007); (3) camouflaging eggs with dirt (A6; Spix's Saddleback Toad, Pombal et al. 1994); (4) carrying eggs wound around the legs until hatching (A15; Midwife Toad, Márquez 1992); (5) carrying eggs in a dorsal pouch-like structure (A16–18; e.g., marsupial frogs like *Gastrotheca*, del Pino 1989); or (6) carrying eggs on the back with no protective structure (A19–20; e.g., backpack frogs like *Cryptobatrachus*, del Pino 1989).

Species with external fertilization, like most anurans, typically use organs other than the oviduct to carry embryos, because zygotes are ingested or deposited only after fertilization. Very few anuran species exhibit internal fertilization, and thus oviductal retention is rare in frogs (but see Sever et al. 2001, Iskandar et al. 2014, Wake 2015; A26). It has been hypothesized that nonoviductal retention was derived from parental care of juveniles, and that oviductal retention is ancestral to viviparity (Lodé 2012). The protection of embryos in maternal organs other than the oviduct (e.g., skin, mouth, stomach) resembles ovoviviparity or viviparity in various ways (see sections on viviparity in caecilians and salamanders above). For instance, male *Rhinoderma darwinii* ingest their embryos and keep them in their vocal sac, where the tadpoles feed on their yolk and secretions from the male's sac until metamorphosis (A22; Goicoechea et al. 1986). Likewise, female *Rheobatrachus silus* give birth to metamorphic young via propulsive vomiting (A21; Corben et al. 1974; Tyler and Carter 1981). Such gastric brooding is possible because developing young secrete a chemical substance that prevents stomach acid production by the mother (Fanning et al. 1982). Unfortunately, further exploration of this fascinating mode of parental care is not possible, as this frog is reportedly extinct, last seen in 1981 (IUCN 2018).

Although egg-brooding anurans often continue parental-care behaviors during tadpole or froglet stages, most egg-attending species do not provide posthatching care, because their eggs are deposited near water and then hatchlings swim away (e.g., *Hyalinobatrachium fleischmanni*: Jacobson 1985). However, a few species do protect their tadpoles or froglets after hatching (*Leptodactylus insularum*, Hurme 2011; *Cophixalus parkeri*, Simon 1983). Other species of parental anurans carry recently hatched tadpoles to bodies of water (A11–12), or hold them on their dorsum or in inguinal pouches, where they are protected until metamorphosis (A23–25; *Cycloramphus stejnegeri*, Heyer and Crombie 1979; *Assa arlingtoni*, Straughan and Main 1966). In some directly developing species that lack a free-living tadpole stage, mothers or fathers transport newly hatched froglets to appropriate habitats (A13–14; *Eleutherodactylus cundalli*, Diesel et al. 1995; *Sphenophryne schlaginhaufeni*, Bickford 2002).

In the Neotropical poison frogs (families Dendrobatidae and Aromobatidae), male tadpole transport was known from natural history observations for over a century (A11; reviewed in Weygoldt 1987), when back-to-back discoveries revealed female offspring transportation (A12) followed by provisioning with unfertilized nutritive eggs in *Oophaga pumilio* (A27; Graeff and Schulte 1980; Weygoldt 1980) and biparental tadpole feeding in *Ranitomeya imitator* (A28; Kneller 1982, as *Dendrobates reticulatus*). These and many other parental behaviors in this group were first described by private breeders (e.g., Polder 1974; Lescure and Bechter 1982; Zimmermann and Zimmermann 1984), who made priceless contributions to the study of amphibian parental care. Observations in situ soon confirmed these data, expanding the knowledge of egg-guarding, tadpole-transportation, and egg-feeding behaviors in many species (e.g., Aichinger 1991; van Wijngaarden and Bolaños 1992; Brust 1993; Juncá et al. 1994; Caldwell 1997; Fandiño et al. 1997). The accessibility of brightly colored and diurnal poison frogs in captivity and in the wild, in combination with their wide array of behaviors, makes them ideal model species for parental-care studies (Weygoldt 1987; Summers and Tumulty 2014; Stynoski et al. 2015). As such, numerous studies have been conducted in this family (Fig. 4), on a diversity of questions, both ultimate (e.g., correlations between the evolution of parental care and egg size or ecological factors; Summers and McKeon 2006; Brown et al. 2010) and proximate (e.g., neural basis of parental decisions; Roland and O'Connell 2015).

Hundreds of important observational studies have added to our knowledge of the natural history and diversity of parental care in anurans in recent decades, and we strongly encourage researchers to continue reporting such crucial observations. On the other hand, since 1950, the study of anuran parental care has truly blossomed in the use of experimental data to test hypotheses directly.

Ultimate questions about adaptive significance.— Rigorous laboratory and field studies have begun to unravel the relative costs and benefits of anuran parental care from the perspectives of both the parent and the offspring. Such research has identified many of the ecological factors and interactions that impact the form, intensity, and diversity of parental care among anuran lineages. It has also illustrated the adaptive significance and selective pressures that have led to the evolution of behaviors and morphologies that facilitate care of offspring.

A fundamental question about the adaptive significance of parental care is whether behavior that appears to play a role in offspring success truly provides measurable benefits. Numerous classic studies have used parent removal experiments to tease apart the adaptive benefits of egg attendance by mothers or fathers and the sources of mortality when a parent experimentally abandons its eggs. Prior to these experiments, many speculated whether egg attendance reduces dehydration, predation, pathogenic infection, or other sources of offspring mortality (e.g., Salthe and Duellman 1973; Vaz-Ferreira and Gehrau 1974; Woodruff 1977; McDiarmid 1978; Jacobson 1985).

The first experimental evidence for benefits of parental egg attendance was found in *Cophixalus parkeri* (Simon 1983) and *E. coqui* (Townsend et al. 1984), in which removal of males from clutches led to high egg mortality via cannibalism, desiccation, fungal infection, and arthropod predation. Similar adaptive benefits have been demonstrated experimentally in many glass frogs (*Hyalinobatrachium fleischmanni*, Hayes 1991; Delia et al. 2013, 2014; *Hyalinobatrachium valerioi*, Vockenhuber et al. 2009; *Hyalinobatrachium orientale*, Lehtinen et al. 2014; *Ikakogi tayrona*, Bravo-Valencia and Delia 2016; *Cochranella granulosa* and *Teratohyla pulverata*, Delia et al. 2017) and other anuran families (*Hylophorbus rufescens* and *Oreophryne* sp., Bickford 2004; *K. eiffingeri*, Chen et al. 2007, 2011; Cheng and Kam 2010; *F. hansenae*, Poo and Bickford 2013; *R. imitator*, Tumulty et al. 2014; *O. pumilio*, Dugas et al. 2016a; *Thoropa taophora*, Consolmagno et al. 2016). These experiments have shown that the source of mortality depends on the selection pressures acting on parents and offspring in a given habitat (Bickford 2004; Bravo-Valencia and Delia 2016), with weather variation (Delia et al. 2013; Lehtinen et al. 2014) and offspring development (Vockenhuber et al. 2009; Bravo-Valencia and Delia 2016; Dugas et al. 2016a) playing important roles in the relative value of parental care. Although the majority of parent removal experiments have been based on studies in which the male adult performs most or all of the egg attendance, some studies have also demonstrated clear adaptive benefits when the female (Poo and Bickford 2013; Bravo-Valencia and Delia 2016; Delia et al. 2017) or both parents (Tumulty et al. 2014) attend offspring.

Other studies have demonstrated other complex ways that parental care can benefit offspring: larger size of brooding males in *A. obstetricans* and *Alytes cisternasii* (Raxworthy 1990; Márquez 1993), sequential vs. nonsequential clutch attendance in *K. eiffingeri* (Cheng et al. 2012), and differences expressed among allopatric color morphs in *O. pumilio* (Dugas and Richards-Zawacki 2015). Such findings suggest that we are only beginning to understand the complex interactions between parental care and offspring fitness in anurans.

The evolution of parental behaviors depends not only on the benefits to offspring, but also the relative costs of that care to parents, who must balance investment in current offspring with investment in future offspring and their own survival (Trivers 1974). For example, Townsend (1986) demonstrated that male *E. coqui* attending eggs lost significant mass and missed numerous mating opportunities, although those costs were compensated by a net fitness gain because of dramatic improvements in offspring survival. Field studies with *O. pumilio* showed that females invest more time in parental care and have a lower potential reproductive rate than males (Pröhl and Hödl 1999). Also, a series of studies based on captive *O. pumilio* demonstrated that the provisioning of nutritive eggs by female frogs is costly and limiting: tadpoles in larger broods received fewer eggs, and females produced fewer clutches when already caring for tadpoles (Dugas et al. 2015a). Furthermore, reproductive rate was negatively correlated with the duration of adult survival (Dugas et al. 2015b), and reproductive success did not improve with parent age or experience (Dugas et al. 2015c). Similarly, *K. eiffingeri* tadpoles in larger clutches grew less, suggesting that nutritive egg production is a limiting factor in maternal care (Kam et al. 1998).

The degree of parental investment in a given species is intricately related to its mating system, and therefore also to the degree of territoriality, resource defense, and mating competition displayed by either of the sexes. In the 1990s and 2000s, a number of reports aimed to quantify and elucidate the relative roles of male and female anurans in light of the impact that investment in parental care could have on the evolution of mating systems. For example, studies have measured territory and home range sizes, reproductive success or skew, choosiness of mates, features of quality such as body size or call traits, and defensive behavior to evaluate whether these factors can be predicted by the intensity of parental care displayed by either males or females. Such hypotheses have generally been tested in dendrobatid and aromobatid species (*A. femoralis*, Roithmair 1992; Ursprung et al. 2011; Ringler et al. 2012; *Dendrobates leucomelas*, *Dendrobates auratus*, Summers 1989, 1990; *Oophaga histrionica,* Summers 1992; *Ranitomeya ventrimaculata*, Summers and Amos 1997; *O. pumilio*, Haase and Pröhl 2002; Pröhl 2002, 2005; Meuche et al. 2011, 2013), and occasionally in other anuran families as well (*A. obstetricans*, Verrell and Brown 1993; *R. darwinii*, Valenzuela-Sánchez et al. 2014; *H. valerioi*, Mangold et al. 2015). Research with *R. imitator*, *Ranitomeya variabilis*, and *Ranitomeya vanzolinii* has also explored the relationship between biparental care and a monogamous or pair-bonded mating system (Caldwell 1997; Caldwell and de Oliveira 1999; Brown et al. 2008a,b, 2009). This work, along with comparative analyses across anurans, suggest that selection to rear offspring in particularly small phytotelmata is associated with biparental care and, accordingly, pair-bonded mating systems (Caldwell and de Oliveira 1999; Brown et al. 2010).

Male tadpole transport without provisioning is thought to be the ancestral form of parental care in dendrobatid frogs (Weygoldt 1987; Summers and Tumulty 2014). Exclusively female or biparental care are thought to be derived (Tumulty et al. 2014). However, parental roles can be flexible. Other anurans, such as *Eleutherodactylus johnstonei*, display dynamic rather than fixed parental roles (amphisexual care; Bourne 1998; Lehtinen 2003), and when male *A. femoralis* were experimentally removed, females stepped in to initiate tadpole transport (Ringler et al. 2015a). Compensatory flexibility may be widespread, considering frequent anecdotal observations of biparental care with high sex bias (see Killius and Dugas 2014; Tumulty et al. 2014). Behavioral flexibility could be a crucial step in the evolutionary transition from uniparental to biparental care in poison frogs (Brown et al. 2010; Ringler et al. 2015a).

Proximate questions about mechanisms.—Proximate studies that clarify the mechanisms and ontogeny underlying anuran parental care have become popular in recent decades. Such work can be categorized into three general themes: (1) histological, physiological, and endocrinological studies to understand the biological tissues and substances associated with parental care; (2) spatial, genetic, and behavioral studies to understand how parent frogs choose where to deposit their eggs or tadpoles; and (3) behavioral, ecological, and chemical studies to understand the provisioning of food, water, and other resources.

Many anurans brood offspring using specialized pouches or organs with modified tissues. For example, in *R. darwinii*, the male swallows egg clutches and rears the young in a pouch in his vocal sac (see above), which becomes extremely distended when brooding young (Garrido et al. 1975). Histological studies examining the ultrastructure of the epithelium and vascularization of the father's pouch as well as the delayed development of the tadpole digestive tract suggest that tadpoles respire and acquire nutrients from fathers while in the pouch (Garrido et al. 1975; Jorquera et al. 1982). Also, Goicoechea et al. (1986) injected fathers with tracers and found those tracers in skin and digestive tract tissues of tadpoles, further supporting transfer of nutrients from fathers to offspring via the brood pouch. Similarly, *R. silus* mothers swallow and hold young in their stomach, where embryos secrete prostaglandin E_2, which inhibits gastric secretions and, along with egg jelly, prevents digestion (Tyler et al. 1983).

Frogs in the family Hemiphractidae have brood pouches in the skin where offspring undergo differing degrees of development (Table 1). These pouches have been classified into six types (del Pino 1980), and produce mucosal secretions in specialized glands to aid the development and attachment of embryos and tadpoles (del Pino 1980; De Pérez and Ruiz 1985). A recent study in *Gastrotheca excubitor* used labeled isotopes to show that both gases and liquids containing nutrients are transferred from highly vascularized maternal pouch tissues to embryos (Warne and Catenazzi 2016).

Anurans in the families Leptodactylidae and Rhacophoridae produce foam nests during oviposition. These nests provide an extra layer of protection for embryos and early-stage tadpoles by providing insulation from desiccation and temperature fluctuations (*Engystomops pustulosus*, Dobkin and Gettinger 1985; Dalgetty and Kennedy 2010; *Rhacophorus viridis*, Tanaka and Nishihira 1987; *Rhacophorus arboreus* Kusano et al. 2006; *Physalaemus fischeri*, *Leptodactylus fuscus*, and *Leptodactylus knudseni*, Méndez-Narváez et al. 2015,). Moreover, by eating the material that forms the foam nest, tadpoles gain nutritional benefits and grow more than when reared outside of the foam nest (Tanaka and Nishihira 1987; Kusano et al. 2006). In *E. pustulosus,* the foam nest is derived from six key proteins that are secreted by oviduct cells into a foam precursor fluid that is beaten during oviposition; some of these foam proteins have antibacterial and antipredator functions (Fleming et al. 2009; Dalgetty and Kennedy 2010).

Anurans are a model system for hormonal control of mating and communication (reviewed in Arch and Narins 2009), so it is surprising that relatively few studies have explored the endocrinology of parental care. Moore et al. (2005) extensively reviewed the literature on the hormonal regulation of behavior in amphibians and did not once mention the words "parent" or "care." A few classic studies offer some clues about the roles that hormones play in the modulation of parental care. For example, estradiol causes the formation of the brood pouch in female *Gastrotheca riobambae* (Jones et al. 1973). Also, brooding male *E. coqui* show lower circulating androgen levels than nonbrooding and calling males (Townsend and Moger 1987). However, implanting males with testosterone pellets did not alter brooding behavior, suggesting that the drop in androgen levels is a consequence rather than a cause of parental care (Townsend et al. 1991). Similarly, male *Limnonectes blythi*, which have lost secondary sex characteristics and transport tadpoles dorsally, exhibit considerably lower levels of androgens than related species that do not exhibit such parental care (Emerson et al. 1993; Emerson 1996).

More recently, Ten Eyck and Haq (2012) demonstrated that arginine vasotocin (AVT, the amphibian homolog of mammalian vasopressin), which generally promotes calling behaviors in anurans, stimulated brooding males to call but not to abandon their egg clutches. Additionally, Schulte and Summers (2017) found that in *R. imitator*, exogenous AVT actually reduced intense egg-care behaviors (but did elevate the expression of some general care behaviors), and that exogenous mesotocin (the amphibian homolog of mammalian oxytocin) reduced the likelihood that males transported tadpoles. They suggest that other hormones such as steroids or prolactin are likely important for the stimulation of early parental behaviors in dendrobatids (Schulte and Summers 2017). However, the hormonal mechanisms that trigger tadpole transport, egg swallowing, and nonparental, mating, and egg-provisioning phases in different taxa remain unexplored. Additionally, it is not known why in some anuran groups the hormonal and morphological prerequisites for parental care appear only in males (e.g., *R. darwinii*, *Anomaloglossus degranvillei*, *Assa darlingoni*, and *D. auratus*), only in females (e.g., *Gastrotheca*, *Flectonotus*, and *Pipa*), or in both sexes (e.g., *R. imitator*, and *Osteocephalus oophagus*).

Many studies have investigated the biotic and abiotic factors that determine where parent frogs choose to deposit eggs or tadpoles. For example, various studies have used experimental pools to show that mother frogs avoid depositing eggs in sites with potential predators (*Dryophytes chrysoscelis*, Resetarits and Wilbur 1989; *Lithobates sylvaticus*, Hopey and Petranka 1994; *Anaxyrus americanus*, Petranka et al. 1994; *R. sirensis*, von May et al. 2009; *Dendropsophus ebraccatus*, Touchon and Worley 2015), infectious pathogens (*Dryophytes versicolor*, Kiesecker and Skelly 2000), or pesticides (*D. versicolor* complex, Takahashi 2007).

Parent frogs also seek out oviposition sites that are less likely to experience desiccation. For example, in *Crinia nimbus*, an Australian direct developer that deposits eggs in sphagnum moss, sites with dense and moist nest material are essential for embryo survival (Mitchell 2002). Phytotelm breeders *O. pumilio*, *Ranitomeya amazonica*, and *K. eiffingeri* are more likely to reproduce in months of the year when desiccation risk is reduced (Donnelly 1989a; Poelman and Dicke 2007; Lin et al. 2008). Also, *R. amazonica* is more likely to deposit eggs and tadpoles in sites with larger water volumes, as well as those that contain detritus, presumably as a food source for offspring (Poelman et al. 2013). Mother frogs are more likely to oviposit in experimental pools with deep water than with shallow water (*Isthmohyla pseudopuma*, Crump 1991; *Hoplobatrachus occipitalis*, Spieler and Linsenmair 1997; *Phrynobatrachus guineensis*, Rudolf and Rödel 2005; *D. ebraccatus*, Touchon and Worley 2015; *R. sirensis*, von May et al. 2009).

Mother frogs also avoid ovipositing in sites that contain potential conspecific competitors or cannibals. For example, mothers were more likely to deposit egg clutches in control pools than in experimental pools with older conspecifics in the water (*D. chrysoscelis*, Resetarits and Wilbur 1989; *I. pseudopuma*, Crump 1991; *H. occipitalis*, Spieler and Linsenmair 1997; *Phrynobatrachus guineensis*, Rudolf and Rödel 2005; *Pleurodema borellii*, Halloy 2006; *Rana japonica*, Iwai et al. 2007; *K. eiffingeri*, Lin et al. 2008; *R. ventrimaculata*, Summers 1999), but not in all cases (*R. variabilis*, Schulte 2014).

In addition to egg deposition, some frogs (e.g., dendrobatids and aromobatids) must also decide which tadpoles to transport (i.e., their own offspring) and where to deposit them. *Ranitomeya variabilis* use chemical cues to distinguish between conspecific and heterospecific tadpoles and to avoid placing tadpoles in dangerous sites with conspecifics (Schulte et al. 2011, 2013, 2015; Schulte and Lötters 2013, 2014; Schulte 2016). Other experimental studies have shown that *R. amazonica* males do not differentiate between their own and foreign clutches (Poelman and Dicke, 2007), whereas *O. pumilio* females (Stynoski 2009) and *A. femoralis* females (Ringler et al. 2016) use indirect recognition via spatial location of clutches and tadpoles to discriminate between their own and unrelated progeny. Research in a few species has shown puzzling evidence of parents preferring to deposit tadpoles along with older tadpoles that are likely to kill and consume their offspring (*D. auratus*, Ryan and Barry 2011; *Dendrobates tinctorius*, Rojas 2014, 2015; *Adelphobates castaneoticus*, Caldwell and Myers 1990; Caldwell and Araujo 1998; *R. ventrimaculata*, Poelman and Dicke 2007). Such a strategy could be intended as food supplementation for older tadpoles, especially when there is more pressure to metamorphose as the wet season ends (*R. amazonica*, Poelman and Dicke 2007; *R. variabilis*, Schulte and Lötters 2013), but not in all cases (*D. tinctorius*, Rojas 2014, 2015). Species differences may exist, however; the larvae of some species eat conspecific eggs and tadpoles (*D. auratus*, Summers 1990; *R. variabilis*, Schulte 2014; *D. tinctorius*, Rojas 2014; *Dendrobates truncatus*, BR, personal observation) and benefit nutritionally (*R. ventrimaculata*, Summers and Amos 1997), whereas other species kill younger intruder tadpoles but do not eat them and larval aggression is unaffected by tadpole hunger level (*O. pumilio*, Dugas et al. 2016b). In some cases, parents avoid depositing tadpoles with conspecifics when given a choice of pools (*R. ventrimaculata*, Summers 1999; *R. sirensis*, Von May et al. 2009; *R. variabilis*, Schulte et al. 2011, 2013; Schulte and Lötters 2014), regardless of relatedness (*R. variabilis*, Schulte and Veith 2014). However, in other cases, cannibalistic tadpoles are deposited irrespective of or even preferring the presence of conspecifics (*Mannophryne trinitatis*, Downie et al. 2001; *D. tinctorius*, Rojas 2014), perhaps because the presence of older tadpoles indicates safety at that site from predators or desiccation (but see *K. eiffingeri*, Chen et al. 2001).

Some species of phytotelm-breeding frogs avoid placing tadpoles in sites with predators (*M. trinitatis*, Downie et al. 2001; *R. variabilis*, Brown et al. 2008b; *A. femoralis*, McKeon and Summers 2013) or low (or too high) volumes of water (*R. sirensis*, Von May et al. 2009; *A. femoralis*, McKeon and Summers 2013; *R. variabilis*, *R. imitator*, Brown et al. 2008b), whereas phytotelm position seems less crucial (Von May et al. 2009; Schulte et al. 2010). The number of sites available for rearing tadpoles generally limits population density, and adding tadpole rearing sites increases local adult density and reproductive activity, whereas adding leaf litter does not (*O. pumilio*, Donnelly 1989b; *D. tinctorius*, Rojas 2015; *A. femoralis*, Ringler et al. 2015b). The distribution of appropriate tadpole rearing sites strongly impacts the distribution of adults in Dendrobatidae (*O. pumilio*, Pröhl and Berke 2001; *R. amazonica*, Poelman and Dicke 2008) and Mantellidae (Heying 2004).

Phytotelm-breeding aromobatids have excellent spatial memory, and use it to return to sites where they deposited egg clutches and tadpoles (*A. femoralis*, Pašukonis et al. 2016, 2017; Ringler et al. 2016). Telemetry has shown that *A. femoralis* follows direct memorized paths to known deposition sites (Beck et al. 2017; Pašukonis et al. 2017). This non-egg-feeding species may use a mental map of tadpole-rearing sites to execute a bet-hedging strategy, distributing the tadpoles from a given clutch among a number of pools to reduce the risk at any one site (Ringler et al. 2013; Erich et al. 2015). Egg-feeding species also use spatial location to identify their tadpoles for intermittent provisioning of nutritive eggs, as opposed to relying on direct offspring recognition (*K. eiffingeri*, Chiu and Kam 2006; *O. pumilio*, Stynoski 2009). It is poorly understood whether spatial memory differs among the sexes, although given evidence of plasticity among the sexes in tadpole transport behavior, spatial abilities may be similar (*A. femoralis*, Ringler et al. 2013, 2015a; Pašukonis et al. 2017). In a visual discrimination task in a laboratory maze, *D. auratus* used a win–stay/lose–shift strategy, demonstrating serial reversal learning and lending further support that dendrobatid frogs have advanced spatial memory (Liu et al. 2016). It remains unclear how flexible anuran spatial abilities are, and whether frogs are capable of planning ahead to optimize risks and costs.

In some species, anuran parental care goes beyond deposition of eggs or tadpoles, to provisioning of eggs. For example, direct developing *E. coqui* fathers provide moisture to eggs, which take up a significant amount of liquid from the father's body (Taigen et al. 1984). Also, *Cycloramphus fuliginosus* males have an iliac gland in the inguinal region that may provision antimicrobial mucus and protein secretions to offspring during egg attendance (Gonçalves and de Brito-Gitirana 2008). In *Xenopus laevis*, antibodies produced in response to an antigen-specific immune challenge in mother frogs were later detected in the eggs (Poorten and Kuhn 2009). In contrast, even though the bacterial assemblages of father *Hyalinobatrachium colymbiphyllum* and their eggs were very similar, removal of fathers did not influence egg bacterial assemblages, suggesting that extended parental care does not influence offspring microbiomes (Hughey et al. 2017). Provisioning can also take the form of active defense against predators, such as with mother *F. hansenae*, which physically interrupt feeding attempts by large arthropods to protect eggs (Poo et al. 2016).

Provisioning can also occur after tadpoles hatch. For example, some species intermittently visit tadpoles to feed them unfertilized nutritive or trophic eggs (reviewed in Weygoldt 1987). In some cases, tadpoles are obligatorily oophagous; they do not readily eat other food items, and stop growing and die before metamorphosis if abandoned by mothers (*O. pumilio*, Brust 1993; Pramuk and Hiler 1999; *K. eiffingeri*, Kam et al. 1997; Liang et al. 2002). In some non-egg-feeding dendrobatids and aromobatids, tadpoles retain yolk that allows them to grow during parental transport for up to a week (*Colostethus inguinalis*, Wells 1980; *M. trinitatis*, Downie et al. 2005).

Many species of anurans provision their eggs with chemical defenses (reviewed in Gunzburger and Travis 2005), but generally such predator defenses diminish as offspring develop. In contrast, nutritive eggs provided by mother *O. pumilio* contain alkaloid chemical defenses that mothers acquire from their own diet of leaf-litter arthropods (Stynoski et al. 2014a). The alkaloids transferred to tadpoles accumulate in poison glands as soon as glands begin to mature around Gosner stage 40 (Stynoski and O'Connell 2017). The chemical defenses are effective in defending tadpoles against spider and ant predators (Stynoski et al. 2014a,b), but not against snake predators (Stynoski et al. 2014b).

Many egg-feeding anurans display complex parent–offspring communication: when the parent frog arrives at the phytotelm, the tadpole exhibits vigorous vibration behavior. In *K. eiffingeri*, tadpoles determine the presence of the adult frog using chemical and tactile—but not visual—cues (Kam and Yang 2002), whereas in *O. pumilio*, tadpoles recognize adults based on visual and tactile—but not chemical—cues (Stynoski and Noble 2012). In both species, multimodal cues that confirm parental presence are needed to stimulate a full begging response, which likely serves to prevent the expression of conspicuous vibration behavior in the presence of a predator (Kam and Yang 2002; Stynoski and Noble 2012). Begging behavior is a reliable indicator of tadpole hunger (*R. imitator*, Yoshioka et al. 2016) and/or quality (*O. pumilio*, Dugas et al. 2017). Mother frogs use tadpole begging signals to make decisions about the allocation of eggs to tadpoles, giving more food to tadpoles that beg more intensely (Yoshioka et al. 2016; Dugas et al. 2017). The fact that tadpole begging is costly, in terms of growth and development (Yoshioka et al. 2016), may have played a role in the maintenance of signal honesty during the evolution of mother–offspring communication in these frogs.

Future Perspectives

It is increasingly evident that amphibians are an excellent system to address timely and relevant questions about the evolution of reproductive strategies, including parental care (i.e., Kupfer et al. 2006; Brown et al. 2010; Poo and Bickford 2013; Reinhard et al. 2013; Stynoski et al. 2014b; Tumulty et al. 2014; Vargas-Salinas et al. 2014; Lehtinen et al. 2014; Rojas 2014; Bravo-Valencia and Delia 2016; Yoshioka et al. 2016; Delia et al. 2017; Ringler et al. 2017; Schulte and Mayer 2017; Stynoski et al. 2018). The advent of new technologies has broadened the range of questions that can be addressed concerning the molecular and physiological underpinnings of parental behaviors (Roland and O'Connell 2015; Fischer et al. 2019). These advances, together with natural history observations, open promising avenues for future research on amphibian parental care. Even more broadly, this research could expand to questions regarding the evolutionary consequences of ancestral parental care for derived taxa, how the evolution of novel parental behaviors influences interspecific relationships (e.g., predator–prey relationships or microbial skin symbionts), and ecological niche use across biological kingdoms (e.g., within ecosystems like phytotelmata). We identify four areas of research that we believe will see rapid progress in the near future.

Multidisciplinary Approaches

Recent work has pushed the envelope on research directions in amphibians given the great variety of reproductive modes, macro- and microhabitats, and life histories that they encompass. Studies on parental care are evolving into multidisciplinary projects that draw a more complete picture by integrating perspectives such as behavioral (what the animals are doing), physiological (how they do it), ecological (in which environments they do it), and evolutionary (how or why did these behaviors evolve and what are the benefits). Such multifaceted issues are best addressed by researchers from many fields working together. We foresee great advances with regards to both the proximate factors influencing parental behaviors and the context in which they evolved. For example, attaching tracking devices to poison frogs has elucidated the movement of individuals around the complex environment of the forest, allowing us to establish where fathers deposit their tadpoles and how far deposition sites are from core areas (Beck et al. 2017; Pašukonis et al. 2019). Tracking methods could also be used to quantify the physiological costs of tadpole transport, and to compare parental investment among species that differ in transport distances. Physiological assays will shed light on the mechanisms underlying hatching plasticity, a behavioral flexibility which is vital for the survival of some glass and hylid frogs (Warkentin 1995, 2011). Likewise, through physiological techniques, we could get a better grasp of the hormonal triggers underlying parental-care behaviors, as well as the parental-care adaptations that have emerged in some amphibian groups in spite of the constraints imposed by ectothermy (Beekman et al. 2019).

Molecular approaches are a powerful way to tackle long-standing questions about animal behavior (Boake et al. 2002). Genotyping adults and young can illuminate parental decisions about offspring distribution across the habitat (Ringler et al. 2018), as well as the genetic relatedness of individuals in the same water body; kinship between offspring and care provider is often assumed but seldom confirmed. Also, parentage analyses will clarify the role of genetic relatedness in the evolution of communal nesting and whether perceived paternity impacts parental-care expression (cf. Neff and Gross 2001; Neff 2003 for similar findings in fish). Going a step further, molecular tools allow us to follow individual young through metamorphosis and dispersal; by sampling individual larvae or tadpoles, any free-living individuals can be subsequently identified genetically at different ontogenetic stages, eliminating the extremely challenging task of tracking each individual in the forest over time (Ringler et al. 2015c). This approach could enable us to measure carry-over effects from the larval to the adult stage, and to link phenotypic shifts across development or among populations or species with genotypic differences.

With an updated amphibian phylogeny (e.g., Jetz and Pyron 2018), it is now possible to delineate evolutionary homologies or analogies among parental care behaviors. Likewise, transcriptomics now allows for the quantification of gene expression (Todd et al. 2016), which is a powerful tool in evolutionary ecology for linking cellular processes with phenotypic traits, behavior, and selection pressures (Sneddon et al. 2005; Wollenberg et al. 2007). The combination of field and lab experiments with molecular techniques will provide answers to questions that are unreachable by either approach on its own, as seen in other taxa such as insects (Benowitz et al. 2017). Therefore, we hope to see the incorporation of transcriptomics in the study of parental care behavior and modes within and across amphibian taxa (Young et al. 2019).

Integrative Experimental Work

Much of the work on amphibian parental care has focused on ultimate questions about its adaptive value and how it has evolved. However, research on the proximate mechanisms underlying how these behaviors function and develop over ontogeny is more limited (Roland and O'Connell 2015; Fischer et al. 2019), partly because they can rarely be answered through observation alone. New technologies and methodological approaches from fields like genomics, endocrinology, and developmental biology hold promise for shedding light on the ways that tissues, hormones, genes, neurons, and regulation mechanisms allow amphibians to perform and moderate the diverse array of parental behaviors known today. Therefore, we emphasize the need for more experimental studies on diverse parental behaviors in amphibians. For example, experiments where begging offspring are reared independently along with electrophysiology or gene expression studies can shed light on individual variation in begging occurrence or intensity. Also, field manipulations can be combined with systems biology perspectives to understand decision making by parents that deposit eggs or tadpoles in diverse microhabitats and how they assess the mid-to-long-term stability of those sites. Furthermore, by combining field manipulations with chemical analysis (see Schulte et al. 2015) and controlled experiments (Saporito et al. 2019), we can uncover the use and significance of specific chemicals in parent–offspring and tadpole–tadpole communication, including in the context of paradoxical behaviors like larval cannibalism. Questions about the direct or indirect benefits of the vertical transfer of antipredator defenses (in *O. pumilio*, Stynoski et al. 2014a,b; Saporito et al. 2019) or skin microbiomes (in *H. colymbiphyllum*, Hughey et al. 2017) are ripe for study. And, controlled manipulations such as translocation or cross-fostering are needed to identify adaptive benefits of communal nesting to parents and offspring.

Parental Care in Times of Population Declines

The world is experiencing an alarming wave of biodiversity loss (Ceballos et al. 2015). In particular, amphibians have declined dramatically in the last four to five decades (Stuart et al. 2004). Approximately 43% of amphibian species worldwide are experiencing population declines (Stuart et al. 2004), due in great part to the spread of chytridiomycosis, a deadly fungal disease (Lips et al. 2006; Lips 2016; Bower et al. 2017; Scheele et al. 2019) and human-mediated habitat loss (Cushman 2006; Becker et al. 2007). Deforestation, for example, directly threatens species that use tree leaves (e.g., glassfrogs, hylids), epiphytes (e.g., some dendrobatids), or tree-holes (e.g., some dendrobatids, hylids, bufonids, hyperoliids, mantellids, microhylids, etc.) to lay or rear offspring. Furthermore, logging alters soils in ways that likely affect terrestrial or burrowing amphibians (e.g., some salamanders and caecilians) and their terrestrial egg nests (Nussbaum 1985; Kupfer et al. 2016). Climate change further destabilizes crucial microhabitats, making treeholes, phytotelmata, and small ponds more prone to desiccation, and limiting the time available for eggs and tadpoles to reach metamorphosis.

Likewise, we urge scientists to investigate the direct and indirect effects of habitat loss and climate change on species that perform parental care experimentally. Do parents alter care behaviors to adapt to higher risk of desiccation? Can parents assess this increasing risk? Do they shift the timing of reproductive cycles to reduce risks? Do they switch to a bet-hedging strategy? What costs do parents incur due to extended searches for suitable offspring deposition sites? Can parental decisions modulate the transmission of infectious diseases among their offspring?

Get Back to Basics: It is Time to Revive Our Interest in Natural History

Indisputably, the basis of everything we know about amphibian parental care is natural history (Fig. 2). However, unsettling formal and informal accounts have noted that natural history is “falling out of vogue” (Anderson 2017:290), and the number of organism-based courses at universities has dropped (Tewksbury et al. 2014). This is troublesome, because natural history is the foundation for new hypotheses in ecology and evolution (Endler 2015). Discoveries of new parental-care behaviors or new taxa exhibiting known parental-care behaviors can lead to novel experimental approaches, which advance our understanding about the adaptive benefits of parental care. Furthermore, cumulative effort in natural history studies permit comparisons across taxa, and thus a more robust understanding of how and why parental care evolved in diverse animal groups. For example, rigorous natural history observations of 40 species along with historical and functional analyses of clutch attendance recently debunked existing beliefs that parental care is rare among glass frogs (Centrolenidae) and is performed exclusively by males (Delia et al. 2017). Likewise, although *A. femoralis* exhibits predominantly male parental care, field observations revealed that females carry out tadpole transport in the male’s absence (Ringler et al. 2013, 2015b), and males cannibalize clutches of former territory holders when taking over their territory (Ringler et al. 2017). Whereas poison frog fathers call to attract additional mates while concurrently caring for offspring, hours of thorough field observations revealed that male Bornean smooth guardian frogs (*Limnonectes palavanensis*) practically do not move or eat for days while caring for clutches (Goyes Vallejos et al. 2018). Considering that these dedicated fathers forego future mating opportunities, it has been suggested that this species is exhibiting sex role reversal (Goyes Vallejos et al. 2018). Surely other instances of unexpected behavioral patterns will be unveiled by thorough observations of focal species in the wild.

Our plea to reinforce natural history observations also applies to over 200 species of caecilians and 700 species of salamanders (AmphibiaWeb 2017), many of which we do not know much about. According to the IUCN (2018), 37% of amphibian species are threatened and over 22% are so poorly documented that we cannot assess their threat status. So-called “basic” descriptive work is valuable and irreplaceable, providing foundational information needed to refine hypotheses about the function and evolution of behaviors and ecology, and thus must continue (e.g., Ferreira et al. 2019; Rojas and Pašukonis 2019; Ospina-L et al. 2019). For example, natural history observations were essential for a recent character state reconstruction illustrating the evolution of parental investment in caecilians (Kupfer et al. 2016), and similar observations are needed to approach such questions in frog and salamander groups.

The historical view of amphibians as simple animals that drop eggs in a pond and hop away has shifted to a more nuanced view of an animal group of over 7000 species (AmphibiaWeb 2017) with incredibly diverse reproductive modes. Most likely, additional novel forms of parental care will be unveiled in the coming years. Clearly, amphibians offer a precious opportunity to test long-standing as well as newly arising hypotheses on evolution and behavior involving an array of parental care modes, especially as amphibian taxonomy is refined and the natural history literature grows.

No less important, amphibians and their fascinating parental behaviors can bring science to a lay audience. Stories about how frogs care for their babies are endearing, and make for elegant outreach opportunities. By sharing those stories through videos, museum exhibits, websites, and colorful magazine and newspaper articles, we can inspire the general public to care, and to take steps in the conservation of threatened species. We encourage researchers in this area to use amphibian parental care in science communication and to have broader impacts outside of the community of academic biologists. Collaborative (rather than competitive) work across research groups, as well as integrative approaches, will further nourish the growth of understanding about the behaviors of these fascinating animals.

Conclusions

Parental care has been studied broadly by many researchers that employ multidisciplinary approaches across many animal taxa. However, certain groups are underrepresented in the literature; one such group is the amphibians. There have been attempts to classify amphibian parental-care behaviors, but because of a steady influx of descriptions of novel behaviors, classifications change frequently. The percentage of species recognized as providing parental care also rises consistently because of new observations and taxonomic discoveries. Currently, approximately 10% of anuran and 20% of urodelian species are believed to provide some type of parental care; there are no estimates for caecilians yet.

In this review, we recognize 28 types of parental care behaviors in frogs, 8 in salamanders, and 4 in caecilians. Parental behaviors have evolved independently several times within the amphibian clade. The focus of studies of amphibian parental care has shifted over time. The first descriptions of parental behavior in anurans, caecilians, and urodeles appeared in the 18th century, followed by decades of natural history notes and taxonomic descriptions. More recently, varied experimental approaches and modern tools have enriched our understanding of the adaptive function of and proximate mechanisms underlying parental care.

It has been challenging to study parental care in caecilians because they are fossorial, but natural history studies and character state reconstruction have provided some insights. The most ancestral form of care in this clade is egg attendance, which provides protection against desiccation and predation, and other caecilian species feed their offspring with intrauterine fluids or maternal skin. Urodeles are an excellent target for studies on the evolution of parental care because of their diverse fertilization mechanisms, mating systems, and associated ecological traits. Parental care has likely evolved independently many times in this clade, with maternal care evolving in species with internal fertilization and paternal care in those with external fertilization. Widespread parental behaviors include egg wrapping, different forms of egg attendance such as egg fanning and coiling around clutches, and ingestion of infected eggs to prevent fungal spread. The transmission of antifungal bacteria to embryos may have favored the evolution of communal nesting in some plethodontids, but more research is needed to clarify those mechanisms. The first description of parental care in anurans was written by a woman, Maria Sibylla Merian, in 1705. Anuran parental care is the most diverse and best studied among the amphibians, consisting of 28 distinct parental modes. Among those modes, egg attendance is the most widespread taxonomically and geographically, both among direct developing species and among species with tadpoles. Other modes include egg transport, either in specialized sacs or attached to the parent's body, and construction of mud and foam nests to protect embryos from predation and desiccation. Some species perform tadpole transport and feeding. Depending on the species, care providers can be female or male, and in a few cases, biparental care has led to the evolution of monogamy.

Anurans have stimulated more hypothesis-driven research than urodeles or gymnophionans. Experimental approaches, molecular tools, and refined phylogenetic relationships have prompted great advances in our understanding of the adaptive value of anuran parental care. In contrast, the study of physiological and morphological correlates of these behaviors has lagged behind. Some anuran clades have received more attention than others, particularly in the Neotropics. Looking to the future, we encourage multidisciplinary experimental studies that explore the role of parental care in adaptation to environmental change. We also call for a revival in the importance of natural history observations. We predict that these research directions will lead to significant advances in the study of amphibian parental care.

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