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Experimentally reducing clutch size reveals a fixed upper limit to egg size in snakes, evidence from the king ratsnake, *Elaphe carinata*

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Abstract

Snakes are free of the pelvic girdle's constraint on maximum offspring size, and therefore present an opportunity to investigate the upper limit to offspring size without the limit imposed by the pelvic girdle dimension. We used the king ratsnake (*Elaphe carinata*) as a model animal to examine whether follicle ablation may result in enlargement of egg size in snakes and, if so, whether there is a fixed upper limit to egg size. Females with small sized yolking follicles were assigned to three manipulated, one sham-manipulated and one control treatments in mid-May, and two, four or six yolking follicles in the manipulated females were then ablated. Females undergoing follicle ablation produced fewer, but larger as well as more elongated, eggs than control females primarily by increasing egg length. This finding suggests that follicle ablation may result in enlargement of egg size in *E. carinata*. Mean values for egg width remained almost unchanged across the five treatments, suggesting that egg width is more likely to be shaped by the morphological feature of the oviduct. Clutch mass dropped dramatically in four- and six-follicle ablated females. The function describing the relationship between size and number of eggs reveals that egg size increases with decreasing clutch size at an ever-decreasing rate, with the tangent slope of the function for the six-follicle ablation treatment being -0.04. According to the function describing instantaneous variation in tangent slope, the maximum value of tangent slope should converge towards zero. This result provides evidence that there is a fixed upper limit to egg size in *E. carinata*.

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1. Introduction

Offspring size is assumed to be fitness related for many organisms, because larger offspring potentially have better performances and hence greater chances to survive (Ferguson and Fox, 1984; McGinley et al., 1987; Sargent et al., 1987; Sinervo and Adolph, 1989; Sinervo, 1990; Reznick, 1991; Einum and Fleming, 2000; Roff, 2002). This assumption implies that a female should, whenever possible, produce large offspring to increase offspring's survival probability which, in turn, enhances her reproductive success. However, as total reproductive resources available to any female are finite, she cannot increase the size of individual offspring without concomitant reduction in the number of offspring produced (Sinervo and Licht, 1991a,b; Bernardo, 1996; Downhower and Charnov, 1998; Einum and Fleming, 1999, 2000; Agrawal et al., 2001). Thus, a female's decision to produce few large or many small offspring reflects a strategy adopted by her to maximize the number of surviving young.

The optimal offspring size theory predicts that offspring size should be optimized through natural selection and offspring number is a consequence of the partitioning of total maternal investment into optimally sized offspring (Smith and Fretwell, 1974). Under this prediction, offspring size should be independent of the amount of resources a female allocates to a particular reproductive episode. However, contrary to this prediction, it has increasingly been reported that offspring size can vary as a function of total reproductive investment or maternal size in many organisms (Congdon and Gibbons, 1987; Reznick and Bryga, 1987; Sargent et al., 1987; Winkler and Wallin, 1987;

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Reznick et al., 1990; Caley et al., 2001). Studies on lizards provide further evidence that offspring size can vary as a response to variation in offspring number induced by hormonal manipulation or follicle ablation (Sinervo and Licht, 1991a,b; Sinervo and DeNardo, 1996; Sinervo and Doughty, 1996; Sinervo, 1998; Olsson et al., 2002). For example, females undergoing follicle ablation (and thus, reduced offspring number) produce larger offspring in Uta stansburiana (Sinervo and Licht, 1991b) and Lacerta vivipara (Olsson et al., 2002), because yolk, normally allocated to a larger clutch, is subsequently apportioned to the fewer, remaining volking follicles. Experimental manipulation of offspring number provides a powerful method which one may use to examine whether a female can adjust offspring size according to faculative fluctuations in reproductive resources available to her and whether there is a fixed upper limit to offspring size for a given species.

Here, we describe a study applying the "follicle ablation" technique to snakes to examine whether follicle ablation may result in enlargement of egg size in this reptilian taxon and, if so, whether there is a fixed upper limit to egg size. Unlike lizards and turtles, snakes are free of the pelvic girdle's constraint on maximum offspring size (Congdon and Gibbons, 1987; Sinervo and Licht, 1991b), and therefore present an opportunity to investigate the upper limit to offspring size without the limit imposed by the pelvic girdle dimension. We used the king ratsnake (Elaphe carinata) as a model animal for two reasons. First, E. carinata is among species where egg size (and thus, hatchling size; Ji et al., 1997; Ji and Du, 2001) varies considerably among females differing in body size and clutch size (Ji et al., 2000). Second, the snake can be easily maintained under laboratory conditions, and is therefore ideally suited to the investigation examining egg size-number strategies.

2. Materials and methods

2.1. Study species

Elaphe cariana is a large-sized [to 170 cm SVL (snout-vent length)] colubrid snake that can be found in a variety of habitats in the hilly countryside in southeastern China including Taiwan, northward to the provinces of Henan, Shaanxi and Gansu; it is also found in northern Vietnam and Japan (Ryukyu Island, including the Senkaku Group) (Huang, 1998). In Zhoushan where we collected snakes, females larger than 108 cm SVL can lay a single clutch of 5-17 pliable-shelled eggs per breeding season stretching from July to August (Ji et al., 2000). Eggs can be incubated successfully at temperatures ranging from 24 °C to 32 °C, with the mean incubation length ranging from 74.0 days at 24 °C to 42.5 days at 32 °C (Ji and Du, 2001).

2.2. Methods

Seventy females (111–149 cm SVL) and ten males (142– 167 cm SVL) were collected in early May 2003 from an island population in Dinghai ($30^{\circ} 02'$ N, $122^{\circ} 10'$ E), Zhoushan Islands (eastern China), and transported to our laboratory in Hangzhou, where females were marked via unique combinations of clipped ventral scales for future identification. In mid-May, females with small sized yolking follicles (c. 15–20 mm length) were equally assigned to five (three manipulated, one sham-manipulated and one control) groups (treatments). Two, four or six yolking follicles in the manipulated females were ablated by removing ~ 0.5 mL yolk from each ablated follicle with sterile syringes. Females in the sham-manipulated group underwent the same protocol without any yolk extraction. Females of different treatments were all maintained in a 24×14×2.5 m enclosure in the backyard of our laboratory. Food (commercially sold eggs of *Coturnix coturnix* and *Gallus gallus domesticus*) was provided ad libitum.



Fig. 1. Adjusted means (and SE) for clutch size, egg mass and clutch mass of females undergoing different treatments, with female SVL being set at 130 cm. Adjusted means with different lettered superscripts differ significantly (Tukey's post hoc test, α =0.05). C: control (*N*=23); 2: two-follicle ablation treatment (*N*=11); 4: four-follicle ablation treatment (*N*=10); and 6: six-follicle ablation treatment (*N*=11).

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