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An overview of parental care in the foam-nesting frogs of the genus *Leptodactylus* (Anura: Leptodactylidae): current knowledge and future directions

Juan F.C. Carrillo[1,*], Diego J. Santana[1], Cynthia P.A. Prado[1,2]

1 - Programa de Pós-Graduação em Ecologia e Conservação, Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Cidade Universitária, 79070-900, Campo Grande, Mato Grosso do Sul, Brazil

2 - Departamento de Morfologia e Fisiologia Animal, FCAV, Universidade Estadual Paulista (UNESP), Professor Paulo Donato Castellane S/N – Vila Industrial, 14884-900, Jaboticabal, São Paulo, Brazil

*Corresponding author; e-mail: jfcuestas@gmail.com

ORCID iDs: Carrillo: 0000-0002-8881-568X; Santana: 0000-0002-8789-3061; Prado: 0000-0002-6105-4921

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Abstract. Amphibians exhibit diverse parental care behaviours, which may be performed by the female, male or both parents. In the Neotropical family Leptodactylidae, frogs in the genus *Leptodactylus* exhibit different parenting behaviours. The repertoire of care behaviours includes egg/nest attendance, nest chamber sealing, tadpole feeding with trophic eggs, and tadpole attendance associated with complex behaviours, such as pumping behaviour and channel digging. Based on the available information, we found that 23.8% of *Leptodactylus* species are known to exhibit post-fertilization parental care. Future studies should focus on mechanisms involved in parent-offspring communication, including acoustic and chemical signals. Moreover, behaviours such as provisioning with trophic eggs are not well understood and deserves further investigation. Because of these complex parental care behaviours, tadpole schooling, and relative easy observation, frogs in the genus *Leptodactylus* represent excellent models for studies interested in parent-offspring communication and evolution of parental care.

Keywords: Amphibia, maternal care, mother-offspring communication, parental investment, tadpole schooling.

Introduction

Parental care can be defined as any behaviour performed after fertilization by an attendant parent that is directed at offspring and is likely to increase offspring lifetime reproductive success (Klug et al., 2012). Although parenting increases offspring growth and survival, it may be costly to parents in terms of future survival and reproduction (Trivers, 1972; Smiseth et al., 2012). Thus, parental care will be favoured only when the fitness benefits outweigh the costs (Klug et al., 2012). Parental care has been mostly studied in mammals and birds, while other groups like amphibians have received less attention (Schulte et al., 2020). Nonetheless, amphibians exhibit a wide variety of parental care behaviours associated with diverse reproductive modes (Haddad and Prado, 2005; Wells, 2007; Nunes-de-Almeida et al., 2021). All three orders of amphibians have species that exhibit parental behaviour with different levels of dedication and complexity (Wells, 2007; Nunes-de-Almeida et al., 2021). Anurans have the greatest number of described care modes (28), followed by Caudata with eight and Gymnophiona with three (Schulte et al., 2020).

Parental care is an important component of the reproductive behaviour of anurans, with 66% of the families presenting at least one type of parental care (Schulte et al. 2020). The caregiver may be the female, the male, or both,

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and the main functions of parenting in anurans include protection against predators, avoidance of egg dehydration and fungal infection, and offspring nourishment (Crump, 1996; Lehtinen and Nussbaum, 2003; Wells, 2007). In general, it is hypothesized that costs and benefits of care, life-history traits, and ecological, environmental and evolutionary dynamics each affected the origin of parental care (Klug et al., 2012).

Recent phylogenetic comparative studies pointed out that parental care in amphibians had variable evolutionary rates (Furness and Capellini, 2019). For instance, simple care behaviours (e.g., egg attendance) are gained and lost at similar rates and evolved at higher rates when compared with more complex adaptations (e.g., viviparity). In contrast, complex adaptations are lost at lower rates than simple attendance (Furness and Capellini, 2019). Additionally, parental care in frogs is related to terrestrial reproduction in humid tropical environments and evolved in association with small clutch size, larger eggs, and reduced adult size (Gomez-Mestre et al., 2012; Vági et al., 2019). Although our knowledge on parental care evolution in amphibians has improved in recent years (Gomez-Mestre et al., 2012; Furness and Capellini, 2019; Vági et al., 2019), considering the great diversity of behaviours, knowledge gaps still remain and further natural observations and experiments with different taxa may help elucidate the origins, functions, and maintenance of parenting in this animal group (Furness and Capellini, 2019; Schulte et al., 2020).

Considering pre and post-fertilization parental behaviours, the Neotropical frog family Leptodactylidae Werner, 1896 (1838) is one of the most diverse, exhibiting five parental care modes (Schulte et al., 2020). Among leptodactylids, parental care is exclusive of the genus *Leptodactylus*, currently composed of 84 frog species (Frost, 2023). In this genus, eggs are deposited embedded in foam nests, which provide protection against egg/embryo desiccation, predation, extreme temperatures and pathogens (Heyer, 1969; Downie, 1988, 1990; Fleming et al., 2009). Foam nest is derived from the mucus secretion produced by the female while releasing the oocytes. Foam production has three main stages: (1) female body arching and oocyte with mucus extrusion; (2) sperm release by the male; and (3) spawn beating with hind legs by the male, forming the foam nest (Heyer and Rand, 1977; Hödl, 1990). The species of *Leptodactylus* are distributed in four species groups, based on molecular, morphological and behavioural data: *L. fuscus*, *L. melanonotus*, *L. latrans*, and *L. pentadactylus* species groups (Heyer, 1969; Wells, 2007; Gibson and Buley, 2004; de Sá et al., 2014). Additionally, the genus is known to exhibit diverse reproductive modes: (1) deposition of foam nests on the water surface and exotrophic aquatic tadpoles (e.g., species in the *L. latrans* group and some in the *L. melanonotus* group); (2) foam nests in water-filled basins at the margins of water bodies and exotrophic aquatic tadpoles (e.g., some species in the *L. melanonotus* and *L. pentadactylus* groups); (3) foam nests in terrestrial basins or burrows and oophagous tadpoles (e.g., some species in the *L. pentadactylus* group); and (4) foam nests in subterranean chambers and exotrophic aquatic tadpoles (e.g., species in the *L. fuscus* group) (e.g., Prado et al., 2002; Silva and Giaretta, 2009; Pereira et al., 2015). All four species groups have species with some degree of parental care, some of them associated with the particular reproductive mode exhibited by each species (Prado et al., 2002), which will be discussed below.

Parental care has already been reviewed on a large scale, including pre and post-fertilization behaviours in all amphibian groups (e.g., Crump, 1996; Wells, 2007; Schulte et al., 2020). The last review reports three modes of post-fertilization parental care for *Leptodactylus* (Schulte et al., 2020). However, complex parent-offspring interactions and behaviours performed during post-fertilization care by attending parents and offspring (tadpoles) have not yet been properly reviewed. Here, we

describe what is currently known about post-fertilization parental care behaviour in *Leptodactylus* species and discuss future directions to advance our knowledge on parenting in this group. Because the genus has undergone taxonomic revisions, we have updated species names accordingly (e.g., Magalhães et al., 2020; Gazoni et al., 2021). The species names reported by the authors on the original descriptions are given in the supplementary table S1.

Duration of parental care

In anurans, time to metamorphosis varies according to environmental and ecological conditions, such as water temperature and competition (Álvarez and Nicieza, 2002), which may affect duration of parental care. Among *Leptodactylus* species, timing of egg hatching, metamorphosis and parental care is variable and poorly documented. Nest care in *L. luctator* (referred as *L. ocellatus*) varies from 6 to 8 days and care of tadpoles from 40 to 50 days (Vaz-Ferreira and Gehrau, 1975). On average, the parental care in *Leptodactylus podicipinus* lasts 28 days, ranging from 25 to 35 days (Martins, 2001). In *Leptodactylus insularum*, parental care may last up to 13 days (Hurme, 2011). In *Leptodactylus fallax* attending females stayed in the burrow tunnel until late larval developmental stages, between 42 to 57 days, before she ceased defending the nest (Gibson and Buley, 2004).

Parental care behaviours

Egg attendance

Egg attendance consists of caregiver guarding and protecting the foam nest during the first embryonic developmental stages, sometimes remaining in the middle of the foam nest with the head out of the water (fig. 1A), as observed in attending females of *L. luctator* (Fernández and Fernández, 1921; Vaz-Ferreira and Gehrau, 1975). Egg attendance was reported for *L. fuscus* (Lescure, 1973; Solano, 1987) and species of both *L. melanonotus* and *L. latrans* groups (e.g., Vaz-Ferreira and Gehrau, 1975; Downie, 1996; Martins, 2001). Both, the participation of females in egg attendance and the occurrence of nest guarding by males in *L. fuscus* deserve further investigation to be confirmed because were rarely observed in the field (table 1; Solano, 1987).

Tadpole attendance

In the groups *L. melanonotus* and *L. latrans*, females attend foam nests and remain with aquatic tadpoles after hatching (Martins, 2001; Rodrigues et al., 2011). Tadpoles form schools and attendance is usually more complex and may include stereotyped behaviours as follows (table 1).

Aggressive behaviour and parental distress call. Attending females may exhibit aggressive behaviour when they feel threatened, such as by attacking intruders. They may use their snout to hit or bite the intruders, or even vocalize to protect their tadpoles (Vaz-Ferreira and Gehrau, 1975; Prado et al., 2002; Rodrigues et al., 2011). Parental distress calls were first reported for *L. luctator* (as *L. ocellatus*) and later extended to *L. latrans* and *L. paranaru*, based on the acoustic parameters of the call and context of emission (Vaz-Ferreira and Gehrau, 1975; Sestito et al., 2016). In *L. latrans*, a distress call performed by the attending female was reported when an observer (representing a threat) approached the female and the school of tadpoles. Female behavioural display included jumping, biting and screaming toward the threat, in this order (Sestito et al., 2016; fig. 1B, table 1).

Pumping behaviour. To maintain school cohesion and guide tadpoles in the aquatic environment, attending females attract tadpoles by rising the hips and hitting the water surface with rhythmic movements, producing waves ("pumping behaviour" sensu Wells and Bard,

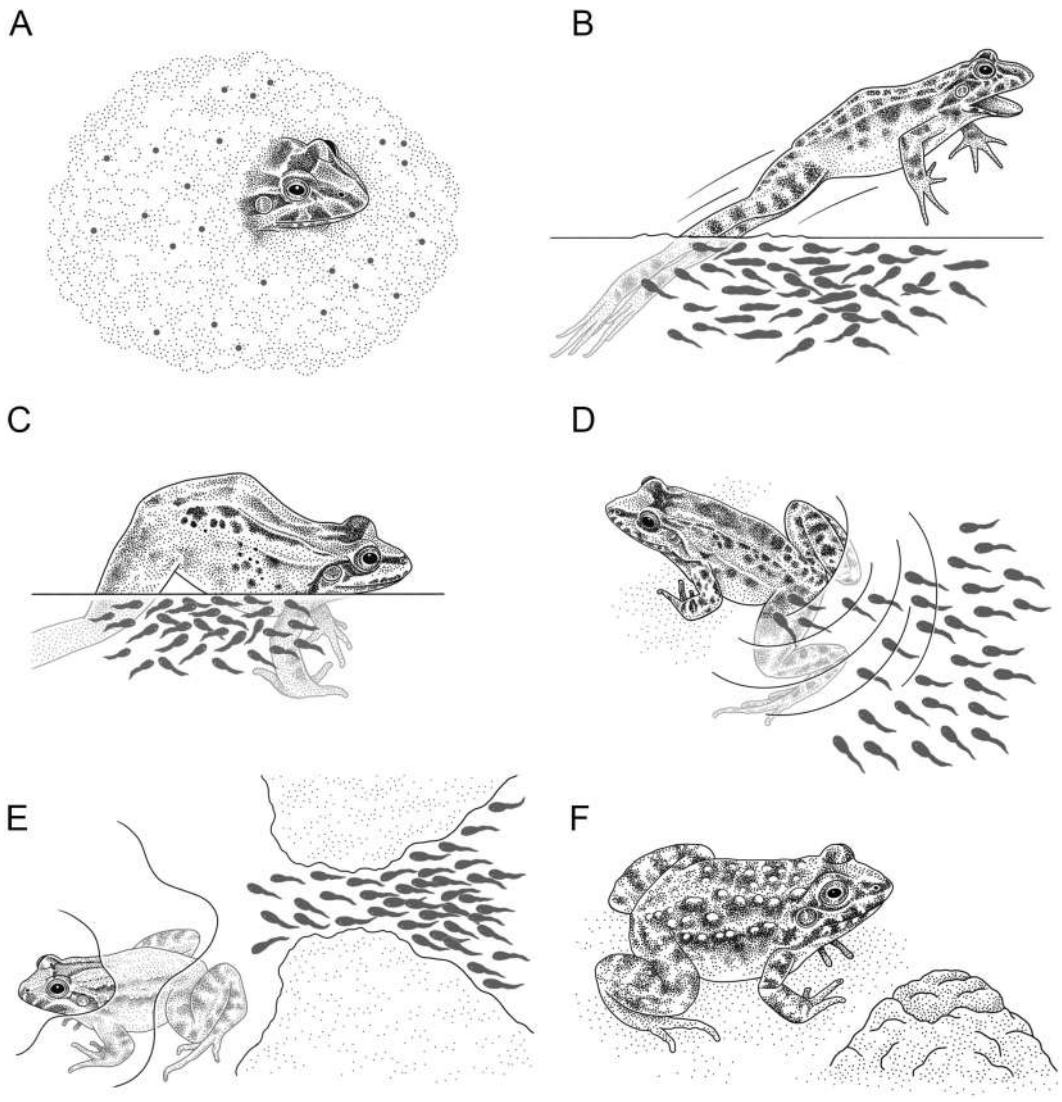

Figure 1. Parental care behaviours observed in species of the genus *Leptodactylus*. A) *Leptodactylus latrans* female attending the eggs in the foam nest (adapted from Zamudio et al., 2016). B) Aggressive behaviour of an attending female of *L. latrans* (adapted from Sestito et al., 2016). C) Attending female of *L. insularum* performing pumping behaviour that attracts the tadpoles (adapted from Wells, 2007). D) Tadpoles of *L. insularum* responding to pumping behaviour by aggregating and scraping attending female's back and legs (adapted from Wells, 2007). E) Channel digging performed by attending female of *L. podicipinus* to connect temporary ponds (adapted from Rodrigues et al., 2011). F) Nest sealing behaviour performed by female of *L. bufonius* (adapted from Crump, 1995; Faggioni et al., 2017). See text for behaviour details. Illustrations by Henrique Folly.

1988; fig. 1C and D). Pumping behaviour was first described for *L. insularum* (referred as *L. bolivianus*) as a stereotyped mechanical communication (Wells and Bard, 1988) and later described for other species in the *L. melanonotus* and *L. latrans* groups (e.g., Downie, 1996; Prado et al., 2000; Rodrigues et al., 2011; Carrillo et al., 2022a). Additionally, because tadpoles may answer by scraping the mothers' skin (table 1), it has been suggested that female chemical compounds might be involved in this communication (Wells and Bard, 1988),

Table 1. Parental care behaviours described for females of species in the genus *Leptodactylus*. Behavioural observations to be confirmed are denoted with (*).

Species Group	Species	Eggs/tadpoles	Behaviour	References
L. fuscus	*L. bufonius*	Eggs	Nest sealing	Cei, 1949; Philibosian et al., 1974; Crump, 1995; Reading and Jofré, 2003; Faggioni et al., 2017
	L. fuscus	Eggs	Attendance*, Nest sealing	Lescure, 1973; Solano, 1987; Lucas et al., 2008
	L. mystacinus	Eggs	Nest sealing	Giaretta and Oliveira-Filho, 2006
L. latrans	*L. insularum*	Eggs/tadpoles	Attendance, Aggressive behaviour, Channel digging, Parental distress call, Pumping behaviour	Wells and Bard, 1988; Vaira, 1997; Ponssa, 2001; Wells, 2007; Hurme, 2011
	L. latrans	Eggs/Tadpoles	Attendance, Aggressive behaviour, Parental distress call	Sestito et al., 2016
	L. luctator	Eggs/tadpoles	Acoustic signalling, Attendance, Aggressive behaviour, Channel digging, Parental distress call	Fernández and Fernández, 1921; Vaz-Ferreira and Gehrau, 1975; Rodrigues et al., 2011
	L. macrosternum	Tadpoles	Attendance, Pumping behaviour, Aggressive behaviour, Skin scraping	Prado el at., 2000; Heyer and Giaretta, 2009; Castro et al., 2013
	L. paranaru	Tadpoles	Attendance, Aggressive behaviour, Parental distress call	Sestito et al., 2016
L. melanonotus	*L. brevipes*	Tadpoles	Attendance, Pumping behaviour, Skin scraping	Carrillo et al., 2022a
	L. colombiensis	–	Attendance*	Estrada, pers. comm. in Ponssa, 2001
	L. leptodactyloides	Tadpoles	Pumping behaviour*	Cocroft and Morales, pers. comm. in Ponssa, 2001
	L. melanonotus	Tadpoles	Attendance, Channel digging, Skin scraping	Hoffmann, 2006
	L. natalensis	Eggs/tadpoles	Attendance, Channel digging, Pumping behaviour, Skin scraping	Santos and Amorim, 2005; Rodrigues et al., 2011
	L. petersii	Tadpoles	Attendance, Pumping behaviour	Lima et al., 2006; Morales et al., 2008
	L. podicipinus	Eggs/Tadpoles	Attendance, Aggressive behaviour, Channel digging, Pumping behaviour, Skin scraping	Prado et al., 2000; Martins, 2001; Prado et al., 2002; Rodrigues et al., 2011
	L. pustulatus	Eggs/Tadpoles	Attendance, Pumping behaviour	de Sá et al., 2007; Castro et al., 2013
	L. validus	Eggs/Tadpoles	Attendance, Pumping behaviour	Downie et al., 1996
L. pentadactylus	*L. fallax*	Eggs/Tadpoles	Attendance, Aggressive behaviour, feeding of tadpoles	Lescure, 1979; Lescure and Letellier, 1983; Davis et al., 2000; Gibson and Buley, 2004
	L. labyrinthicus	Tadpoles	Feeding of tadpoles	Prado et al., 2005; Shepard and Caldwell, 2005; Silva and Giaretta, 2008
	L. riveroi	Tadpoles	Attendance*	Lima et al., 2006

which could benefit tadpoles' nutrition (Hoffman, 2006).

Acoustic signalling. Acoustic communication between mother and tadpoles is a particular behaviour described only for *L. luctator* (table 1). Tadpoles emit harmonic sounds described as "falling drops over an incandescent surface" (Vaz-Ferreira and Gehrau, 1975), with a maximum frequency of 6.0 kHz and maximum duration of 0.24 seconds. This sound is followed by low frequency waves, allowing tadpoles to locate and aggregate with their conspecifics and females to locate schools (Vaz-Ferreira and Gehrau, 1975). Females, in turn, produce a pulsed call composed of two notes, both with maximum frequency of 3 kHz and maximum duration of 0.032 and 0.016 seconds, respectively (Vaz-Ferreira and Gehrau, 1975). The authors described the possible anatomical mechanism of the attending female call and suggested that the calls' main function is to provide female-offspring cohesion (Vaz-Ferreira and Gehrau, 1975). This may be especially important in areas with dense vegetation where visual communication is limited.

Channel digging. Frog species that reproduce in temporary ponds may eventually need to move their offspring from a drying pond to another one to avoid tadpole desiccation. For that purpose, it has been reported that attending females of the species *Leptodactylus podicipinus*, *L. melanonotus*, *L. luctator*, and *L. insularum* use the posterior limbs to construct channels that allow tadpoles to have access to adjacent water bodies (Hoffman, 2006; Rodrigues et al., 2011; fig. 1 E, table 1). Channel digging is eventually complemented with pumping behaviour to attract tadpole schools to larger temporary ponds (JFC Carrillo, pers. obs.). Additionally, Hoffman (2006) reported the construction of a tunnel by *L. melanonotus* female under experimental conditions.

Nest chamber sealing

Males of species in the *L. fuscus* group construct a subterranean chamber where the foam nest is deposited by the amplectant pair (Crump, 1995; Martins, 1988; Lucas et al., 2008). After oviposition, females of *L. bufonius* have been observed closing the opening of the chambers by pushing mud from the ground up to the top of the chamber (Crump, 1995). When necessary, attending females may use bladder water to moisten the mud (Crump, 1995). Nest chamber sealing is considered a female facultative behaviour for *L. bufonius* (Crump, 1995; Reading and Jofré, 2003; Faggioni et al., 2017), as well as for *L. fuscus* (Lucas et al., 2008; fig. 1F, table 1), and probably *L. mystacinus* (Giaretta and Oliveira-Filho, 2006).

Feeding of tadpoles

Foam nests of some species in the *L. pentadactylus* group are deposited in burrows far and more independent from water bodies (Prado et al., 2002; table 1). In *L. fallax*, females remain in the burrows after fertilization, getting in and out frequently and probably reducing their feeding time (Gibson and Buley, 2004). Although free from aquatic predators because of water body independence, attending females of *L. fallax* must provide unfertilized oocytes to feed the tadpoles (Gibson and Buley, 2004). Provisioning events occur on average every three days, with longer intervals of 11 days (Gibson and Buley, 2004). Trophic eggs have also been observed in foam nests of *L. labyrinthicus* (Prado et al., 2005; Shepard and Caldwell, 2005; Silva and Giaretta, 2008). Previous studies on *L. labyrinthicus* estimated that only 5% to 19% of the oocytes found in the nest were fertilized, with remaining unfertilized oocytes serving as food to tadpoles (Prado et al., 2005; Shepard and Caldwell, 2005; Silva and Giaretta, 2008). However, whether trophic eggs are laid by the female during the amplexus, or produced and laid afterwards, remains unknown for *L. labyrinthicus* and is further discussed

below (Prado et al., 2004; Silva and Giaretta, 2008).

Functions of parental care in *Leptodactylus* species

The roles of parental care in *Leptodactylus* include not only defence against predators (Vaz-Fereira and Gehrau, 1975; Rodrigues et al., 2011), but also protection against adverse environmental conditions (Reading and Jofré, 2003; Gibson and Buley, 2004; Faggioni et al., 2017). In larger species, such as those of the *L. latrans* group, the aggressive behaviours may be effective against large predators, such as birds, fishes, and snakes (Vaz-Fereira and Gehrau, 1975; Rodrigues et al., 2011; Sestito et al., 2016), whereas females of smaller species (e.g., *L. melanonotus* group) protect their offspring by eating small predators, such as insects and spiders (see Vaz-Ferreira and Gehrau, 1975; Martins, 2001; Carrillo et al., 2022b). However, the main function of maternal care in species of the *L. melanonotus* group seems to be related to guidance of tadpoles to safety from predators (Prado et al., 2000; CPA Prado, pers. obs.). The guidance of tadpoles to escape from drying ponds in seasonal environments by digging channels is another function of parental care in the genus (Hoffman, 2006; Rodrigues et al., 2011). Channel digging has been reported for *Leptodactylus* species with maternal tadpole attendance, both in the *L. latrans* and *L. melanonotus* groups (Hoffman, 2006; Rodrigues et al., 2011). Similar parental behaviour has also been observed in other anuran families, such as in males of African bullfrog, *Pyxicephalus adspersus* (Pyxicephalidae; Cook et al., 2001), and females of African shovel-nosed frog, *Hemisus marmoratus* (Hemisotidae; Kaminsky et al., 1999).

Nest chamber sealing is a facultative behaviour performed by females of the *L. fuscus* group (*L. bufonius*, *L. mystacinus* and *L. fuscus*), providing protection against predation (Giaretta and Oliveira-Filho, 2006; Lucas et al., 2008; Faggioni et al., 2017). Moreover, closed chambers may also prevent extreme temperatures and egg/embryo desiccation in seasonal dry environments, such as the Chaco and the Cerrado, where these species occur (Reading and Jofré, 2003; Lucas et al., 2008; Faggioni et al., 2017; Frost, 2023). In *L. bufonius*, although open chambers provide a stable environment in terms of temperature variation (Reading and Jofré, 2003), closed chambers maintain even lower temperatures inside the nest during the hottest hours of the day (Reading and Jofré, 2003; Faggioni et al., 2017). In a population of *L. bufonius* from central Argentina, the sealed chambers were found farther away from the water bodies than the unsealed ones, thus suggesting that this facultative behaviour may serve as an extra protection against extreme temperatures and offspring desiccation (Reading and Jofré, 2003).

Trophic egg provisioning was described for *L. fallax* (Gibson and Buley, 2004), but it is suggested as a possible behaviour for *L. pentadactylus*, *L. knudseni*, and *L. labyrinthicus* (Hero and Galatti, 1990; Prado et al., 2002; Prado et al., 2005), all species of the *L. pentadactylus* group (de Sá et al., 2014). *Leptodactylus labyrinthicus* inhabits seasonal open habitats with unpredictable rainfall in Brazil, Argentina and Paraguay (Frost, 2023). Breeding occurs in the rainy season and foam nests are typically deposited in terrestrial basins at the margins of water bodies, where tadpoles feed and complete metamorphosis (Prado et al., 2005; Shepard and Caldwell, 2005). As mentioned above, only 5% to 19% of the oocytes are fertilized in *L. labyrinthicus* and the remaining are consumed by the tadpoles (Prado et al., 2005; Shepard and Caldwell, 2005; Silva and Giaretta, 2008). An experimental study with this species showed that tadpoles may survive for up to 70 days feeding only on trophic eggs, being able to complete metamorphosis without additional food supply (Prado et al., 2005). Thus, authors argued that the provisioning of

trophic eggs may represent a reproductive strategy for seasonal habitats where the species occurs (Prado et al., 2005). Similarly, under low rainfall conditions in Panama, *L. pentadactylus* can deposit foam nests inside burrows and it has been reported the coexistence of eggs and tadpoles inside the nests, suggesting egg consumption as plausible (Muedeking and Heyer, 1976). In *L. fallax*, tadpoles complete development inside terrestrial burrows, avoiding risks such as drought of ephemeral ponds and aquatic predators (Gibson and Buley, 2004). As burrows have no contact with the exterior or adjacent ponds, feeding of tadpoles with trophic eggs is required. Only females of *L. fallax* have been reported returning to the nests to deposit trophic eggs (Gibson and Buley, 2004), whereas for the remaining *Leptodactylus* species the frequency of this behaviour and details regarding the deposition of trophic eggs remain unknown (Prado et al., 2004; Prado et al., 2005; Silva and Giaretta, 2008).

Feeding of free-living tadpoles occurs in only 6 out of 56 frog families, including Leptodactylidae (Schulte et al., 2020). Trophic egg provisioning is common in species that reproduce in phytotelmata (e.g., bromeliads, tree holes), such as frogs in the families Dendrobatidae (e.g., Pröhl and Hödl, 1999) and Rhacophoridae (e.g., Kam et al., 1996), probably related to limited food resources in these microhabitats (Wells, 2007; Brown et al., 2008). However, tadpoles developing in phytotelmata may benefit from reduced aquatic predation and competition (Magnusson and Hero, 1991; Brown et al., 2008; Zamudio et al., 2016). In leptodactylids, foam nests protect offspring from aquatic predators and desiccation (Downie, 1988, 1990) and divergence time estimates suggest that this trait evolved in the warm climates of the Eocene, followed by rapid diversification during a cold and dry period at the Oligocene/Miocene transition (Fouquet et al., 2013). Thus, we hypothesize that provisioning of tadpoles with trophic eggs in some *Leptodactylus* species has coevolved with the foam nest as a strategy to survive in seasonal habitats, with unpredictable rains (e.g., Prado et al., 2005), which deserves investigation.

Future directions

Based on the available information, 23.8% of *Leptodactylus* species exhibit some form of post-fertilization parental behaviour, including species within all four species groups (table 1). The complexity of parental care in *Leptodactylus* includes behaviours such as nest chamber sealing, aquatic tadpole attendance, channel digging, feeding of tadpoles with trophic eggs, and alloparental care (Prado et al., 2000; Gibson and Bulley, 2004; Rodrigues et al., 2011; Faggioni et al., 2017).

The low percentage of *Leptodactylus* species known to have parental care reveals that more natural history studies, with direct field observations, are still needed (Schulte et al., 2020). For instance, maternal care needs to be confirmed and described in more detail for *L. colombiensis*, *L. leptodactyloides*, *L. riveroi*, *L. petersii*, and *L. fuscus*, species for which parental care has been mentioned in literature only as "personal communication" or as part of natural history notes (Solano, 1987; Ponssa, 2001; Lima et al., 2006). Also, it is important to clarify if males exhibit some degree of parental care in *Leptodactylus* species, such as *L. fuscus*, *L. melanonotus* and *L. riveroi* (see Lescure, 1973; Solano, 1987; Ponssa, 2001; Hoffman, 2006; Lima et al., 2006). We suggest that male territorial and aggressive behaviours could have been misinterpreted as parental care (see Solano, 1987; Hoffman, 2006; Gibson and Buley, 2004). Additionally, we need more behavioural details and experimental studies about the mechanisms involved in mother-offspring communication, alloparental care and kin recognition, and provisioning of trophic eggs, as well as estimates of the costs and benefits of such behaviours (e.g., Rodrigues et al., 2011; Carrillo et al., 2022b).

The evolution of parental care in *Leptodactylus* has never been directly investigated. Previous studies at broader scales have used parental care information known for *Leptodactylus* to investigate, for instance, the evolution of reproductive modes in Leptodactylinae (Pereira et al., 2015), or the evolution of reproductive modes, parental care, and reproductive tradeoffs in amphibians as a whole (e.g., Gomez-Mestre et al., 2012; Furness and Capellini, 2019; Furness et al., 2022). Thus, the origins and maintenance of parental behaviours in *Leptodactylus* are poorly understood and need to be addressed in a phylogenetic context. Moreover, studies elucidating the genes involved in parenting behaviours, as well as on female anatomical adaptations for parental care, could open new avenues of investigation. Lastly, considering that terrestrial reproductive modes and hidden eggs favoured egg attendance evolution in amphibians (Furness and Capellini, 2022), the variation in levels of hidden reproductive modes exhibited by *Leptodactylus* species (Prado et al., 2002) offers an excellent opportunity to further understand the evolution of parental care in amphibians.

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