

— SHORT COMMUNICATION —

## Multi-maternal nesting behaviour and a potential adaptive signal for its evolution in the Argentinean geckonid lizard *Homonota borelli*

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Multi-maternal nesting behaviours (or communal nesting) represent a remarkable expression of prenatal parental care. In squamate reptiles (lizards and snakes) this mode of parental care has been reported in different lineages. Nevertheless, the causes behind its origin remain largely unexplored, and hence, poorly understood. Here, we study parental care in the Argentinean geckonid species *Homonota borelli*. We found that this lizard nests communally, which represents the first report of communal nesting for this species and one of the first within the genus. The facts that the number of potentially suitable places for nesting is much higher than the number of nests observed and that eggs from the same nests eclose asynchronously, suggest that the evolution of this behaviour would be mediated by the fitness advantages of oviposition in sites where eggs have previously been laid. Therefore, communal nesting in *H. borelli* would be adaptive.

**Key words:** parental care, communal nesting, adaptation, lizards, Gekkonidae, *Homonota*.

### INTRODUCTION

Selection favours the evolutionary fixation of parental care behaviours that enhance offspring fitness. Therefore, different strategies can evolve in response to different selection regimes, which has resulted in an extraordinary diversity of parental care modes widely spread across the animal kingdom (Clutton-Brock, 1991). Such diversity covers all possible combinations of parental care, including uniparental care (care by females or males exclusively) and biparental care (care by both females and males), before and after birth (Clutton-Brock, 1991). Remarkably, there are also some parental care strategies that involve groups of conspecific parents cooperatively helping in communal nesting and breeding (Brown, 1987; Clutton-Brock, 2002). This form of multi-parental care has in-

creasingly attracted the interest of evolutionary biologists, who have devoted several studies to report the occurrence of this behaviour across a wide diversity of species, and to explore their causes and evolutionary consequences for the individuals that express this trait (Doody *et al.*, 2009).

Traditionally, most research on parental care has concentrated in bird and mammal clades (Clutton-Brock, 1991, 2002; Koenig & Dickinson, 2004). In contrast, a comparatively much lower volume of literature has focused on the general phenomenon of parental care in reptiles. Several reasons are likely to explain this pattern, the most obvious one being that parental care, in its different forms, is rare among these animals. In fact, parental care is only widespread in crocodiles, being unknown in turtles and sporadic among squamates (lizards and snakes) (Somma, 1990; O'Connor & Shine, 2004). In spite of this situation, multi-maternal nesting behaviour (or communal nesting, where two or more females lay their eggs in

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the same place, but not necessarily at the same time) has been reported in lizards and snakes (Graves & Duvall, 1995; Doody *et al.*, 2009). However, only a few observational studies have been devoted to investigate the origin of this mode of parental care, which remains therefore poorly understood (Graves & Duvall, 1995; Radder & Shine, 2007; Doody *et al.*, 2009). Two major hypotheses have been formulated to explain the occurrence of communal nesting in reptiles, one involving cooperative benefits mediated by selection (adaptive hypothesis), and the other stochastic environmental constraints (constraint hypothesis) (James & Henderson, 2004; Radder & Shine, 2007).

The first hypothesis suggests that communal nesting behaviour evolves adaptively because developing eggs deposited in egg-clusters laid by multiple females have fitness advantages over eggs laid in single-female nests (*e.g.*, higher protection, better thermal conditions). Alternatively, the constraint hypothesis predicts that communal nesting results from limited availability of suitable places to lay the eggs that females may encounter in a given space and time, and hence, females are forced to nest communally in the few available places (*i.e.* there are more females than nesting places).

In this paper, we report for the first time multi-maternal nesting behaviour in the Argentinean geckonid *Homonota borelli*, and discuss a possible adaptive signal behind the evolution of this behaviour. The significance of these observations rely on the facts that this is one of the few known studies aimed to elucidate the potential factors involved in the establishment of communal nesting behaviour among lizards in general (Radder & Shine, 2007), and that the reproductive biology of lizards in southern South America, especially in the Argentinean-Chilean geographical region, remains poorly known. Only a few studies on the reproductive biology of *Homonota* species are known (see Cei, 1993; Abdala, 1997, for reviews), and only one case of multi-maternal nesting has been reported (*Homonota uruguayensis*, see Carreira *et al.*, 2005).

## MATERIALS AND METHODS

*Homonota borelli* is a small bodied (snout-vent length up to 42 mm) geckonid endemic to eastern-central and northern Argentina. In this subtropical area, it is found occupying nonvegetated microhabitats, such as open ground and stones (Gallardo, 1977; Cei, 1993), although it is regularly observed using both inhabited

and abandoned human constructions, being therefore considered an 'anthropophilic' lizard (Cei, 1986, 1993). The reproductive mode of this species is oviparity. Females lay only one egg each year, during the warm, dry season (between December and January approximately) (Gallardo, 1977; Cei, 1986, 1993; Abdala, 1997). In some areas of its distribution, *H. borelli* is a poorly abundant species, which makes difficult the conduction of scientific studies, and, at the same time, increases the urgency to investigate fundamental aspects of its biology, such as parental care behaviour and the mechanisms shaping its either evolutionary or plastic expression. This and further observations might result in essential tools for developing conservation programs, and as such, are potentially of critical importance.

We carried out field observations of the nesting patterns of a population of *H. borelli* from eastern Godoy Cruz town, Mendoza Province, Argentina (32° 56' 31" S, 68° 49' 5" W), during January and February 2009. In this area, *H. borelli* inhabits abandoned human constructions made of adobe (*i.e.*, bricks made from sand, clay, water and fibrous organic materials such as sticks, straws or dung, and dried in the sun). Parts of the external layer of the walls were randomly chosen and removed by hand, leaving exposed the interior of the walls, which consists of several small cavities connected by the irregular surface of the inner structure of the adobe bricks. These cavities and connecting surface irregularities are used by *H. borelli* to dwell and lay eggs. We analyzed all *H. borelli* nests found in these walls, for which we recorded (1) the total number of eggs, (2) the number of whole eggs and empty eggshells per nest, (3) the spatial distribution of the nests in the walls surface. In addition, we carried out lab observations to investigate the variation in the age of the eggs in each nest. To achieve this, we took the nests to the lab and carried out daily observations to record egg eclosion. All hatchlings were then released in the same place where the nests were found.

## RESULTS AND DISCUSSION

Our observations revealed that females *H. borelli* lay eggs communally, as evidenced by aggregations of both whole eggs and eggshells found in the same nests. A total of four nests were found in the above described wall cavities (average elevation of nests:  $955.0 \pm 147.2$  mm; cavity height:  $86.7 \pm 42.6$  mm, width:  $25.0 \pm 2.9$  mm, depth:  $116.7 \pm 31.8$  mm), always in the wall side

TABLE 1. Summary of *Homonota borelli* nests reported in this study. Asterisks indicate multi-maternal nests, where the number of eggs equals the number of females involved

Month	Number of eggshells	Number of whole eggs	Total number of eggs found
January	5	2	7*
January	2	6	8*
January	0	1	1
February	2	0	2*

facing sun (no nests were found in the wall side unexposed to sunshine), despite the fact that the species is observed foraging on both exposed and nonexposed sides. In three of these nests at least two eggs were found (*i.e.*, at least two females involved), while only one egg was observed in the remaining nest (*i.e.*, only one female involved) (Table 1). It is worth noting that although only four nests were observed, the effective size of our sample is substantially larger as we recorded 18 eggs in total, which means that our study encompasses 18 nesting females. Therefore, the total of four nests studied implies replicated cases of communal interactions among several pregnant females (17 in total, after excluding the only non-communal nest found; see Table 1). These findings represent one of the first reports of multi-maternal nesting in a species of the genus *Homonota*, and the first in a gecko of the Argentinean-Chilean biogeographical region of South America, where the geckonid, and in general lizard fauna is unique (Pincheira-Donoso *et al.*, 2008).

A fundamental question is whether the multi-maternal nesting behaviour in *H. borelli* is an evolutionary adaptation (adaptive hypothesis) or a circumstantial consequence of the limited availability of spatial conditions for nesting (constraint hypothesis) (*e.g.*, Radder & Shine, 2007). Our field observations suggest that this behaviour would be an adaptation resulting from the fitness advantages of nesting communally. This conclusion of a potential adaptive signal derives from the fact that the adobe walls where the nests were found showed abundant empty cavities with the same characteristics of the cavities used for nesting. Indeed, as detailed above, while adults *H. borelli* actively forage on both sides of the walls, nests were only observed on the side of the walls directly exposed to sunshine (*i.e.*, females appear to select similar thermal environments for their eggs), where the availability of empty cavities was much higher than the number of nests recorded. This situation might reasonably be interpreted as an 'adaptive preference' of females *H. borelli* to lay eggs in cavities where other

females have previously laid their eggs. This claim is supported by the observation of both whole eggs and empty eggshells in the nests with the highest total number of eggs (Table 1), which confirms the asynchronous egg eclosion that might be expected from communal nesting where females lay eggs at different times. Our lab observations strengthen this conclusion, as we found that eclosions of eggs from the same nest actually occurred at different times. All these findings taken together suggest that multi-maternal nesting behaviour in *H. borelli* is likely to be adaptive, as shown in a few other lizards (Radder & Shine, 2007; see Graves & Duvall, 1995; Doody *et al.*, 2009, for reviews).

Potential fitness advantages of communal nesting have been speculated to result from a number of benefits offered by sites with existing eggs, such as easier nest excavation for mothers (which is not the case for *H. borelli*), lower mortality risk by predation, better incubation conditions based on nest choice by more experienced mothers, and better social conditions for offspring development (Graves & Duvall, 1995; Marco *et al.*, 2004; Branchi & Alleva, 2006; Radder & Shine, 2007; Doody *et al.*, 2009). Radder & Shine (2007) suggested that oviposition where eggs have previously been laid may enhance maternal fitness by affecting hatchling phenotype (*e.g.*, body size), as a possible consequence of effects of communal nesting on water uptake by eggs. The most likely selective factor behind the evolution of communal nesting in *H. borelli* requires, however, further research. How females decide where to lay the first egg of a (future) communal nesting in a given available site remains an open question that deserves further empirical investigation.

Our observations suggest that *H. borelli* might be an appealing model species to explore the evolution of parental care, as well as other associated problems (*e.g.*, the reproductive behaviour of males and females in relation with parental care; Williams, 1966; Clutton-Brock, 1991). However, as in many other species, biological information on this gecko is still seriously

limited, and programmes of conservation of its natural populations are required. In fact, the importance of *H. borelli* does not only rely on its potential as a model system, but also, on its ecological impact as a natural predator of the vinchuca (*Triatoma infestans*: Reduviidae), the most important vector of Chagas Disease. Our observations coupled with previous studies (Williams & Ghilini, 1979), reveal that *H. borelli* may play an important role in controlling population size of this insect.

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