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Maternal Care and Obligatory Oophagy in *Leptodactylus fallax*: A New Reproductive Mode in Frogs

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Leptodactylus fallax **is an endangered frog (Leptodactylidae) found only on Montserrat and Dominica in the eastern Caribbean. Here we report the first captive breeding of this species and document a unique reproductive strategy with an unprecedented level of maternal care. Male frogs fought and dominant animals occupied a nesting burrow. Males enticed females into the burrow with a trilling bark call (100–120 calls/min). A terrestrial foam nest was produced after 9–14 h. Female frogs remained close to their foam nests and defended them aggressively throughout larval development (42–57 days). Females fed larvae (26–43 per nest) trophic (unfertilized) eggs. Many provisioning events (10–13) were recorded, supplying a total of 10,000—25,000 eggs. Male frogs also remained close to the burrow and defended the site. Trophic eggs were the exclusive food source for the developing larvae, and** ***L. fallax*** **is therefore probably displaying a new form of amphibian endotrophy.**

TWENTY-NINE different modes of reproduction have been documented in anurans (Duellman and Trueb, 1994). The most advanced forms of anuran reproduction are those independent of any water body (Duellman, 1992). The trend toward increasing terrestriality in the Leptodactylinae has three main stages: (1) foam nest on water, tadpoles aquatic and feeding (Modes 8 and 9) such as *Leptodactylus pentadactylus*; (2) foam nest on land, tadpoles aquatic and feeding (Mode 21) such as *Leptodactylus fuscus*; (3) foam nest on land, tadpoles terrestrial and nonfeeding (Mode 22) such as *Adenomera marmorata* (Duellman and Trueb, 1994).

Leptodactylus fallax is a large frog with average adult snout–vent length of 135 mm (Brooks, 1982). Its use as a food item and its preferred mountainous habitat have led to it being known throughout its distribution as the ''mountain chicken.'' Now found only on Montserrat and Dominica in the West Indies, it was extirpated from Martinique, Guadeloupe, St. Kitts, and St. Lucia in the early 20th century as a result of deforestation, introduced predators and competitors, habitat disturbance, and hunting for human consumption (Kaiser, 1994; Lescure and Letellier, 1983). Recently, the Montserrat population has been further threatened by activity of the Soufrière Hills volcano, which has destroyed much of the frog's habitat.

Lescure (1979) and Lescure and Letellier (1983) classified the reproductive mode of *L. fallax* as one in which tadpoles survive in the foam nest solely on egg yolk reserves until metamorphosis (Mode 22 in Duellman and Trueb, 1994). However, tadpoles were reported to grow to 110.5 mm while eggs were < 3 mm in diameter (Lescure and Letellier, 1983). It is unlikely that an egg of this size can contain the reserves necessary to produce a tadpole so large. This suggests that larvae obtain food for development from another source. From examination of two three-week-old wild nests Davis et al. (2000) concluded that *L. fallax* tadpoles were unlikely to be nonfeeding because none had any remaining yolk, and six weeks remained to metamorphosis. Muedeking and Heyer (1976) suggested that *L. pentadactylus* larvae in terrestrial nests distant from water bodies ingested eggs. Both Davis et al. (2000) and Prado et al. (2002) hypothesized that this might explain larval nutrition in *L. fallax*.

In this paper, we describe reproductive behavior in a captive population and present information on maternal care of larvae. This is the first study to describe the breeding strategy for this species. By analysis of video footage of frog reproduction, we examine the hypothesis that *L. fallax* tadpoles exhibit oophagy during development. A new mode of endotrophic anuran reproduction is identified, obligatory oophagy in a subterranean foam nest.

MATERIALS AND METHODS

Study animals (seven males, six females) were captured on Montserrat in November 1999 and subsequently housed at Jersey Zoo, British Channel Islands. Five large (2 × 2 m) indoor enclosures were established to house the frogs. Photoperiod (14:12 to 12:12 h), day and night temperatures (22–28 C), humidity (60–80%), and rainfall (warm water irrigation system) were controlled to reproduce the Montserrat montane forest climate. Enclosures were provided

TABLE 1. DATA ON STUDY NESTS SHOWING FREQUENCY AND NUMBER OF PROVISIONING EVENTS, NEST DEVELOPMENT TIME, AND METAMORPH NUMBER AND MASS.

		Provisioning events				Metamorphs		
			Time between events (days)				Mass (g)	
Nest	Date produced	Total	Range	Mean ± SD	Total nest development time (days)	*n*	Range	Mean ± SD
1	5/15/2000	10	2–7	3.0 ± 1.7	42	40	1.8–3.3g	2.8 ± 0.4
2	6/29/2000	11	1–5	3.3 ± 1.4	57	34	1.6–3.1g	2.5 ± 0.4
3	7/4/2000	12	1–11	3.2 ± 2.9	45	43	1.8–3.1g	3.1 ± 0.3
4	5/9/2001	13	2–4	2.4 ± 0.7	44	25	2.1–3.6g	3.0 ± 0.3

with a deep (5–40 cm) substrate of compost, bark-chippings, and leaf litter, and hollow logs, cork-bark tubes, and a large (50 × 50 cm) shallow (4 cm) water bowl. Frogs were fed crickets (*Acheta domestica*, *Gryllus bimaculatus*), locusts (*Locusta locusta*, *Schistocerca migratoria*) and occasionally small mice (*Mus musculus*). Insects were offered five nights per week and small mice once every two weeks. All food items were liberally supplemented with Nutrobal™ vitamin and mineral supplement.

The animals were initially housed in three of the five enclosures in groups as follows: two groups of two male:two female and one group of three male:two female. The remaining two empty enclosures were later used to accommodate males and females introduced for breeding purposes.

General observations of activity and behavior of the species, including calling, were made throughout the study period (November 1999 to December 2001) on an informal basis by both authors and other staff responsible for the care of the frogs.

Wild *L. fallax* foam nests commonly are constructed under rocks or logs, in tree stumps, in covered hollows or underground burrows (Brooks, 1982; Lescure, 1979), or may be associated with human-made structures (Davis et al., 2000). We constructed artificial nesting sites in all five enclosures from opaque plastic boxes (35 × 25 × 25 cm) containing a shallow (1.0 cm) layer of moist bark-chippings. Each box was fitted on one long side with a length (70 cm) of 10-cm diameter drainpipe that was partially covered with wood chips and leaf litter. This created a dark subterranean burrow with a single tunnel entrance. These burrows were checked briefly (< 1 min) each day and after suspected maternal activity. An infrared camera with microphone (GET GCCTVS10) was fitted to a later version of the burrow set-up. The camera was fitted to an aperture cut in the box lid and connected to a monitor and video recorder (Phillips TL24A/00T). The monitor allowed nests to be observed without physical disturbance. A later nest box was fitted with a glass bottom so that we could examine the underside of the nest and determine clutch size without disturbing it.

Between May through August 2000 and 2001, we repeatedly paired similar-sized males between 1600 and 1800 h in isolation from females in one of the two breeding enclosures. This was done to stimulate male-male interaction. After 2–4 days, we introduced a single female into each enclosure with the two males during the late afternoon (1630–1830 h). If no reproductive activity had occurred after 5–7 days, frogs were returned to their original communal enclosures. In the event of nest production, all three frogs were left undisturbed for the life of the nest.

A sample of five tadpoles was briefly removed (< 10 min) from one nest for examination and measurement. Eggs were also removed from the same nest for measurement. Tadpoles were removed after hatching and on subsequent occasions immediately after female attendance at the nest. They were measured with 150-mm dial calipers (CAMLAB, Cambridge, UK). Tadpoles were examined, and eggs were measured under a binocular microscope, 10× magnification (Prior SM3S) with micrometer. Tadpoles were only removed when the female was in the tunnel rather than the nest box itself because of the potential risk of nest abandonment.

RESULTS

Between May and August 2000 and May and August 2001, males were introduced to a female 28 times. Four successful breeding events involving four different females (Nests 1–4, Table 1) took place. Although nesting burrows were available in both communal and breeding enclosures, the only nests produced were in breeding enclosures. Nests 1 and 2 were produced in burrows without cameras and video recorders. Courtship, mating, nest production, and female nest attendance were recorded on videotape for

Nests 3 and 4. Nest 4 was produced in the burrow fitted with a glass bottom and was the nest from which tadpoles were removed for examination and measurement.

Male calling.—Males uttered loud ''whooping'' calls at all times of day and night in both the communal enclosures and the breeding enclosures. Details of these calls have been documented and analyzed by Davis et al. (2000). In this study, calls were made at a rate of 45–50 calls/min and calling duration varied from only a few seconds to > 2 h. Calls were more common during early morning and late afternoon and increased in regularity and duration during May and June; calling regularity decreased again toward the end of June. This pattern of calling corresponds with the seasonal pattern recorded in Montserrat with calling regularity increasing toward the end of the dry season from April to June (KRB, unpubl.).

Male-male interactions.—We observed agonistic interactions between males on four occasions during late afternoon (1600—1800 h) when males had been placed with each other in breeding enclosures. Only once was a nest produced after such an interaction when a female was introduced (Nest 2). Males ''stood'' almost upright on their hind legs facing each other, supported by each other's own body weight. Interactions began with vigorous pawing and pushing with forelimbs followed by bouts of clasping beneath the forelimbs and attempting to wrestle one another to the ground. When the physical interaction had finished the ''whooping'' call described above was heard from just one of the two males on three of the four occasions. This included the occasion followed by nest production. On the fourth occasion, both males called. Calling lasted from 10–23 min ($n = 5$).

Courtship.—On 19 of the 28 occasions that a female was introduced to two males, there was an obvious change in both male's use of the enclosure. Prior to the introduction of a female the two males did not seem to occupy a defined area within the enclosure. However, within 24 h of a female's introduction to the enclosure one of the males seemed to dominate and to occupy the nesting burrow area.

Courtship was recorded on videotape for Nests 3 and 4. Males called from nesting burrows. The ''whooping'' call increased in rate to a rapid ''trilling bark'' (100–120 calls/min) lasting until the female entered the burrow (11 min and > 8 h [$n = 2$]). At this time, the male stopped calling and attempted to amplex the female. The male moved on top of the female thrusting his whole body forward and backward in a frantic motion and reaching over the head of the female so that his rostrum almost touched the ground in front of her. Jerking motions were coupled with rapid undulations of the abdomen (3–6 undulations/sec, 3–5 sec duration). Orientation of frogs varied greatly during this activity from head-to-head to head-to-vent. Both frogs moved about the nest chamber often rotating in place. This created a shallow depression or clearing in the substrate lining the burrow. In both recorded instances, nest production did not occur during the initial encounter; the female broke loose and left the chamber. Departure of the female again triggered rapid calling by the male, which stopped when the female reentered the burrow. The females left the burrow two and five times ($n = 2$) before stable axillary amplexus (head-to-head) was achieved and nest production started.

Mating/nest production.—In the cases of Nests 3 and 4, foam nest production started when the amplectant male seemed to stimulate the female to expel fluid by bringing both hind feet up to touch the female's cloaca. Subsequently, the male paddled simultaneously with both hind legs, side-to-side, over the female's cloacal region. Paddling motions occurred in bouts every 8–75 sec (24 sec ± 13 sec; $n = 249$), on average consisting of 9 ± 2 movements; range 5–12, $n = 250$. Prior to each bout males twice pushed both legs together into the accumulating foam mass, lifting them again so they were in contact with the female's cloaca. Immediately after this behavior and prior to the next bout of paddling the female expelled further fluid from the cloaca.

Foam was evident 39 and 125 min ($n = 2$) after paddling started and formed behind the male and above the posterior end of the female's dorsum. Completion of the foam nest took 9.25 h and 14 h ($n = 2$) from the first attempt at amplexus. Both sexes called quietly and intermittently during nesting. The male abandoned the burrow soon (< 5 min) after the nest was completed leaving the female sitting in the foam. The female moved off the nest 23 and 46 min later ($n = 2$) and sat beside the nest in the burrow. Foam nests had developed a strong but flexible ''skin'' within 24 h when they were physically examined. The ''skin'' was resilient enough to support a female sitting on the nest.

Nest 4 was produced in a glass-bottomed nest burrow enabling the eggs to be counted without disturbing the nest. It contained 45 eggs, 26 of which subsequently hatched. Fertility of the other 19 eggs in the clutch could not be determined.

Nest defense.—Parental males remained close (< 1 m) to the site of each nesting burrow throughout larval development but never were observed entering the tunnel. Human interference around Nests 1, 2, and 4 elicited attacks from the males, which surged forward and butted with their heads. Direct interference with the burrow, either through the tunnel or through the removable lid, triggered the same response from the female, which remained within the tunnel or burrow. Other males in the same enclosure, known not to be the father, were not defensive and never were observed near an active nest. Parental defensive behavior directed toward these males was never observed. No frogs attacked staff servicing the enclosure unless there was an active nest in the enclosure.

Females were observed outside nest burrows on only five occasions during the entire developmental period for Nests 1–4. On each occasion, they were observed sitting in the water bowl in the early morning (0700–0830 h). The females never were observed feeding. However, females might have left the burrows more frequently and fed unobserved during the night when the burrows and enclosures were not monitored. The fact that females did not appear emaciated by the end of a breeding cycle implies that they did feed. Both males in the enclosures fed normally throughout the nesting period.

Larval nutrition.—Larvae were first detected by movements in the foam after six days in Nest 3 and 10 days in Nest 4. Once larvae had hatched, females repeatedly provisioned nests during larval development. First provisioning of nests took place 7–12 days (10 days ± 2.5 days; $n = 4$) after nest production. The occurrence of provisioning events was determined by daily physical checks for Nests 1 and 2 but could be detected on the video monitor for Nests 3 and 4. Eight of these provisioning events were captured on videotape; three events for Nest 3 (7, 9, and 10), and five events for Nest 4 (6, 7, 9, and 12). All events recorded were of larvae in stages 26–42 (Gosner, 1960) and lasted 38 min ± 19 min (range 15–90 min; $n = 8$).

The female entered the nest box and maneuvered herself over the nest/tadpoles; she then contracted the inguinal area of her abdomen. Fluid mixed with eggs (mean diameter of ovum and capsule, 1.6 mm ± 0.1 mm; $n = 15$) was expelled in short bursts. Tadpoles immediately oriented to the cloaca of the female and used rapid wriggling movements of their tails to move toward the emerging eggs. Tadpoles clustered around the female's vent and swallowed whole eggs. During provisioning, the female regularly swept her hind legs, each in turn, across her cloaca. This distributed the emerging eggs through the nest and displaced those larvae nearest the cloaca. The movements of the long-tailed larvae and the leg movements of the female renewed the foam in the nest.

Between provisioning events, the foam gradually became viscous fluid. The volume diminished so that tadpoles sometimes were exposed to the air with no foam covering. Therefore, the occurrence of other provisioning events, not recorded on videotape, was easily detected by regular checks on the state of the foam.

Females reprovisioned every 3 ± 1.3 days (range 1–7 days, $n = 42$). Feeding frequency did not seem to increase as larvae matured. On one occasion (Nest 3; Table 1) 11 days elapsed between provisioning events. Tadpoles seemed unaffected by such a long period between feeding events and progressed to metamorphosis normally.

Larvae were removed from Nest 4 and examined after provisioning events 3, 4, 6, 7, and 10 (Table 2). The gut of stage 25/26 (Gosner, 1960) tadpoles after the third provisioning event contained a creamy-white fluid identical in color to infertile eggs from the same nest. Tadpoles examined after the fourth provisioning event contained whole eggs. The approximate number of whole eggs ingested, counted through the transparent skin of the belly (Fig. 1), increased with tadpole development from 35 ± 3 eggs ($n = 5$) at 17 days to over 70 ± 9 eggs ($n = 5$) at 33 days. Larvae grew from 27 ± 1 mm total length at 12 days to 127 ± 5 mm total length at 33 days (Table 2).

Larval development.—During the first 4–5 weeks of development, tadpoles examined from Nest 4 were transparent and their internal organs were clearly visible. Larvae examined through the glass bottom of Nest 4 prior to the first provisioning event were inactive and seemed to contain nothing in their intestinal tract other than yolk residue.

The time from nest completion to metamorphosis ranged from 42–57 days (Table 1). Differences in developmental rates within a nest resulted in metamorphosed frogs emerging from the nest during 2/3 days. On leaving the burrow they had to squeeze past the female that

TABLE 2. GROWTH AND DEVELOPMENT OF FIVE LARVAE REMOVED FROM NEST 4 AT INTERVALS DURING DEVELOPMENT.

Age of larvae[a] (days)	Approx. stage Gosner (1960)	Snout–vent length (mm) Mean ± SD; $n = 5$	Tail length (mm) Mean ± SD; $n = 5$	Total length (mm) Mean ± SD; $n = 5$	Provisioning event number	Estimated eggs in gut Mean ± SD; $n = 5$
12	25–26	—	—	27 ± 1	3	[b]
17	25–26	—	—	83 ± 4	4	35 ± 3
22	26–30	20 ± 2	88 ± 3	108 ± 4	6	50 ± 6
26	37–38	23 ± 2	96 ± 4	119 ± 5	7	55 ± 6
33	41–42	26 ± 2	101 ± 4	127 ± 5	10	70 ± 9
44	44–46	30 ± 2	0	30 ± 2	—	—

[a] At age 44 days, larvae were fully metamorphosed.
[b] No whole eggs observed in gut.

remained wedged in the nest tunnel during the late stages of the development of her offspring. After emergence of the metamorphosed frogs the female stopped aggressively defending the nest and abandoned the burrow system to resume seemingly normal nonreproductive behavior.

The number of frogs metamorphosing ranged from 25–43 (Table 1). In Nest 4, in which 26 eggs were confirmed hatched, a total of 25 young frogs emerged (96% survivorship). Survivorship in the other three nests could not be calculated but only three dead larvae were retrieved from the four nests (two from Nest 1 and one from Nest 4). Emergent frogs began feeding on small crickets (*Acheta domestica* and *Gryllus bimaculatus*) 5–7 days after leaving the nest.

DISCUSSION

Although this study refers to a relatively small number of frogs in a captive environment, we think our observations are a valid representation of the reproductive mode of *L. fallax*. The study animals had only recently been brought into captivity and the unique behavior described is complex and unlikely to be an artifact of keeping the animals in captivity. Factors that might be influenced in captivity include clutch size, development time, and survival of larvae.

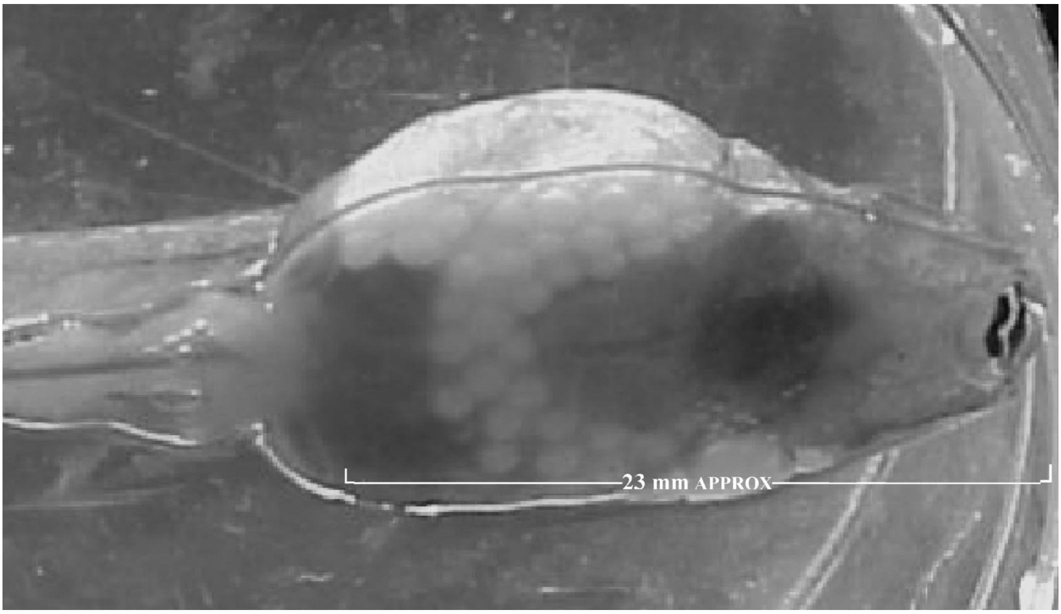

Fig. 1. Tadpole aged 26 days (approximate Gosner stage 37/38) from nest 4.

Nest production.—Davis et al. (2000) could not determine whether burrows used by wild *L. fallax* were exclusively naturally occurring or whether frogs sometimes made them. Each of the four incidences of nesting observed in this study occurred in artificial burrows. Despite the availability of a variety of substrates of depths up to 40 cm no evidence of attempted burrow construction was found.

The process of foam-nest production observed in Nests 3 and 4 resembles those described for *L. pentadactylus* (Rivero and Esteves, 1969; Heyer and Rand, 1977) and *Physalaemus ephippifer* (Hödl, 1990). Hödl (1990) defined three parts to each bout of foam-nesting activity: (1) female signal position; (2) male response (''basket formation''—male brings feet up to female's cloaca); (3) foam-beating. Mating male *L. fallax* observed in this study clearly demonstrated this ''basket formation,'' but no female signal was observed. Foam-beating behavior, the movement of the male's legs, seems to be the same ''windshield wiper action'' as described in *L. pentadactylus* (Hödl, 1990).

Nest defense.—Maternal defense of nests and tadpoles was reported in *L. fallax* (Lescure, 1979; Davis et al., 2000). It is also known in other *Leptodactylus* species. *Leptodactylus validus* females remain with aquatic tadpoles which move about in a dense mass (Downie et al., 1996). *Leptodactylus ocellatus* females also remain with aquatic tadpoles and attack wading birds attempting to feed on them (Vaz-Ferreira and Gehrau, 1975). Simulated predator attacks on *Leptodactylus bolivianus* caused females to jump toward the attacking object (Vaira, 1997). *Leptodactylus podicipinus* females attending tadpoles behave aggressively toward observers, jumping toward a stick held near the tadpoles and butting it with their heads (Prado et al., 2000).

Leptodactylus fallax females defend their nests/tadpoles aggressively, and for the first time in a *Leptodactylus* species, there also seems to be defensive behavior in males, although currently there are no observations in nature to support ours in captivity.

Nest provisioning and oophagy.—Maternal use of oocytes for provisioning of larval frogs was first documented for the Strawberry Poison-Dart Frog *Dendrobates pumilio* (Weygoldt, 1980). Subsequently, it has been described in several other frog species of the Hylidae, Dendrobatidae, and Mantellidae among species with arboreal aquatic tadpoles including *Osteopilus brunneus* (Lannoo et al., 1987), *Chirixalus eiffingeri* (Kam et al., 1996), *Osteocephalus oophagus* (Jungfer and Weygoldt, 1999), *Anotheca spinosa* (Jungfer, 1996), *Dendrobates vanzolinii* (Caldwell, 1997; Caldwell and deOliveira, 1999), *Colostethus beebei* (Bourne et al, 2001), and *Mantella laevigata* (Heying, 2001).

Tadpoles of at least two species of leptodactylids eat eggs of other frog species (Cardoso and Sazima, 1977; Downie, 1990) but no leptodactylids are known to eat conspecific eggs or demonstrate maternal provisioning. The provisioning events described here for *Leptodactylus fallax* also represent the first example of maternal nutritive egg provisioning for terrestrial larvae.

With a shift to a more terrestrial mode of reproduction, parental care in frogs tends to increase as clutch size decreases. Nutritional content of individual eggs increases and the overall energetic expenditure remains about the same for a frog of a given size (Crump and Kaplan, 1979). However, *L. fallax* produces only a small clutch of small (1.6 mm) presumably low energy fertilized eggs. This small energetic effort is subsequently increased with thousands of nutritive eggs. Although *L. fallax* conforms to the observed terrestrial breeding trend in increasing parental care, it fails to conform to the trend of decreasing clutch size and increasing egg size. Clutch size is small, but egg size is also small. Jungfer and Weygoldt (1999) have suggested that the correlation between decreasing clutch size and increasing egg size does not generally apply to those species with oophagous tadpoles. They hypothesize that, when most eggs are used as food, selection favors small eggs more easily swallowed by smaller larvae. Oophagy may have evolved in response to low food availability and quality in small arboreal water bodies such as bromeliads and tree holes (Lannoo et al., 1987). Limited food supply might also be typical of a terrestrial nesting frog, the tadpoles of which remain in the nest throughout development.

During early provisioning events by *L. fallax* eggs are not eaten whole presumably because larvae are too small (27 mm body length) to ingest whole 1.6 mm diameter eggs. Jungfer (1996) and Jungfer and Weygoldt (1999) showed that newly hatched tadpoles of *Anotheca spinosa* and *Osteocephalus oophagus* attach themselves to an egg and bite on it with their keratinized mouthparts. They then appeared to suck out the contents of the ovum, discarding the empty egg capsule. By the time larvae were provisioned with eggs for the second time they were capable of swallowing whole eggs. *Leptodactylus fallax* tadpoles may employ the same technique. The serrated keratinized structure of the beak

(Davis et al., 2000) suggests that they are capable of feeding in this manner. Additionally, our observations in larvae too small to swallow whole eggs of distended stomachs full of a substance identical in color to whole eggs support this suggestion.

Estimates of egg numbers released at sequential provisioning events suggest that females adjust the number they produce at each feeding. Given the large number of eggs (~70) consumed by each tadpole in a clutch of larvae 33 days old it is clear that fewer are being released for younger larvae. Surplus uneaten eggs would otherwise foul the nest or perhaps render it vulnerable to attack by insects with larvae that feed on amphibian eggs (e.g., Downie et al., 1995).

Based upon our limited data (Table 2) of eggs provided by females to larvae in our study, we can estimate the total number of eggs provided by a female caring for a clutch of tadpoles. We estimate that a nest of 26–43 tadpoles receives 910–1505 eggs at the fourth provisioning, 1300–2150 eggs at the sixth, 1430–2365 eggs at the seventh, and 1820–3010 eggs at the 10th. Allowing an arbitrary figure of 150 eggs for each of the first three provisioning events and using the values estimated above to represent the fifth, eighth, and ninth, and all subsequent events respectively, we can estimate that female *L. fallax* carrying out 10–13 provisioning events (Table 1) would provide nests of 26–43 tadpoles with at least 10,000—25,000 eggs during their development.

Females may be stimulated to provision their nests in response to cues from tadpoles. In videoed provisioning events, there was a marked increase in tadpole activity immediately prior to females starting to provision. Jungfer (1996) observed a similar increase in activity in *A. spinosa* tadpoles prior to feeding when females provided eggs for tadpoles in response to larvae sucking and biting around the female's cloaca.

The method by which foam is regenerated at each provisioning event is not clear. Downie (1984, 1989) demonstrated that tadpoles of *L. fuscus* could create new foam nests independent of water or of their mother with spitting movements of the mouth and wriggling of the tail. *Leptodactylus fallax* tadpoles in this study never regenerated foam nests between provisioning visits by the female. However, the activity of the larvae combined with fresh fluid provided by the female led to replenishment of the foam in the nest within minutes of the start of provisioning. Therefore, it is unclear whether the secretions of the adult female or of the larvae are necessary for foam production after initial nest production.

Reproductive mode and endotrophy.—Terrestrial reproduction in Leptodactylinae is best developed in the genus *Adenomera* (e.g., *Adenomera marmorata, Adenomera hylaedactyla*). Tadpoles of these species remain in the foam nest and develop through to metamorphosis using only their yolk; reproductive mode 22, nidicolous endotroph (Altig and Johnston, 1989; Duellman and Trueb, 1994). This reproductive mode had been assigned to *L. fallax* by Lescure and Letellier (1983).

In other cases of anuran larval nutrition via maternal provisioning with oocytes, larvae are free swimming in arboreal water bodies. Their mode of reproduction was not considered endotrophic because tadpole stomachs contained vegetation and other detritus presumably of some nutritional value (e.g., Lannoo et al., 1987; Jungfer, 1996; Jungfer and Weygoldt, 1999). In our study of *L. fallax,* there is no evidence that tadpoles gain nutrition from any source other than their own yolk (before the first provisioning event), and subsequently, from nutritive eggs deposited in the nest at intervals by their mother.

Given our observations on the novel reproductive behavior of *L. fallax* it is now possible to extend Duellman and Trueb's classification of amphibian reproductive modes. A new endotrophic reproductive mode: ''Foam nest on land, tadpoles terrestrial and show obligatory oophagy'' is demonstrated by *L. fallax.*

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