

Maternal behaviour in response to predation threats in a vulnerable lizard from Patagonia, Argentina

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Abstract

Climatic and ecological conditions can determine the existence and degree of parental care. In species that live in cold-temperate environments and exhibit high reproductive effort it is expected that parental care would have greater selective value. In this study, we aimed to detect maternal behavioural responses to predation threats in the lizard *Phymaturus spectabilis* from cold-climate environments of Patagonia, Argentina. Seventeen females with their offspring each were exposed to four treatments in the laboratory: first a treatment with no stimulus, and then in a random order a carnivorous sympatric lizard, a conspecific male and a simulated flight of a museum mount of a raptor. We analysed the occurrence of 11 specific behaviours. Two clearly different parental responses occurred. In the presence of the raptor, mothers stayed near the offspring and remained motionless longer than in the other treatments. Their freezing response is consistent with their cryptic coloration and this species may rely on this strategy to avoid raptor predation. In contrast, in the presence of the predator lizard, mothers presented higher frequencies of flights, tail waves and head bobs. Head bobs are commonly interpreted as dissuasive signals to the predator to discourage attack. The behaviours observed in *P. spectabilis* together with similar behaviours observed in congeneric species would suggest the existence of a common pattern of parental care related to the high reproductive investment in *Phymaturus*.

Introduction

Reproductive investment is a key life-history trait that involves the energetic costs of gametogenesis and embryogenesis, and in some species includes the effects on fitness associated with parental care, in its diverse forms (Low, 1978). Parental care encompasses those behaviours that increase the fitness of offspring by providing protection and/or nutrition (Pike *et al.*, 2016). In a strict sense, parental care refers only to the protection of eggs and/or offspring after hatch or birth (Clutton-Brock, 1991), and studies on lizards have focused mainly on female egg guarding (O'Connor & Shine, 2003, 2004; Huang, 2006) or assistance in hatching (Lanham & Bull, 2000). However, although offspring disperse soon after birth in most lizards (Shine, 1988), in a few species offspring establish long-term associations with their mothers (e.g. *Xenosaurus newmanorum*, Lemos-Espinal, Smith & Ballinger, 1997; *Cordylus cataphractus*, Mouton, Flemming & Kanga, 1999; *Egernia saxatilis*, O'Connor & Shine, 2003, 2004, 2005; *Egernia striolata*, Bull *et al.*, 2001; *Egernia stokesii* and *Tiliqua rugosa*, Main & Bull, 1996). The extended parent–offspring relationship enhances offspring fitness by providing protection against

predation, and access to food and thermal resources (O'Connor & Shine, 2004), which in turn can benefit growth and performance (Sinervo, 1990; Mautz, Daniels & Bennett, 1992; Autumn & De Nardo, 1995; Niewiarowski, 2001).

Harsh environmental conditions, high predation pressure and resource competition have been pointed out as the main driving forces behind the evolution of parental care (Shine, 1988; Clutton-Brock, 1991). Many species of *Phymaturus* lizards live in extreme environments, characterized by cold and snowy winters, and short activity seasons with high daily thermal amplitudes, where resource competition and parental care behaviours are expected. In fact, preliminary studies in captive *Phymaturus* have shown evidence of females taking care of offspring (*Phymaturus antofagastensis*, *Phymaturus punae*, *Phymaturus calcogaster* and *Phymaturus aguanegra*; Halloy *et al.*, 2005, 2006). In Liolaemidae, the parental care behaviours observed in response to predator stimuli included head bobs, mouth opening, chasing of the intruder, mothers staying in proximity to offspring and mothers covering offspring with their bodies (Halloy *et al.*, 2013). Also, in *P. calcogaster* and *P. palluma*, offspring climbed onto the back of the mother, a manoeuvre perhaps used as an alternative to crypsis that may

function to dissuade a predator that is not willing to attack an adult lizard (Eisenberg & Werning, 2012; Halloy *et al.*, 2013).

The aim of this study is to contribute to the understanding of maternal antipredator behaviour and social interactions in lizards by analysing the responses of *Phymaturus spectabilis*' females with their offspring when exposed to different types of predation stimuli in laboratory conditions. We expect that the antipredator behavioural repertoire will vary depending on whether the predation stimulus is terrestrial or aerial, and predict displays of active antipredator behaviours in the presence of a terrestrial predator (head bobs, tail waves, flights), but motionless cryptic behaviour (freezing) when exposed to an aerial threat.

Materials and methods

Study area, lizard capture and conditions of captivity

We captured by noose or hand 17 females of *P. spectabilis* determined to be pregnant by inspection of external abdominal morphology and corroborated by abdominal palpation (Boretto *et al.*, 2014a,b). At the moment of capture, we georeferenced (GPS Garmin Map 60C Sx) the exact site of capture in order to return the female and her offspring to the same location after experimentation. Captures were made January 28–29, 2013, in a rocky outcrop 25 km south-west from Ingeniero Jaccobacci, Río Negro Province, Argentina (41°25'40" S; 69°45'07" W; 983 to 1064 m asl). This biotope lies within the occidental district of the Patagonian steppe, characterized by open ground, with gravel and effusive rock substrate. The dominant vegetation is composed of cushion plants in sparse large clumps; the Floristic Physiognomy Dominions (*sensu* Cabrera, 1971) are low–medium shrubby grass steppes. The climate is arid, with very cold winters and dry, windy summers. The mean annual precipitation ranges between 150 and 210 mm and is mainly restricted to winter. The mean air temperature of the warmest month is 26°C, and the mean air temperature of the coldest month is –0.8°C, registering an absolute minimum of –30°C (Bustos, 1995).

Pregnant females were transported within 24 h of capture 220 km to a laboratory at Centro Regional Universitario Bariloche (CRUB), Universidad Nacional del Comahue. Each female body length was measured (snout-vent length, SVL) with a digital calliper (Lee Tools®, ±0.02 mm) and weighed with a 50-g spring scale (Pesola®, ±0.5 g). The lizards were placed individually in plastic terrariums (floors 37 × 22 cm, walls 25 cm high) with a sandy substrate and a shelter consisting of a rock extracted from their habitat. Individuals from different terrariums were never in direct contact and never placed together in the same terrarium. After birth, offspring remained in the same terrarium as the mother. The sides of the terrariums were lined with paper to prevent visual contact among individuals. Heat was provided daily from 09:00 to 17:00 h by an infrared lamp situated in one corner of each terrarium to generate a thermal gradient for thermoregulation (22–39.5°C). In addition, we provided a 14:10 h light:dark regime complemented with 6 h of UV radiation daily from a source (Sylvania-Reptistar®) located 30 cm from the lizards

(*sensu* Lindgren, 2005). Water was provided *ad libitum* and lizards were fed every 2 days with vegetables and fruits, and with mealworms *Tenebrio molitor* dusted with vitamins and calcium. Females took in average 23.75 days (range: 8–37 days) to give birth. Litter size ranged from one to three offspring with a median value of two offspring. Immediately after birth, we weighed post-partum females with a 50-g spring scale (Pesola®, ±0.5 g) and recorded offspring body mass (10 g spring scale, Pesola®, ±0.5 g) and SVL (digital caliper; Lee Tools®, ±0.02 mm). Adults and offspring fed normally during captivity and there was no significant change in mean body mass from the date of birth to the date of release in either group (paired *t* tests, mothers: $t_{16} = 1.810$, $P = 0.089$, $\text{mean}_{\text{mothers_postpartum}} = 20.165 \pm 0.467$ g, $\text{mean}_{\text{mothers_release}} = 19.718 \pm 0.574$ g; offspring: $t_{32} = 1.587$, $P = 0.122$, $\text{mean}_{\text{offspring_at_birth}} = 4.548 \pm 0.094$ g, $\text{mean}_{\text{offspring_release}} = 4.342 \pm 0.091$ g). Mothers and offspring remained a maximum time of 45 days in captivity until all the births have occurred and all the experiments had been carried out. Finally, each family was released at the same location of capture.

Experimental procedures

The experiments were conducted within 48 h of birth in a plastic terrarium 55 cm high, 35 cm long and 24 cm wide covered with a sandy substrate. A video camera (Sony Handycam DCR-SR45) was placed approximately 1 m directly above the terrarium. We first introduced the mother and her offspring (usually a litter of two offspring but occasionally one or three) and left them for 5–10 min without any stimulus. Each family was manipulated with a unique pair of gloves in order to avoid confounding effects due to human or lizard scent. This 5–10 min period was chosen because it has been observed in other studies of lizard behaviour that this time is sufficient for lizards to accustom themselves to the enclosure and to interact normally (O'Connor & Shine, 2004; Labra, 2006; Aguilar, Labra & Niemeyer, 2009). A subsequent 10-min period was considered as the baseline control treatment (BCT). After BCT, three types of stimuli were presented one at a time for 10 min each and in a random sequence with 15 min of rest (no stimulus) between each 10-min treatment. The three stimuli were: (1) predator lizard treatment (PLT): an individual of the carnivorous lizard *Pristidactylus nigroiugulus*, natural predator of *P. spectabilis*' offspring (J. A. Scolaro, personal communication), collected from the same rocky outcrop as the pregnant females was used as stimulus of terrestrial predation; (2) control lizard treatment (CLT): an adult male of *P. spectabilis* was used as a control of the PLT considering that *P. spectabilis* does not represent a threat because it is predominantly herbivorous and there are no reports of cannibalism or aggression against juveniles in this species; (3) raptor treatment (RT): a museum mount of *Elanus leucurus*, an opportunistic raptor that prey on the most abundant and vulnerable species in each feeding area and is common at the study site (Bó, Baladrón & Biondi, 2007; Narosky & Yzurieta, 2010) that represented the risk of aerial predation that this species experience in their habitat. In the PLT and the CLT, the stimulus was introduced

in a corner of the terrarium away from the mother and offspring, and tethered at their waist constraining their radius of movement to approximately half of the terrarium. The raptor stimulus was passed over the terrarium by an unseen operator once per minute to simulate flight, following the methodology used to threaten lizards in other behavioural studies (Halloy, Boretto & Ibagüengoytia, 2007; Ventura *et al.*, 2017).

Videos analyses, variables recorded and sampling and recording rules

The videos were analysed by a single observer (Facundo Cabezas-Cartes) and we used focal animal sampling of each mother. The videos were viewed twice: first we used time sampling recording of some of the categorical behaviours and then we used continuous recording for occurrences of the other categorical behaviours (Martin & Bateson, 2007; see Table 1).

Data analyses

Principal component analysis (PCA) was used to develop integrative measures of the behaviour of mothers during the experimental treatments. We performed one-way repeated measures analysis of variance (RMANOVA) with four treatments: BCT,

PLT, CLT and RT to compare the effect of the treatments in the behavioural variables. In order to perform all pair-wise comparisons of treatment means *a posteriori*, we used the Tukey's multiple comparison test. Normality and homogeneity of variance assumptions were tested using Kolmogorov–Smirnov test and Levene's test respectively. We used the statistical software Canoco 5.03[®] (Microcomputer Power, Ithaca, NY, USA) and Sigma Plot 11.0[®] (Systat Software Inc., San Jose, CA, USA).

Results

Exploratory analyses revealed that some of the behavioural variables were correlated with one another, so we used PCA to develop integrative measures of behaviour and reduce the number of variables analysed. We kept the principal component 1 (PC1) and the principal component 2 (PC2) since their eigenvalues were higher than the mean of the overall eigenvalues (Table 2; $\text{eigenvalue}_{\text{mean}} = 0.193$). The variables 'association with one offspring', 'mother over offspring' and 'offspring over mother' were removed from the analyses since they presented loadings lower than 0.4 and higher than -0.4 in PC1 and PC2.

Principal component 1 showed negative loadings from some exploratory behaviours such as 'motion', 'wall scratching' and

Table 1 Description, sampling and recording rules, and type of measure (*sensu* Martin & Bateson, 2007) of the behavioural variables analysed in *P. spectabilis* mothers

Behaviour	Description	Sampling and recording rules, and type of measure
Association with one offspring	Defined when at least one offspring remains within a radius of 9 cm (a standard adult SVL of the species, <i>sensu</i> Halloy & Halloy, 1997) of its mother for more than 8 s of the interval	Focal animal sampling of the mother with one-zero sampling with an interval of 15 s. The score obtained was expressed as the proportion of all sample intervals during which the behaviour pattern occurred
Association with both offspring	Defined when both offspring remain within a radius of 9 cm (<i>sensu</i> Halloy & Halloy, 1997) from their mother for more than 8 s of the interval	
Motion	Defined when the mother spent more than 8 s of the interval moving, including walking, adjustments of body posture and displacements of the body's centre of gravity (Labra, 2006)	
Head bob	Stereotypical up and down motion of the head (Martins <i>et al.</i> , 2004)	Focal animal sampling of mother and continuous recording. The scores obtained were the total number of occurrences in 10 min
Tongue-flick towards terrarium	Protrusion and rapid retraction of the tongue towards the terrarium walls or floor, a behaviour considered to be an indicator of chemical exploration (Mason, 1992)	
Tongue-flick towards offspring	Protrusion and rapid retraction of the tongue towards offspring	
Tail wave	Fast swinging of the tail from its base and side to side (typically four or five times)	
Mother over offspring	Mother covers an offspring with her body, forming a bridge over it (<i>sensu</i> Halloy <i>et al.</i> , 2007)	
Offspring over mother	Mother is mounted (on her back) by at least one offspring (<i>sensu</i> Halloy <i>et al.</i> , 2013)	
Wall scratching	Movement of the anterior limbs towards the terrarium walls in a vertical position of the lizard's body, probably trying to climb the wall and explore other places	
Flight	Burst run ('sprint run', <i>sensu</i> Cabezas-Cartes <i>et al.</i> , 2014) directed away from a given predation stimulus	

Table 2 Loading scores and eigenvalues of principal components 1 and 2 (PC1 and PC2) for the behavioural variables analysed during the experimental trials

Variable	PC1	PC2
Association with both offspring	0.4620	-0.1109
Head bobs	-0.1626	0.8420
Tongue flicks towards terrarium	-0.8125	-0.2032
Tongue flicks towards offspring	-0.4016	-0.2062
Tail waves	-0.1771	0.7131
Motion	-0.9253	-0.1257
Wall scratching	-0.8165	-0.1157
Flights	-0.1843	0.7827
Eigenvalues	0.3312	0.2444

'tongue-flicks towards terrarium' (Fig. 1; Table 2) and positive loading from 'association with both offspring'. The raptor treatment differed significantly from the rest of the treatments (RMANOVA: $F_{3,64} = 37.044$, $P < 0.001$; Table 3; Fig. 2). We considered the PC2 to be a proxy of active antipredator behaviours since this axis showed positive loadings from the variables: 'head bobs', 'tail waves' and 'flights' (Table 2). There were differences among the treatments in the values obtained for each mother (RMANOVA: $F_{3,64} = 11.885$, $P < 0.001$); specifically the predator lizard treatment differed from the rest of the treatments (Table 3; Fig. 3).

Discussion

Phymaturus spectabilis females with their offspring displayed behavioural repertoires likely related to parental care when

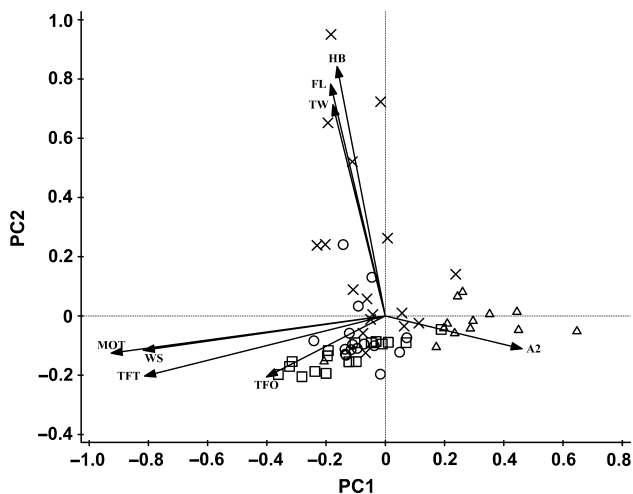


Figure 1 Principal component analysis (PCA) correlation biplot obtained from the data of the frequency of the behavioural variables displayed by *Phymaturus spectabilis* mothers under the different treatments. Squares represent the samples of BCT, crosses of LPT, empty circles of LCT and triangles of RT. A2: association with both offspring, HB: head bobs, TFT: tongue flicks towards terrarium, TFO: tongue flicks towards offspring, TW: tail waves, WS: wall scratching, MOT: motion and FL: flight.

they were exposed to predation stimuli. Although our study cannot determine whether the mothers' behaviours were caused by the presence of offspring because we did not observe females without offspring as a comparison group, we were able to describe how mothers behave under the threat of predation. Specifically, two types of displays were observed which depended on the type of predator. On the one hand, in the presence of a terrestrial predator (the carnivorous lizard *P. nigroigulus*), we observed a higher frequency of active antipredator behaviours such as head bobs, tail waves and flights. On the other hand, when the predation stimulus came from the air, females reduced exploration and activity, and spent more time close to their offspring.

Head bobs are common in lizards and they have been proposed as part of species-specific elaborated communication systems in some species (Carpenter, 1978; Fox, McCoy & Baird, 2003), used in territory defence, courtship and other social roles such as the identification of gender and individual identity (i.e. Carpenter & Ferguson, 1977; Martins, 1991, 1993). Also, head bobs might be part of the behavioural repertoire associated with parental care as are other behaviours such as mouth gaping, chasing and biting (Halloy *et al.*, 2013). In *P. spectabilis*, the higher frequency of head bobs by the mother in the presence of a terrestrial predator could be interpreted as a signal to offspring of the potential danger that the predator represents, although further studies are necessary to test this hypothesis. Nevertheless, head bobs could play an additional role in the presence of the predator lizard, functioning as a dissuasive signal, as well as tail wave displays, that communicate to the predator the prey's ability to escape and a lower likelihood of successful capture and handling of prey, as the hypothesis of pursuit-deterrent signal predicts (Hasson, 1991; Caro, 1995).

In the presence of an aerial predator, the behavioural responses of the mothers in our experiment were different than when facing a terrestrial predator. Specifically, the mothers remained in place for long periods, stifling even subtle movements such as tongue flicking (Labra & Niemeyer, 2004), and in close proximity to their offspring (<9 cm away). The freezing behaviour can be interpreted as an antipredator behaviour, as observed in other species (Vitt & Congdon, 1978; Schwarzkopf & Shine, 1992), while the close association between mother and offspring for a prolonged period of time has been proposed as an indirect form of parental care in other species of *Phymaturus* (Halloy *et al.*, 2005), in the high-altitude viviparous lizard *Liolaemus huacahuasicus* (Halloy & Halloy, 1997), and in *L. elongatus* from Patagonia (Halloy *et al.*, 2007). Our field observations confirm that this type of behaviour is also common in the natural environment given that most of the mothers released in the field after our experiments remained close to their offspring for more than 30 min and some mothers were observed to walk up to 10 m away from their offspring, in an apparent exploration, only to return to their offspring at the original location (Cabezas-Cartes, 2016).

The differences observed in maternal antipredator displays in *P. spectabilis* are related to the kind of behavioural repertoire that a terrestrial and an aerial predator can trigger in lizards. Lizards use three strategies to escape from predators: 'flight',

Table 3 *P* values of *a posteriori* multiple comparison procedures (Tukey's tests) among the four treatments (BCT, LPT, CLT and RT) for each principal component analysed

	PC1				PC2		
	Baseline control	Control lizard	Raptor		Baseline control	Control lizard	Raptor
Control lizard	0.538	–	–	Control lizard	0.691	–	–
Raptor	<0.001	<0.001	–	Raptor	0.369	0.946	–
Lizard predator	0.237	0.953	<0.001	Lizard predator	<0.001	<0.001	0.003

Bold values indicate significant differences ($P < 0.05$).

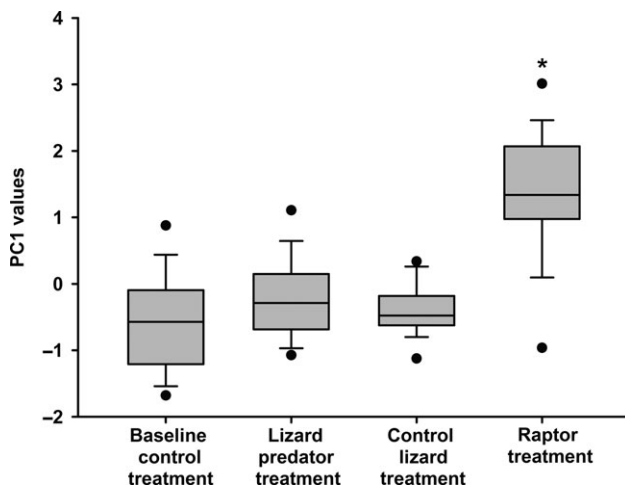


Figure 2 Box plot diagram of the effect of treatments on the PC1 values (negative loadings from exploratory behaviours and positive loadings from 'association with both offspring') of the PCA carried out to analyse the behavioural variables displayed by *Phymaturus spectabilis* mothers under the different treatments. The medians, 10%, 25%, 75% and 90% percentiles of the frequencies of occurrence are indicated. Asterisks indicate treatments that differ significantly from the other treatments ($P < 0.05$).

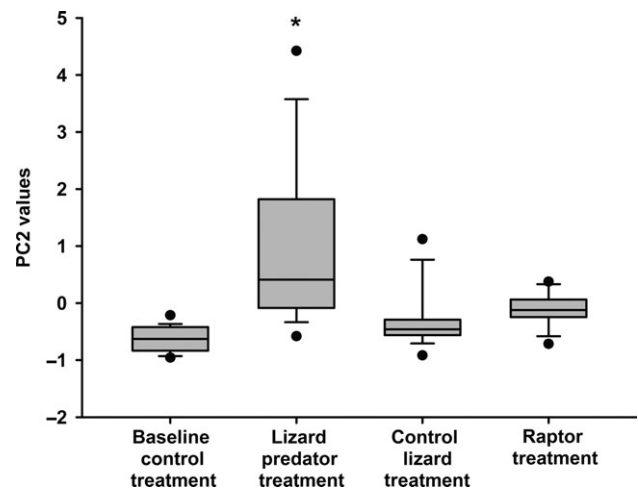


Figure 3 Box plot diagram of the effect of treatments on the PC2 values (positive loadings from antipredator behaviours) of the PCA carried out to analyse the behavioural variables displayed by *Phymaturus spectabilis* mothers under the different treatments. The medians, 10%, 25%, 75% and 90% percentiles of the frequencies of occurrence are indicated. Asterisks indicate treatments that differ significantly from the other treatments ($P < 0.05$).

in which lizards are wary and flee long distances from predators; 'crypsis', in which lizards present colour patterns that blend with their environment and they remain motionless (frozen) to avoid detection when approached; and 'known escape route', which occurs when lizards flee short distances to an apparently pre-selected refuge (Vitt & Congdon, 1978; Schwarzkopf & Shine, 1992). Considering the cryptic coloration of *P. spectabilis* from the air, this species likely would adopt the 'crypsis' strategy when faced with aerial predators, while in the presence of a terrestrial predator in the field it has been observed that they used the 'known escape route' strategy, as they select rocky habitats with many crevices that they use as refuges (Cabezas-Cartes, Kubisch & Iburgüengoytía, 2014). Our results support this idea, since mothers in the presence of the terrestrial predator presented a higher frequency of flight behaviour than in the other treatments. However, as our experimental set up did not allow them to escape or hide from predator, they also displayed active antipredator behaviours such as head bobs and tail waves which might function as dissuasive signals as we have explained above.

Evidence of parental care behaviour recorded by Halloy and her co-workers for some species of *Phymaturus* (Halloy *et al.*, 2005, 2013), and the displays observed herein, reflects the relevance of these behaviours for the general theme of enhancing offspring survivorship in the genus, and suggest the idea of a common pattern of parental care in *Phymaturus*. In particular, parental care is likely an important component of the reproductive investment of *P. spectabilis* in addition to the relatively high reproductive effort and the high relative litter mass (Cabezas-Cartes, 2016).

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Graphical Abstract

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The aim of this study is to contribute to the understanding of maternal antipredatory behaviour and social interactions in lizards by analyzing the responses of *Phymaturus spectabilis* females with their offspring when exposed to different types of predation stimuli in laboratory conditions. Two clearly different parental responses occurred: in the presence of the raptor, mothers stayed near the offspring and remained motionless longer than in the other treatments; in contrast, in the presence of the predator lizard, mothers presented higher frequencies of flights, tail-waves and head-bobs. Our results together with similar behaviours observed in congeneric species would suggest the existence of a common pattern of parental care in *Phymaturus*.