



# Do Brooding Pythons Recognize their Clutches? Investigating External Cues for Offspring Recognition in the Children's Python, *Antaresia childreni*

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## Abstract

Parental care provides substantial benefits to offspring but exacts a high cost to parents, necessitating the evolution of offspring recognition systems when the risk of misdirected care is high. In species that nest, parents can use cues associated with the offspring (direct offspring recognition) or the nest (indirect offspring recognition) to reduce the risk of misdirected care. Pythons have complex parental care, but a low risk of misdirected care. Thus, we hypothesized that female Children's pythons (*Antaresia childreni*) use indirect cues to induce and maintain brooding behavior. To test this, we used a series of five clutch manipulations to test the importance of various external brooding cues. Contrary to our hypothesis, we found that female *A. childreni* are heavily internally motivated to brood, needing only minimal external cues to induce and maintain egg-brooding behavior. Females were no more likely to brood their own clutch in the original nest as they were to brood a clutch from a conspecific, a pseudoclutch made from only the shells of a conspecific, or their clutch in a novel nest. The only scenario where brooding was reduced, but even then not eliminated, was when the natural clutch was replaced with similarly sized stones. These results suggest that egg recognition in pythons is similar to that of solitary-nesting birds, which have similar nesting dynamics.

## Introduction

Parental care provides substantial benefits to offspring in the forms of energy provisioning, thermal regulation, water balance, and protection (Clutton-Brock 1991; Deeming 2004), and such offspring benefits have led to parental care being widespread across taxa. However, costs to the parent are substantial, making it critical for the parent to identify its offspring (Waldman 1988). This is particularly important, because parents often leave their offspring to return at a later time (e.g., foraging behavior). When offspring are nest bound, parents can use cues from either the offspring (direct offspring recognition) or the nest environment (indirect offspring recognition) to correctly allocate care.

The evolution of offspring recognition is driven by two nesting scenarios (Huang & Pike 2011). Direct offspring recognition is expected to occur in species with a high risk of misdirected care, such as exists in colonial nesting species (Medvin & Beecher 1986; Pitcher et al. 2012) or species with high rates of nest parasitism (Stokke et al. 2007). When such selection pressures are weak or absent, indirect offspring recognition is expected to predominate, as it does in solitary-nesting birds (Waldman 1988), fish (Perrone & Zaret 1979), and amphibians (Stynoski 2009). Each type of offspring recognition may entail a different set of proximate mechanisms (i.e., external and internal cues) regulating the behavior.

External cues that induce and maintain parental care may be visual (Underwood & Sealy 2006),

auditory (Illmann et al. 2002), chemical (Reebs & Colgan 1992), or a combination of these (Wolski et al. 1980). In direct recognition systems, these cues may be produced by the offspring or applied to the offspring by the parent (Gubernick 1980), but parents utilizing indirect recognition systems often rely on features of the nest environment (Waldman 1987). However, regardless of the source, external cues are likely supplemental to strong internal stimuli to provide parental care (Rothstein 1975; Peterson 2000).

While post-paritive (i.e., after oviposition or birth) parental care is atypical of reptiles, it has been documented in numerous species (reviewed in Greene et al. 2002; Somma 2003; Stahlschmidt & DeNardo 2010). Where it does occur, little is known about offspring recognition. The few existing studies on the subject, focusing on scincid lizards, suggest that indirect offspring recognition is important in reptile parental care (Vitt & Cooper 1989; Huang & Pike 2011). Pythons provide the most complex form of post-paritive parental care described among reptiles in that females tightly coil around their clutch typically until hatching. During this time, pythons use behavioral adjustments to influence embryonic temperature, hydration, and respiratory gas exchange (Aubret et al. 2005; Stahlschmidt & DeNardo 2008; Stahlschmidt et al. 2008, 2011).

While a considerable amount of information has been gathered regarding these physiological trade-offs, little is known about the proximate mechanisms that regulate these parental behaviors, including recognition of the offspring. Brooding pythons may periodically leave their clutch temporarily to thermoregulate (Shine 2004; Stahlschmidt, pers. comm.), thus necessitating some degree of clutch recognition. However, because python nests are solitary and the offspring are immobile during this time, there is minimal risk of a female python misdirecting her care. We hypothesized that female pythons possess a strong drive to coil on their clutches and that clutch recognition would be predominantly indirect. That is, as with many solitary-nesting birds, female pythons would recognize their nesting site, but have limited ability to distinguish specifics of their clutch.

We explored the extent to which post-oviposition Children's pythons (*Antaresia childreni*) recognize their clutches by performing a series of experimental clutch-nest substitutions. We predicted that an altered nest site would reduce or eliminate brooding behavior, but that a female would not be able to differentiate her clutch from other similar stimuli (e.g., another female's clutch).

## Methods

### Husbandry

We used reproductive female Children's pythons (*A. childreni*,  $n = 7$ ) from a captive colony at Arizona State University (ASU). *Antaresia childreni* are medium-bodied (<1 m; 500 g) snakes native to rocky areas in the wet-dry tropics of northern Australia (Wilson & Swan 2008). Females brood their clutches (egg count =  $8 \pm 1$  eggs, clutch mass =  $83.3 \pm 8.4$  g, Stahlschmidt et al. 2011) throughout incubation (approximately 50 d). While brooding, females adjust their posture frequently and exhibit exploratory behavior (Stahlschmidt et al. 2008), and it is thought that they periodically bask as other pythons have been documented to do in natural environments (Slip & Shine 1988). Toward the end of gravidity (approximately the last 10 d), females were maintained in 1.9 l cylindrical brooding containers supplied with hydrated air within an environmental chamber maintained at  $30.5 \pm 0.3^\circ\text{C}$  (approximating the species' preferred incubation temperature, Lourdaïs et al. 2007) and a 14:10 L:D photoperiod. Females oviposited within the brooding container.

### Experimental Substitutions

We initiated experimental trials with female *A. childreni* within 2 d of oviposition. During the trials, females were maintained in a temperature controlled ( $31.5 \pm 1^\circ\text{C}$ ) chamber with the lights off. Each female was put through a series of five trials in random order, with one control trial and four trials in which one variable in the nest-clutch environment was substituted. To make a substitution, the female was temporarily removed from her nesting container and placed in a holding container while the manipulation was being made. Each substitution was completed within 2 min of opening the brooding female's nesting container. Trials lasted 8 h and were conducted in a temperature controlled chamber ( $31.5 \pm 1^\circ\text{C}$ ) with the lights off. During the trial, the female's behavior was recorded using infrared cameras and time lapse videography (Ganz CTR-030NC-2 Infrared Camera; CBC Corp., Torrance, CA, USA; SSC-960 VHS VCR; Samsung, Seoul, Korea). After each trial, the female was placed with her clutch in her original nesting container, and she was allowed to brood undisturbed for at least 24 h between successive trials. Behavior was categorized as either brooding (coiled around the clutch with little to no movement, Stahlschmidt et al. 2008) or exploratory (greater than one-third of the female's body

moving). For each trial, we recorded the time until the female began brooding and the total time spent brooding. Each trial is described below.

#### *Replacement of the clutch with a conspecific clutch*

The clutch of the female in the trial was replaced with a clutch from a non-study conspecific female that had laid within 5 d of the female in the trial. The conspecific clutch was removed from its female immediately prior to the substitution and placed within the trial female's nest container in approximately the same position as the original clutch. While we made efforts to approximate the surrogate clutch size to that of the trial female's clutch, clutch size was often not the same between the two clutches, because the eggs within an *A. childreni* clutch adhere to each other and prevented us from removing or adding eggs to the surrogate clutch. All females were able to completely coil around conspecific clutches despite differences in clutch size ( $2.1 \pm 0.6$  eggs; maximum difference = 5 eggs) and mass ( $33.4 \pm 9.9$  g; maximum difference = 63 g).

#### *Replacement of the clutch with an odor-cleansed pseudoclutch*

A pseudoclutch was prepared from a clutch of a female not included in these trials. A small opening ( $\sim 1$  cm<sup>2</sup>) was made in each egg, and the contents were drained without altering the shape of the clutch. Snakes have been shown to produce water insoluble lipids that mediate their interactions with each other and their environment (Mason 1993). To remove these, the empty shells were washed twice in distilled water (dH<sub>2</sub>O) for 5 min, followed by a 5 min hexane wash (Mallinckrodt Baker Inc., Paris, KY, USA), and then another dH<sub>2</sub>O wash for 3 min. Sterilized forceps were then used to fill each wet eggshell with thin cotton strands (Safeway 100% pure Jumbo Cotton Balls; Safeway Inc., Pleasanton, CA, USA) that had been soaked in a 70% mixture of Plaster of Paris (DAP Inc., Baltimore, MD, USA), and the entire clutch was dried at 58°C for 3 h (Isotemp Oven Model 203; Fisher Scientific, Pittsburgh, PA, USA). For the trials, the female's clutch was replaced with the pseudoclutch as described for the conspecific clutch replacement. The same pseudoclutch was used for all females, but, between uses, the pseudoclutch was rinsed for 30 s in hexane, followed by 30 s in dH<sub>2</sub>O, and then dried.

#### *Replacement of the nest environment*

A new nesting container of the same size and shape as the female's original container was prepared by wash-

ing it with distilled water for 5 min, then hexane for 5 min, and then distilled water again for 5 min before allowing it to air dry. A new lid was treated in the same manner. For the trials, a female was separated from her own clutch, which she had been brooding in her original laying container. The clutch was placed at the center of the new container, and the female was placed near the side of the container. Thus, this manipulation was intended to remove any chemical cues in the nesting environment.

#### *Replacement of the clutch with a stone clutch*

We used an artificial stone clutch to provide an object similar in shape to a clutch but without any chemical cues inherent to actual eggs. The stone clutch approximated the general size and shape of an average clutch and was prepared by selecting six smooth stones that had dimensions similar to those of *A. childreni* eggs. To remove any water soluble and lipid soluble chemicals from the surface of the stones, they were washed for 5 min in dH<sub>2</sub>O, followed by a 5 min hexane wash, and another 5 min wash in dH<sub>2</sub>O. The stones were then cemented into a clutch formation using a 70% mixture of Plaster of Paris. For the trials, the natural clutch was replaced with the stone clutch as described for the conspecific clutch replacement. For consistency, the same stone clutch was used for all females, but, between uses, the stone clutch was rinsed for 30 s in hexane, followed by 30 s in dH<sub>2</sub>O, and then dried.

#### *Control manipulation*

As a positive control, the brooding female underwent manipulations similar to those described for the clutch replacement trials, but, in this case, the female's clutch was simply handled and returned to the nesting container, and then the female was returned to the nesting container.

#### **Statistical Analysis**

Statistical analyses on behavioral data were performed using GraphPad Prism vers. 4 (GraphPad Software Inc., San Diego, CA, USA). We examined the effect of the manipulations on the amount of time it took females to achieve a tight coil by performing a repeated measures analyses of variance (rmANOVA). We repeated this analysis for the percent of time females spent tightly coiled during a trial; however, percent data were arcsine transformed. For both analyses, the level of statistical significance was set at

$\alpha < 0.05$ . Each rmANOVA provided three p-values – one for the within-subjects effect, one for the between-subjects effect, and one for the interaction between the two. As our study design had all subjects being treated similarly (i.e., each snake was exposed to all five manipulations), we expected and the results demonstrated that there were no between-subjects effects or any significant interactions between the within-subjects effect and the between-subjects effect. Therefore, in accordance with the study design, we only present the p-values for the within-subjects effect (i.e., the effect that the various manipulations had on the subjects). *Post hoc* analyses to determine differences among manipulations were performed using Tukey's Multiple Comparison Test. Data are presented as  $\bar{x} \pm \text{SE}$ .

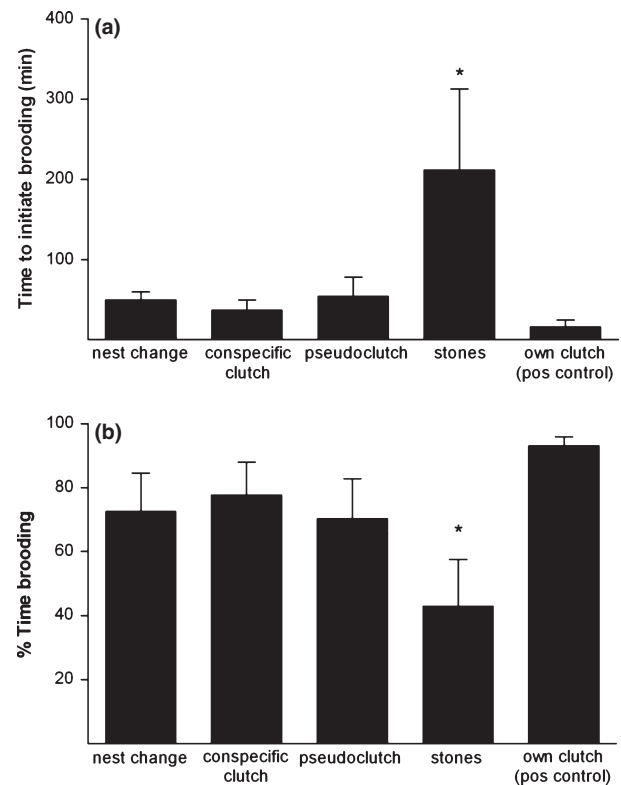
## Results

All females brooded to some extent in all trials. However, there was a significant effect of manipulation type on the time to initiate brooding ( $F_{4,24} = 1.64$ ,  $p = 0.035$ ; Fig. 1a). *Post hoc* analysis revealed that the time to initiate brooding was longer in the stone clutch ( $34.3 \pm 18.5$  min) compared with all other manipulations. There was no significant difference in time to initiate brooding for the positive control manipulation ( $1.7 \pm 0.5$  min), the nest replacement manipulation ( $9.2 \pm 2.5$  min), the conspecific clutch manipulation ( $6.2 \pm 2.3$  min), and the pseudoclutch manipulation ( $8.6 \pm 4.4$  min).

Similarly, there was also a significant effect of manipulation type on the percent of time spent brooding ( $43 \pm 16\%$ ;  $F_{4,24} = 4.34$ ,  $p = 0.009$ ; Fig. 1b), with *post hoc* analyses revealing that time spent brooding was significantly less for the stone clutch ( $43 \pm 16\%$ ) than it was for all other manipulations. There was no significant difference in time spent brooding for the positive control ( $93 \pm 3\%$ ), nest replacement ( $73 \pm 13\%$ ), conspecific clutch ( $78 \pm 11\%$ ), and pseudoclutch ( $70 \pm 14\%$ ) manipulations.

## Discussion

Female Children's pythons demonstrated a very limited ability to distinguish their clutch from other clutches. In fact, only the replacement of the female's clutch with similarly shaped stones significantly reduced, but still did not eliminate, brooding efforts (Fig. 1). Females also showed no reduction in brooding effort in a new nest environment. These results suggest that external cues for clutch recognition are of limited importance in Children's python brooding



**Fig. 1:** Female Children's pythons (*Antaresia childreni*,  $n = 7$ ) (a) took longer to achieve an initial coil ( $F_{4,24} = 1.64$ ,  $p = 0.035$ ) and (b) spent significantly less time brooding ( $F_{4,24} = 4.34$ ,  $p = 0.009$ ) the stone clutch, but there was no significant difference among any of the other nest-clutch substitution. Asterisks indicate statistical differences using rmANOVA at a significance level of  $p = 0.05$ . Values are presented as  $\bar{x} \pm \text{SE}$ .

behavior. Thus, it is likely that strong internal cues (presumably hormonal) provide a resilient drive to brood and only minor external cues are needed to initiate and maintain brooding behavior, at least for the short duration used in this study.

During early reproduction, female garter snakes (*Thamnophis sirtalis*) produce skin secretions that attract males, stimulate male sexual behavior, and enable males to trail them (Mason et al. 1990; LeMaster & Mason 2001). It is possible that skin secretions continue to be produced post-parturition to aid in maintenance of brooding or returning to brood a clutch. However, the importance of chemical cues in brooding is questionable because females brooded novel artificial clutches that had been washed in water and hexane to remove chemical cues. The lack of a reduction in brooding after changing the nesting container suggests that the nest does not provide an indirect cue. While the small size of the nesting chamber forced females to be in close proximity to the

'clutch' at all times, brooding posture can be easily differentiated from a resting posture adjacent to or on top of the clutch. Brooding entails the female coiling her body in a stack of concentric rings around the eggs (Stahlschmidt et al. 2008). Post-reproductive females, non-reproductive females, and males never assume this posture regardless of the tightness of their confinement.

As our replacement nest containers were identical in size and shape to the original nest containers, our results cannot eliminate the possibility that some spatial aspect of the nest environment acts as a brooding cue. It is possible that females use some form of spatial orientation to familiarize themselves with their original nest environment. Such a spatial cue may be important for females navigating back to a dark subterranean nest after basking. Alternately, brooding may result from multiple cues such that the presence of her clutch was sufficient to stimulate brooding despite the loss of an indirect cue from her nest environment. It would have been informative to utilize an additional manipulation where females were presented with a conspecific clutch in a novel nest container, as such a manipulation would replace both direct and indirect cues from the female's brooding environment.

Our study also cannot eliminate the possibility that the Plaster of Paris used in the pseudoclutch and stone clutch manipulations might have acted as an attractant or repellant to the females. For example, calcium may provide females with a brooding cue, because it is present in squamate eggshells in the form of calcite (Packard & DeMarco 1991) and in the Plaster of Paris as calcium sulfate. However, there is no evidence of calcium as an attractant, especially because it can be prevalent in the abiotic environment. Also, the results from our manipulations that used Plaster of Paris were distinct, as the pseudoclutch did not alter brooding while the stone clutch extended the time to initiate brooding and reduced the percent time spent brooding.

The type of parent-offspring recognition a species uses suggests different evolutionary pathways (Huang & Pike 2011). Indirect offspring recognition in a species may imply that parental care was driven by nest-site defense. For example, python parental care could have initially consisted of simply lying in close proximity to the clutch to deter predation. In this scenario, females would have originally cued on features within the nest environment and maintained this cue as the behavior became more complex and associated with offspring development. Our results are interesting as they suggest that at some point female *A. child-*

*reni* may have transferred the brooding cue from the nest environment directly to the clutch, perhaps as their parental care became more associated with physiological benefits (e.g., hydric). Additionally, with this increase in parental care complexity, females developed strong internal cues to motivate them to brood with only limited external stimuli.

In summary, our results suggest that offspring recognition in pythons is similar to that of solitary-nesting birds, at least during the egg-brooding phase. In both cases, females care for immobile offspring that are isolated from other conspecific offspring. Additionally, in both cases albeit more so in birds, the female periodically leaves her brood. Given these similar nesting dynamics, it is not surprising that both taxa show strong drives to brood with only limited ability to specifically recognize their eggs. However, the inability to recognize one's own eggs can put the female at risk of nest parasitism, where another species might deposit eggs into a nest. Nest parasitism has been well-documented in birds (Payne 1977), but has not been documented in snakes and is unlikely under natural conditions because of the fact that snakes oviposit their entire clutch at one time. However, female pythons readily accept eggs that are experimentally added to alter clutch size (Aubret et al. 2003). Given the lack of strong external cues in regulating python egg brooding, future studies should investigate internal cues that might drive brooding behavior in pythons.

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