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# Prolonged parental behaviour by males of *Limnectes palavanensis* (Boulenger 1894), a frog with possible sex-role reversal

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## ABSTRACT

In sex-role-reversed systems, males carry out all parental care duties, forgoing further mating opportunities. Cases of complete sex-role reversal have not been reported in anurans. We describe the parental care behaviour of the leaf-litter frog *Limnectes palavanensis*, a Bornean endemic with egg-guarding and tadpole transport, possibly the first anuran with sex-role reversal. In this study, we tested one of the predictions of the sex-role reversal hypothesis: males invest more in parental care than females do, and this prevents them from quickly acquiring additional mates. We observed egg-guarding behaviour in captivity to determine the length and intensity of parental care. Also, we describe the tadpole climbing and tadpole transport behaviour. We found that males perform all of the parental duties, remaining with the clutch until hatching. They do not call during this time, nor do they care for more than one clutch at a time. Observations of tadpole transport in the field indicate that all tadpoles in the clutch are retrieved at once. The behaviour of males during tadpole retrieval suggests that they stimulate synchronous hatching. Together, these results indicate that the male parental expenditure in this species is high, resulting in lost mating opportunities. The prolonged male-only parental care behaviour of this species satisfies an important criterion for the occurrence of sex-role reversal.

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tadpole transport; frogs;  
parental investment

## Introduction

The strength of sexual selection acting on each sex is determined by the relative parental investment of males and females in their offspring, which in turn influences which sex becomes the limiting resource for reproduction. If paternal investment is costly and limits the availability of males, females will compete for access to the males and they become the choosy sex (Trivers 1972). This process is known as sex-role reversal. Within the vertebrate clade, cases of sex-role reversal have only been observed in fishes (sea horses and pipefishes) and birds (jacanas and phalaropes) (Reynolds 1987; Vincent et al. 1992; Emlen et al. 1998).

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Confirming sex-role reversal requires that (1) males invest in parental care more than females do, forfeiting additional mating opportunities to care for their offspring; (2) receptive females outnumber receptive males, so males become a limiting resource for mating; and (3) more than one female should approach a male and show some degree of competition among them. In addition, (4) males should behave as the choosy sex since they are investing more per mating event (Trivers 1972; Summers 1989; Wells 2007).

One of the most studied vertebrate examples of sex-role reversal is the family Syngnathidae, which includes the pipefishes and seahorses. Laboratory and field studies have shown that several species in this family are completely or partially sex-role reversed. In these species, males carry the eggs in a special pouch where they brood them until they hatch (Berglund et al. 1986). In most populations, reproductively active females are more abundant than males and compete with each other for access to males. Thus, when the operational sex ratio is female biased, males become the choosy sex, usually choosing larger females (Berglund 1993, 1995). In some species, sex roles in courtship change seasonally as the sex ratio becomes biased towards females late in the breeding season. Males with specialised brood pouches have a limited amount of space to carry the eggs, and they have to care for them until hatching. In contrast, females usually lay more than one clutch with more than one male, indicating that their reproductive rate exceeds that of the males (Berglund and Rosenqvist 1993). The behavioural characteristics of these species are consistent with the sex-role reversal hypothesis.

In anurans, the poison frog *Dendrobates auratus* was thought to present some degree of sex-role reversal, because males invest in parental care and female–female competition occurs (Wells 1978). However, males compete with each other for mating opportunities as well and can take care of several clutches at a time (Summers 1989). Consequently, even though females take an active role in courtship and also compete aggressively with other females for access to males, this example is not a clear case of sex-role reversal (Summers 1989; Summers and Tumulty 2013). To date, no frog species meets the criteria of a sex-role-reversed mating system despite the widespread occurrence of male parental care throughout the clade.

Most studies of anuran species with parental care have focused on the members of the family Dendrobatidae, known for attendance of terrestrial eggs and transport of tadpoles to water, by either males or females (Grant et al. 2006). Egg attendance and tadpole transport similar to that of dendrobatids has been briefly described in two species of guardian frogs from Borneo, *Limnonectes palavanensis* and *L. finchi* (Dicroglossidae) (Inger et al. 1986; Inger and Voris 1988). At present, very little is known about the behavioural ecology of these species; however, several aspects of the natural history of *L. palavanensis* are consistent with a sex-role-reversed mating system: (1) males call infrequently from widely separated locations on the forest floor and do not exhibit territorial behaviour; (2) females of *L. palavanensis* call at much higher rates than males and often vocalise spontaneously, sometimes in the absence of a calling male; (3) calling females outnumber calling males in the field; and (4) females form small groups of two or three individuals near individual males, suggesting the potential for female competition for mates (Goyes Vallejos et al. 2017).

*Limnonectes palavanensis* is found throughout the northern part of Borneo, including Brunei Darussalam, the Malaysian state of Sarawak, and part of western Kalimantan,

Indonesia, as well as Palawan Island, of the Philippines. Inger et al. (1986) reported the first observation of frogs carrying tadpoles in Borneo. Later, Inger and Voris (1988) briefly described the parental behaviour of *L. palavanensis* in Danum Valley Field Centre (4.962°N, 117.689°E) in Sabah, Malaysia. They observed two adults attending eggs and three males transporting tadpoles. Despite these descriptions, nothing is known about the time the care-giving parent invests attending the eggs, and details of tadpole transport behaviour are still lacking.

Here, we document the details of parental care by *L. palavanensis* and test one of the predictions of the sex-role reversal hypothesis. The evolution of sex-role reversal requires that parental investment from the father exceeds maternal investment, either because paternal care of the offspring is energetically expensive with further reproduction incurring a net cost, rather than a benefit, or because paternal care removes males from the mating pool for an extended period of time. Therefore, we hypothesise that males of *L. palavanensis* provide extended care to their offspring, forfeiting the opportunity to mate with additional females and indicating a key characteristic of a sex-role-reversed mating system.

## Methods

### *Study site*

We studied the reproductive and parental behaviour of *L. palavanensis* on the island of Borneo at the Kuala Belalong Field Studies Centre (KBFSC), Temburong district, in Brunei Darussalam (4.547°N, 115.157°E and 50–200 m above sea level). The yearly rainfall at the site varies between 4400 and 6800 mm, with no distinct dry season. The field station is located at the northern end of the Ulu Temburong National Park. The vegetation around the field station is composed of dipterocarp primary rainforest and low-density understory vegetation. The topography is steep, with soils composed of sedimentary rocks and clay and a shallow layer of leaf litter.

### *Egg attendance in the laboratory*

Mated pairs lay eggs on land, hidden under the leaf litter, and therefore egg clutches are extremely difficult to find in the field. Hence, in order to observe egg attendance behaviour we observed clutches obtained in captivity. From August to December 2014, we conducted acoustic encounter surveys in the area adjacent to the field station (ca. 1.3 ha) looking for calling males and females to form mating pairs. In this species, males and females vocalise throughout the night, with the males producing a long, loud trill advertisement call, and the females producing a short, soft chirp (Goyes Vallejos et al. 2017). The difference between the calls allows us to easily differentiate between males and females. Surveys were done from 1700 h until 2300 h using three main transects within the study area. When a male or a female was found, we took snout-urostyle measurements with a calliper (to the nearest 0.1 mm) and body mass using a digital portable scale (to the nearest 0.1 g). Both males and females were marked with a four-digit identification number by clipping a toe for each hand and each foot. They were brought to the outdoor area of the lab and put together (one female and one

male) in glass terraria (40 × 30 × 25 cm) with a plastic mesh cover and left alone overnight. The terraria were provided with a layer of clay soil, leaf litter and small invertebrates found in the forest to simulate the frogs' natural habitat. The terraria were sprayed with water every day to maintain 90% relative humidity inside, measured daily with a digital hygrometer. The next morning, if a clutch was found, we removed the non-attending adult, recorded the sex of the attending adult using the toe-clip number, counted the number of eggs, and initiated behavioural observations of the parent. The non-attending adults were released at night at the point of capture.

Every 6 h we observed the clutches for 5 min and recorded whether the attending parent was with the egg clutch. We made observations every day until the eggs hatched or the clutch was abandoned. We calculated the proportion of observations in which the adult was attending the clutch. For some individuals, we used focal animal sampling *ad libitum* (constant observation up to 5 h) using a Sony HDR-XR550V Handycam HD with the 'NightShot' setting to record in absolute darkness. We include descriptions of the hatching and climbing behaviour of the tadpoles. Immediately after the tadpoles hatched, the parent with all the tadpoles on its back was returned to the point of capture.

### ***Tadpole transport in the field***

During the 2014 field season, we visited the study area almost every night from 1700 h to 2300 h looking for adult *L. palavanensis* transporting tadpoles. When an adult was found, we approached it carefully and determined the number of tadpoles by photographing the back of the frog. In addition, we also photographed the front and hind feet to determine if the individual had been previously marked. We recorded the time and location. Individuals carrying tadpoles are very easily disturbed and are more sensitive to threats than are non-carrying individuals (J. Goyes Vallejos pers. obs). The slightest disturbance makes them flee very quickly, so we could not follow the tadpole-carriers to determine either the distance travelled or the tadpole deposition location.

### ***Ethics statement***

All the behavioural observations and experimental methods were conducted in accordance with the University of Connecticut's Institutional Animal Care and Use Committee (approved protocol A12-028) and followed the guidelines for the Treatment of Animals in Behavioural Research and Teaching from the Animal Behaviour Society. All necessary permits were obtained for the described study, which complied with all relevant regulations.

## **Results**

### ***Clutch size and egg attendance behaviour***

On 23 November 2013, we found an adult male in the field attending a clutch of eggs at 2000 h. The clutch had 14 eggs and it was located where a female had been calling 9 days before. The eggs were on top of a leaf and the male was covering the egg mass

with his body and hiding under the leaf litter. The clutch hatched at around 0000 h, but we did not observe when the tadpoles climbed onto the back of the parent. This was the only observation of an egg clutch in the field in three field seasons.

Both males and females hide deep in the leaf litter, so amplexus, fertilisation and egg deposition were never observed. Nine clutches of eggs were produced in terraria from 21 August to 3 December 2014. Eggs were deposited in leaf litter, and in all instances, the caregiving parent was a male. The mean  $\pm$  standard deviation (SD) number of eggs per clutch was  $15 \pm 4$  (range: 10–21 eggs,  $N = 9$ ). *Limnonectes palavanensis* exhibited sexual dimorphism in size; measurements of snout–urostyle length ranged from 26.0 to 28.6 mm for males and 29.0 to 33.0 mm for females. There was no correlation between number of eggs and female body size ( $P = 0.36$ ,  $r = 0.35$ ) or male body size ( $P = 0.43$ ,  $r = 0.32$ ). Hatching occurred  $10 \pm 1$  days (range: 9–11 days,  $N = 7$ ) after oviposition, between 1500 h and 0000 h. Tadpole size at hatching measured 2.61–2.73 mm (mean  $\pm$  SD =  $3.69 \pm 0.14$  mm) from the snout to the base of the tail, and a total length of 11–13 mm (mean  $\pm$  SD =  $11.89 \pm 0.72$  mm) ( $N = 11$ , one clutch). The maximum width of the body was 2.72–2.84 mm. Tadpoles hatched at Gosner (1960) stages 24–25, and their guts were full of yolk reserves, with the ventral intestinal coil beginning to form 24 h after hatching.

We considered egg attendance as any behaviour where the male was covering the clutch partially or completely at a fixed location, or when he was less than 1 cm away from the clutch (Crump 1996) (Figure 1). In three of the observed nine clutches, the male was not observed attending the egg clutch. In one case, the male escaped when we were trying to remove the female. We put him back in the terrarium, but he did not



**Figure 1.** Male of *Limnonectes palavanensis* attending a clutch of eggs.

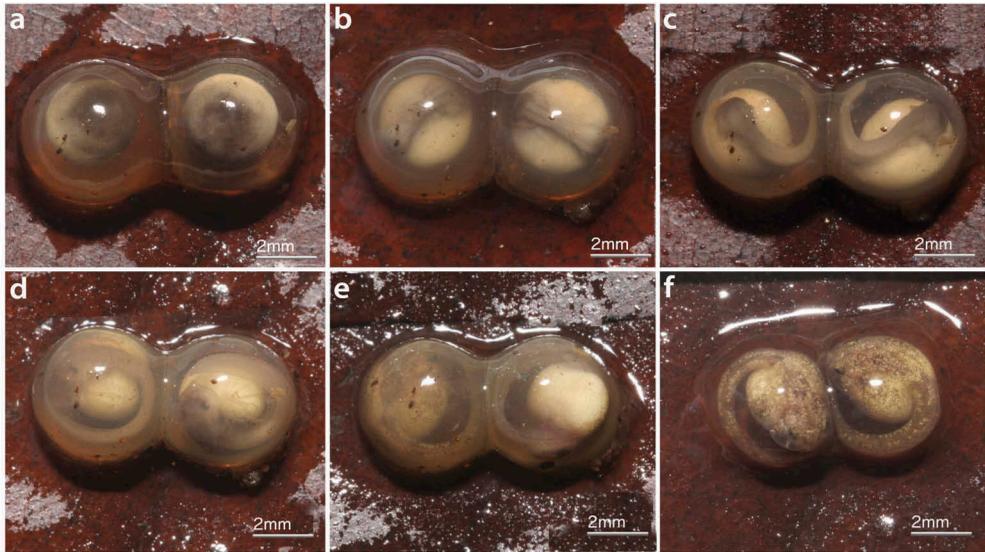
return to the clutch and was not observed attending the clutch at any time. However, the clutch of 14 abandoned eggs continued its normal development. After 9 days, 11 tadpoles broke free of their egg capsules, two appeared to be unfertilised, and one did not develop (Figure 2). In the other two cases, the clutches were not fertilised and were never observed to have a male attending them.

In one of the six remaining clutches, the male spent only 51% of the observations with the clutch of eggs. This particular clutch had 13 eggs, but from the day of oviposition, the eggs had been deposited in a scattered fashion and did not develop well. By day 11, most of the eggs looked decomposed and covered in fungus. At dusk, the male returned to the clutch site and retrieved two surviving tadpoles. For the rest of the observed clutches, the percentage of observations where the male was attending the clutch ranged between 79 to 98% (five clutches, 198 observations). Nearly all of the observations when the male was not with the clutch were due to previous disturbances from the observers when the male had been attending the eggs. We did not observe males of *L. palavanensis* eating unfertilised or infected eggs, nor did they exhibit disturbance-induced oophagy. Two of the total number of clutches observed had all the eggs develop into tadpoles. On average, egg-hatching success, defined as the percentage of eggs hatched per clutch, was  $72.23 \pm 31.25$  % (N = 9 clutches).

Approximately 24 h after fertilisation the eggs undergo rapid division with a clear differentiation of the vegetal pole and the animal pole (Figure 3(a)). After 3 days, neural folds have developed and fused to form the spinal cord and the brain (Gosner stage 15; Figure 3(b)). Head formation and tail elongation started 4 days after fertilisation [Gosner stage 18–19 (tailbud stage); Figure 3(c)]. When the embryos are 6 days old, the external gills are visible and eyes become apparent (Gosner stage 21–22; Figure 3(d)). By day 9, the eyes of the tadpoles are completely formed; their guts are full of yolk and they move inside the egg capsule when light is shined on them (Gosner stage 24–25; Figure 3(e)). After 10 days the clutch is ready to hatch, the egg capsules seem to become thinner, and the tadpoles can break free (Figure 3(f)).



**Figure 2.** Abandoned clutch of *Limnonectes palavanensis*. (a) Abandoned clutch of 14 eggs; note the formation of the animal pole (darkened area). (b) The clutch continued its normal development (7 days old). Two eggs did not develop (yellow arrows) and one egg stopped developing after day five (black arrow). The tadpoles hatched on their own after nine days.

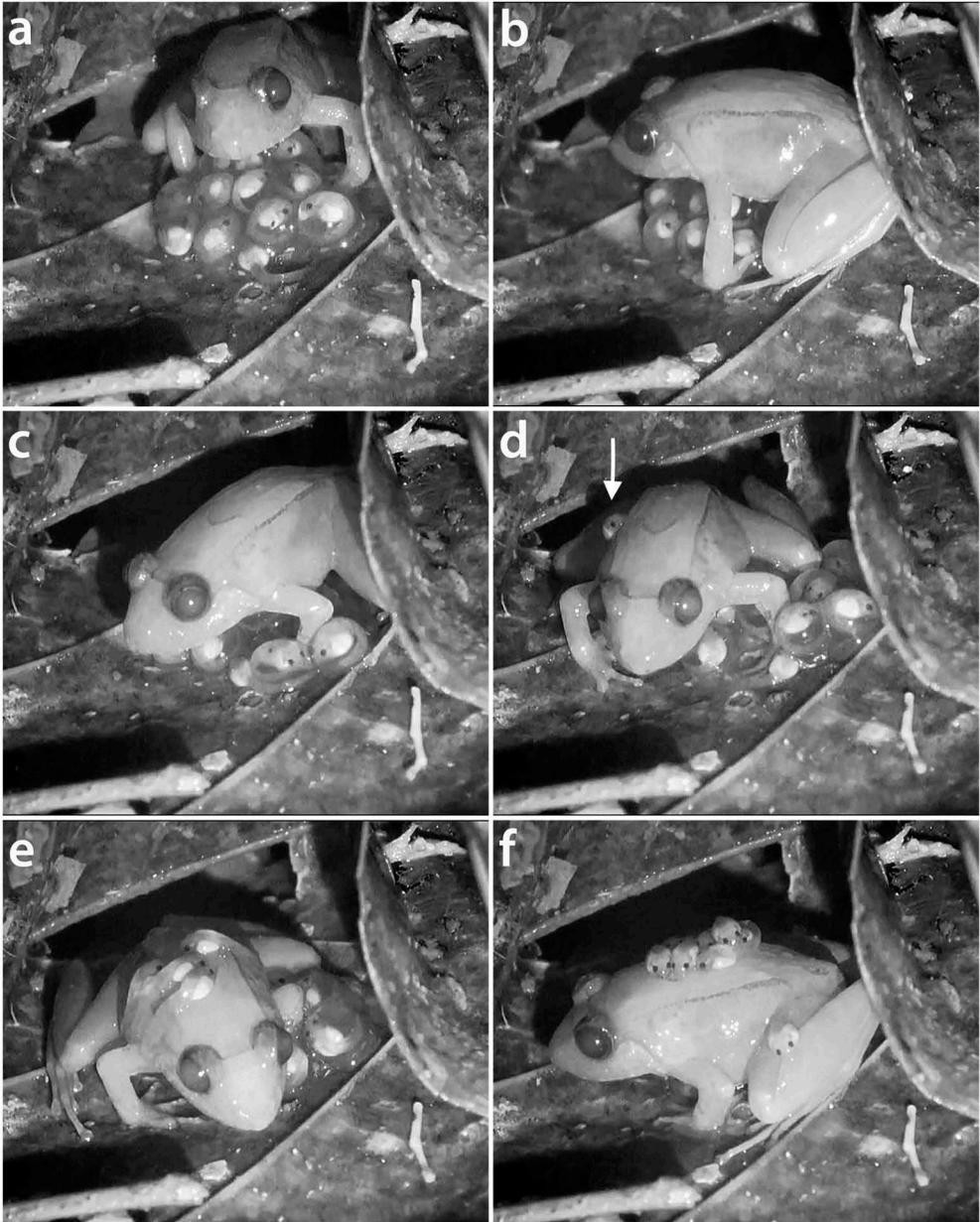


**Figure 3.** Embryonic development of the eggs of *L. palavanensis*. (a) The vegetal pole differentiates from the animal pole 24 h after fertilisation. (b) Neural folds develop, Gosner stage 15 (3 days old). (c) The head forms and the tail elongates around the yolk sac, Gosner stages 18–19 (4 days old). (d) Eyes become apparent and external gills are visible, Gosner stages 21–22 (6 days old). (e) The tadpoles are now sensitive to light, the eyes are completely formed and the gills are not visible anymore, Gosner stages 24–25 (9 days old). (f) The tadpoles are ready to hatch (10 days old).

During the continuous focal observations ( $N = 4$ ), attending males stayed with or near the clutch ( $< 1$  cm) during the whole observation period (sampling period = 50 min, 52 min, 85 min, 302 min, respectively). Males did not call while attending a clutch of eggs, despite the fact that some females were calling in adjacent terraria. Attending males were observed feeding on small invertebrates only if the prey animals crossed directly in front of them.

### ***Tadpoles climbing on males***

We observed tadpoles climbing on a male for three of the clutches in the laboratory and filmed a complete sequence (Figure 4; Supplementary video S1). Even though tadpoles were capable of breaking free from the egg capsule, males apparently initiated hatching with physical stimulation of the eggs by gently touching the eggs with their fingers and their chins. They rotated and tapped the eggs, and the tadpoles responded by spinning inside the egg capsule. Subsequently, the male positioned himself with the clutch under his abdomen, twitching his abdomen and fingers, and rotating his body on top of the eggs. He stepped several times on the eggs, separating them and seemingly breaking the egg capsule in the process. Once free, the tadpoles wriggled onto the back of the male while he remained still for several seconds. The male started a series of 45–90° turns left to right or right to left, waiting for several seconds after each turn for more tadpoles to climb onto his back. The tadpoles moved around on the back of the male continuously, rearranging themselves. Elapsed time



**Figure 4.** Climbing behaviour of the tadpoles of *L. palavanensis*. (a) The male stimulates hatching by touching the eggs with its chin and fingers. (b) The male positions himself on top of the eggs and twitches his abdomen and fingers. (c) He steps on the eggs, breaking the egg capsule and separating them. (d) The first tadpole starts climbing (indicated by the arrow). The male sits on top of the now free tadpoles and waits for them to climb. (e) The male starts to turn around while the tadpoles wriggle onto his back. After every turn he remains still for a few seconds while the tadpoles climb. (f) The tadpoles move around and rearrange themselves while the last tadpole makes it to the top.

from the moment the male stimulated hatching until the male left the oviposition site was 48, 50 and 87 min.

### ***Tadpole transport in the field***

During the 2013 and 2014 field seasons (ca. 10 months of fieldwork), we found only 10 males transporting tadpoles (Figure 5). All of the observations occurred between 2000 and 2200 h. In seven of these cases, it was possible to confirm the identity and sex of the transporting adult because it had been previously marked, and all seven were males. The average ( $\pm$  SD) number of tadpoles transported was  $13 \pm 2$  (range: 8–15). There was no correlation between body size and number of tadpoles ( $P = 0.25$ ,  $r = -0.49$ ,  $N = 7$ ). Since the frogs were already transporting tadpoles when discovered, it was not possible to determine the duration of tadpole transport.

We found one male in a pig wallow with approximately 19 tadpoles on his back. The male had its hind limbs and fore limbs completely submerged and the tadpoles were in contact with the water. The tadpoles spun their tails several times before slowly dislodging from the back of the male. Not all of the tadpoles detached at once. Upon detaching, some of the tadpoles swam away, but others stayed underneath the male, which remained motionless for 7 min. Unfortunately, the male jumped away before depositing the rest of the offspring, and we were not able to find it again.



**Figure 5.** A male (striped morph) *Limnonectes palavanensis* transporting tadpoles on his back.

## Discussion

In this study, we estimated the parental care investment (measured as days devoted to care for their offspring) of males of *L. palavanensis*, a possibly sex-role-reversed species. Males of *L. palavanensis* exhibit prolonged attendance of eggs, staying with them during the entire embryonic development period until hatching. In addition, males do not call while attending the eggs, indicating that males do not attract additional females, so they guard and transport one clutch at a time. This extended care period suggests that male investment in care surpasses female investment and that males are effectively forfeiting additional mating opportunities.

Males did not leave the clutch for foraging or other activities, but did eat prey opportunistically if small invertebrates passed close by. In a few instances, a male was observed shedding its skin and eating it. Males remained inactive during this time, presumably expending little energy. In *Eleutherodactylus coqui*, a Neotropical frog with exclusive male egg attendance, males remain with their clutches for a period of 20 days. While the food intake is reduced in brooding males vs non-brooding males, the losses in body mass and percentage of fat are small in brooding males (Townsend 1986). Males of *L. palavanensis* remain with the clutch for ca. 10 days; therefore, the energetic cost of egg attendance probably is minimal. Thus, the main cost of parental care to the males is loss of mating opportunities. In some species of dendrobatids in which the male guards the eggs and transports the tadpoles, males resume calling shortly after fertilisation and acquire additional mates, attending between two and five clutches at a time, thereby reducing the cost of paternal care (Roithmair 1994; Pröhl and Hödl 1999; Brown et al. 2008a; Ursprung et al. 2011; Forti et al. 2013). The ability to acquire additional mates plays a critical role in predicting a species' mating system. In most animal species, females have a higher parental investment; thus, sexual selection typically acts more strongly on males, making the females choosy. But if male parental investment is so high that limits the potential for additional mating opportunities, males can become the choosy sex. Exclusive parental care of eggs and/or tadpoles by males has evolved several times independently in amphibians. However, *L. palavanensis* is the only species that has spontaneous female calling, paternal care, and a female-biased operational sex ratio occurring simultaneously (Goyes Vallejos et al. 2017). The occurrence of these behaviours influences the shift of sex roles. Our study provides detailed information about the parental care of *L. palavanensis*, which is imperative for understanding its mating system and how it could have evolved into a sex-role-reversed species.

Observations of a clutch abandoned due to our disturbance of the male showed that, in the absence of predators, eggs can continue their normal development and can break free of the egg capsule without aid. However, without a male to retrieve and transport them to water, the aquatic tadpoles cannot complete development. Males carry the entire clutch of tadpoles at once and may induce synchronous hatching by physically stimulating the eggs. In *Ranitomeya imitator* and *R. variabilis* males have been observed touching the eggs with their hind legs to free the tadpoles from the egg capsule (Brown et al. 2008b). Whether or not physical stimulation by males of *L. palavanensis* is critical for synchronous hatching deserves further examination.

The number of tadpoles on the backs of males observed in the field was similar to the clutch sizes obtained in the lab, which suggests that males transport only one clutch at a

time. Tadpole retrieval is a lengthy process that can take up to 1.5 h before the males can begin their search for deposition sites. We do not currently know the tadpole transport distances that males of *L. palavanensis* travel before finding suitable pools to deposit their offspring. In *Colostethus panamansis*, a dendrobatid frog of similar size, females were found carrying large number of tadpoles, suggesting that the mother also carries the entire clutch at once. In this species, tadpoles grow while on the female's back, depending on their yolk reserves while she transports them to water, a process that can take up to 9 days (Wells 1980a, 1980b). Tadpoles of *L. palavanensis* hatch with their guts full of yolk reserves, possibly allowing them to stay on the male for several days without feeding. Thus, tadpole transportation in *L. palavanensis* could last several additional days depending on the ability of the male to find tadpole deposition sites. Proper determination of the length of tadpole transport and the effect of the availability of suitable tadpole depositions sites on parental expenditure will likely increase our estimates of the duration of male parental care in *L. palavanensis*, thereby providing further evidence of prolonged paternal care in this species.

In species with a sex-role-reversed mating system, male parental investment is so high in terms of time or energy expenditure that it limits the potential for additional mating opportunities. Thus, the time devoted to gamete production and parental care of the males is longer than for the females, and males become the limiting resource for reproduction (Parker and Simmons 1996). Here, we described the parental care behaviour of *L. palavanensis* and provided evidence that males care for their offspring virtually continuously for at least 10 days, and males do not acquire additional clutches. This is the first study providing information of the time from oviposition to hatching and the intensity of egg guarding by male *L. palavanensis*. The extended male parental care effectively removes males from the mating pool for a considerable amount of time. Therefore, the number of males that are not attending eggs at a given time may be limited and females will have to compete for access to the males if their potential reproductive rate is higher than that of the males as observed in species with a sex-role-reversed mating system. We hypothesise that *L. palavanensis* females can produce multiple clutches during the male egg attendance period. In other words, the potential reproductive rate of the females is higher than that of the males. The time interval at which females produce consecutive clutches remains unknown. Therefore, future research should focus on determining the time it takes a female to develop a new clutch after oviposition, and estimating the potential reproductive rate of the females.

In addition to high male parental investment, females in sex-role-reversed mating systems are more abundant and often exhibit characteristics generally associated with males. Our results, paired with the fact that females of *L. palavanensis* are highly vocal and more abundant in our study population, demonstrate that this species complies with some of the criteria for the occurrence of sex-role reversal. A case of true sex-role reversal in anurans has not been documented because no system has been found that satisfies the conditions for it. *Limnonectes palavanensis* is the strongest candidate to date. With its prolonged male parental care and particular female behaviour, *L. palavanensis* offers a unique opportunity to test predictions of sexual selection theory and determine they key factors responsible for the evolution of sex-role reversal.

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## Disclosure statement

No potential conflict of interest was reported by the authors.

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