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Maternal Investment in *Physa acuta*

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Effects of maternal investment on offspring viability in *Physa acuta*

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Introduction

In many animal species there is a critical tradeoff between maternal investment and offspring viability. In animals such as birds that lay eggs serially to produce offspring that are raised simultaneously, there has been evidence of hatching asynchrony, where the first laid offspring is the largest and therefore likely to be the strongest at birth, which each subsequent sibling receiving fewer maternal resources and a corresponding decrease in viability[1]. In clutch laying animals such as certain reptiles and amphibians there has been a clearly defined relationship between offspring size and viability[2]. Using size as an indicator of maternal investment and potential viability, the trade-off observed between clutch size and egg size has been defined as a relationship between the number of offspring and their viability.

In an attempt to examine if a similar relationship exists in mollusks, we examined individuals of the species *Physa acuta,* a freshwater snail (Mollusca: Gastropoda) [3]. These snails, which are common across much of North America and Europe, are hermaphroditic and capable of both self and cross fertilization[3]. They lay 5-50 eggs at a time, and can continuously lay egg clutches every 12-24 hours. Each egg is contained within a separate capsule, all of which are suspended in a gelatinous masses. Development is direct and a juvenile snail will emerge from the egg capsule (Figure 1).

Experiments have shown that larger hatchlings had a significantly greater chance of suvivorship over a 9 week period[4]. Therefore, using juvenile size as a predictor for future survivorship we related differences in egg capsule size, and therefore amount of intracapsular fluid, to juvenile size in *Physa acuta.* Furthermore we sought to experimentally test this relationship by artificially manipulating the volume of capsular fluid and observing any effect on juvenile size.

Materials and Methods

Culture Conditions

Individuals of *Physa acuta* were collected on 6.17.2010 from Lake Evergreen in McLean County, IL. The largest four individuals were segregated in to individual containers where they were kept at 27 °C in a temperature controlled chamber with a 12L:12D light cycle. Twice daily each container was checked for egg masses. Once a clutch was found the approximate time of laying was estimated individual egg capsules were then separated from the gelatinous mass encasing, and the shortest (Figure 2; d_1) and longest (Figure 2, d_2) diameter of each egg capsule was measured using an ocular micrometer at the total magnification of 100x Eggs were monitored regularly until all of the individuals hatched or died. Hatched individuals were frozen (-10°C). The long and short axes of the juvenile shells were measured at 100x magnification. This process was repeated until 4-5 clutches had been obtained from four separate adult individuals.

Modification of Intracapsular Material

Egg capsules produced by two different adults were collected and measured as described above. Using a glass micropipette, each capsule was pierced and a volume of the intracapsular material was removed. The difference in the capsular volumes between the pre- and post-removal were used to estimate the volume of material removed. After material removal, the capsules were monitored daily until hatching or death. After hatching, each individual was measured as described above.

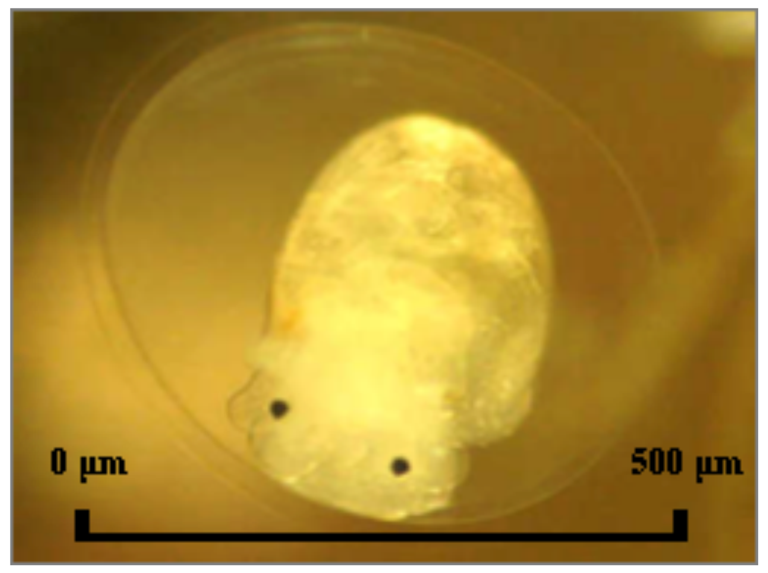

Figure 1. Egg capsule and pre-emergent juvenile near hatching

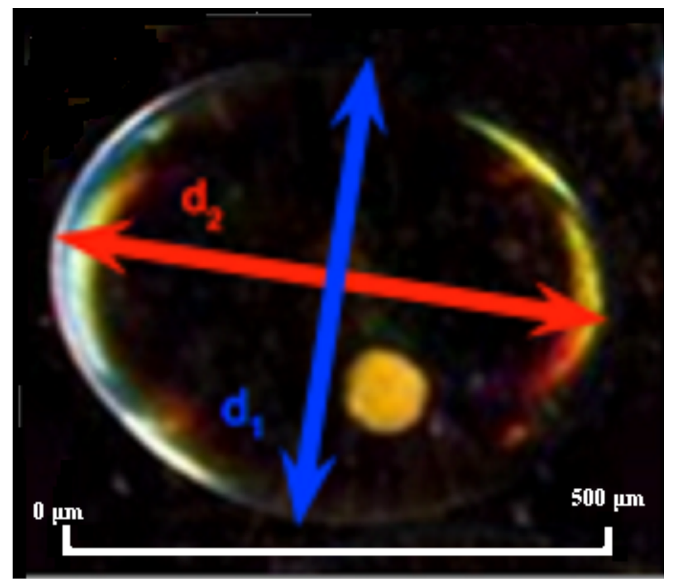

Figure 2. Egg capsule, marked for diameter measurements

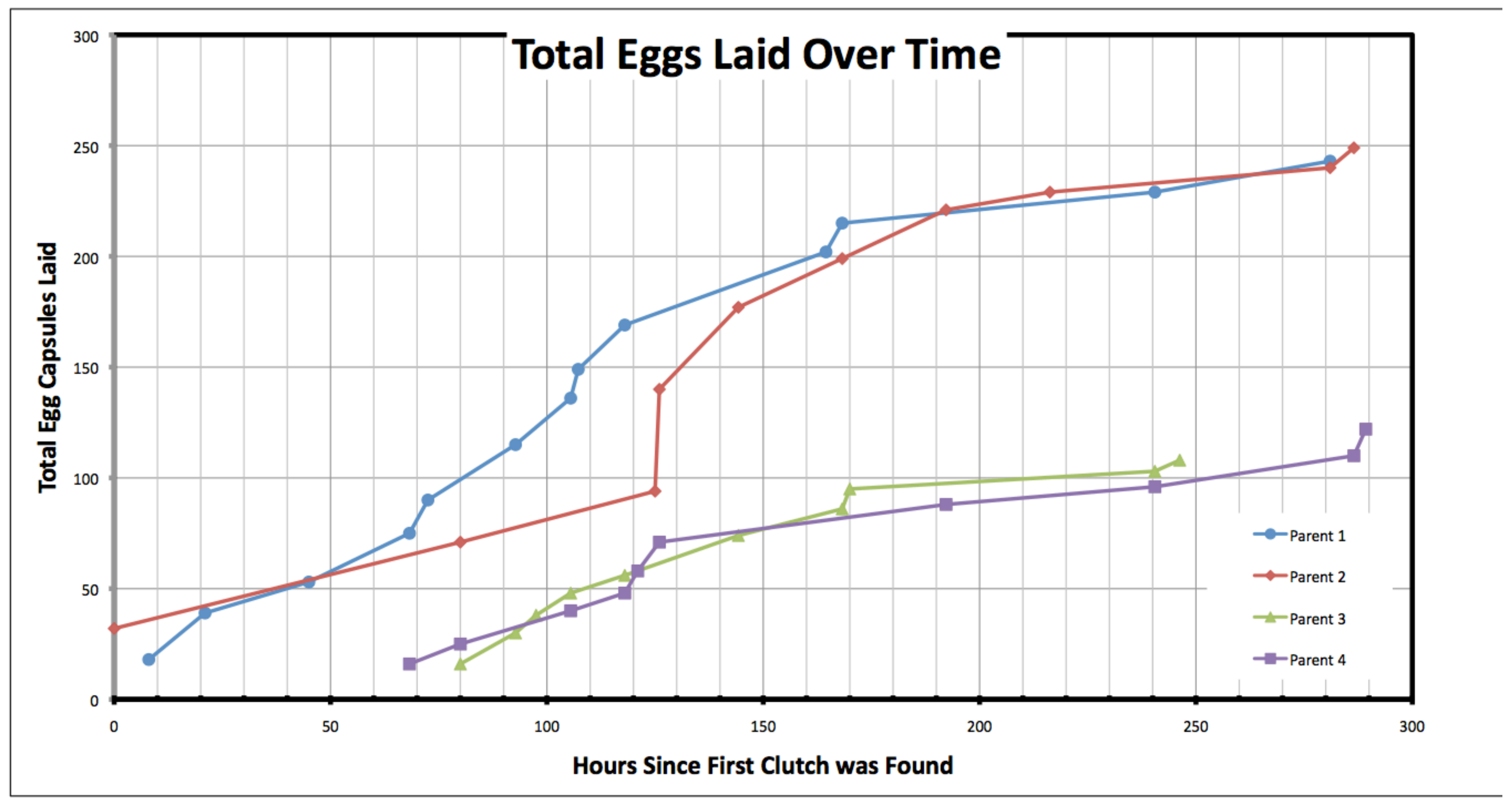

Figure 3. Total egg capsules produced during a 12 day period as a function of time

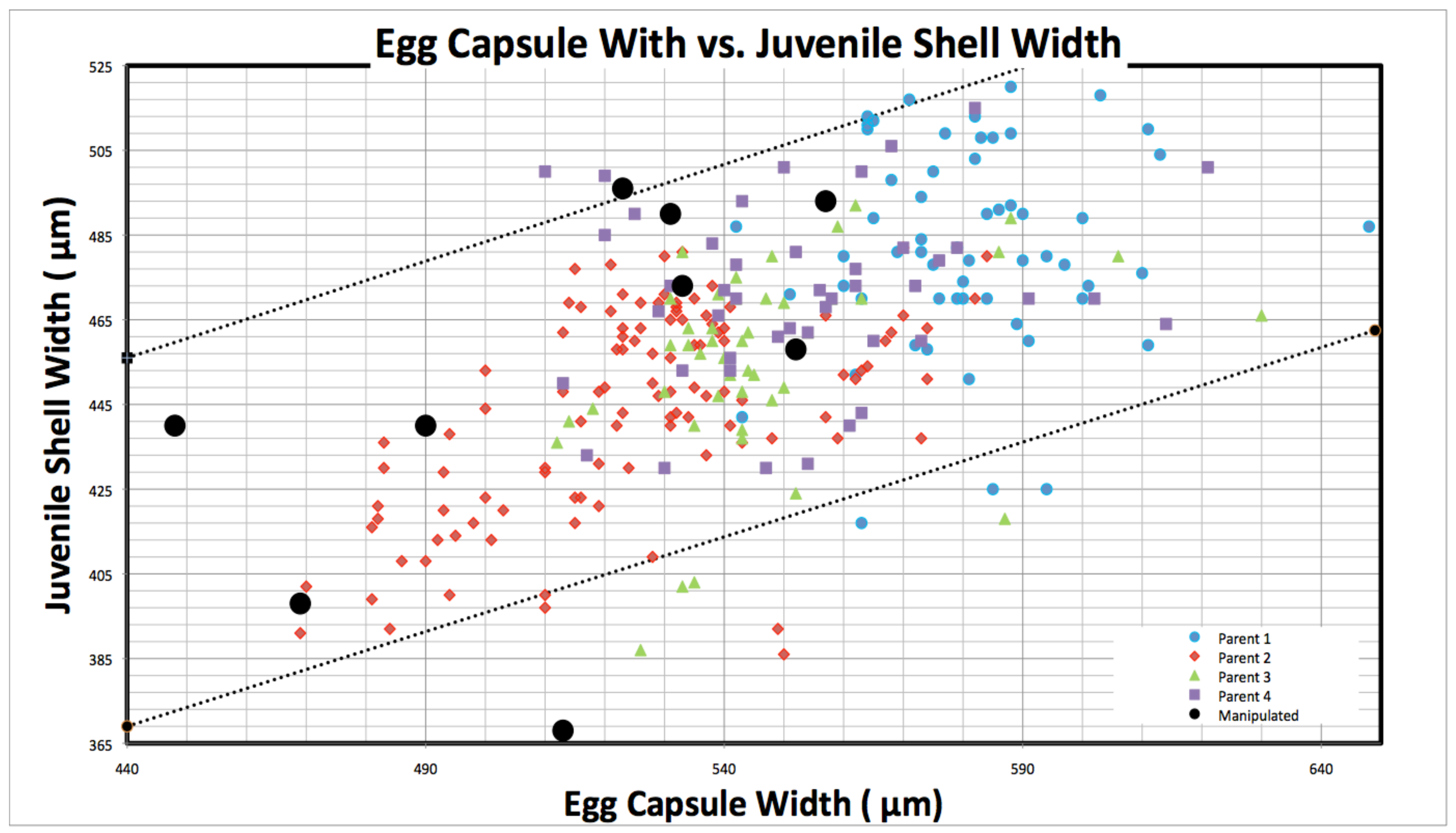

Figure 4. Egg capsule width vs. Juvenile shell length with upper and lower 95% confidence bounds. In the case of manipulated individuals the capsule width after manipulation is used.

Juvenile Identifier	A	B	C	D	E	F	G	H	I	J	K	L
% Change in Capsule Volume	39	68	53	18	45	52	38	42	22	30	31	38

Table 1. Percent of capsular fluid removed from the 12 individuals that survived manipulation until hatching.

Results

Due to the small number of parents sampled statistical comparisons were not informative, however the following observations were evident from the data.

- There was no relationship between parental wet weight or size and:
  - Juvenile size upon hatching
  - Interclutch time period
  - Number of egg capsules per clutch
  - Average capsule volume
  - Total volume of egg capsules produced
- There appears to be a similarity in the laying trends of all parents over time, however a larger sample size and longer observation time are necessary to support this observation (Figure 3).
- There is no consistent relationship between clutch size and average capsule size within individuals.
- Among parents there was no difference in the length to width ratio of juvenile egg capsules ($F=1.244$, $p=0.293$) i.e. there was no difference in capsular shape.
- There was a significant difference in the average capsular lengths ($F=38.862$, $p<.01$) and capsular widths ($F=22.570$, $p<.01$) produced by the four parents.
- Among parents egg capsule width and hatchling shell length were positively correlated with one another ($r=0.558$, $p<0.01$). Egg capsule width was also positively correlated with hatchling shell length ($r=0.569$, $p<0.01$).
- Removal of up to 67.6% of capsular volume was performed without affecting juvenile viability. All twelve individuals that survived manipulation hatched (Table 1).
- Nearly all of the manipulated individuals fell within the 95% confidence bounds for predicted shell lengths and widths (Figure 4).

Discussion

It is of interest to note that the differences observed in juvenile characteristics between parents do not appear to correlate with parental size, so although each parent lays eggs of a fairly consistent size and shape, this size is not a function of parental size. Factors such as age, diet, and method of fertilization before collection could all contribute to this variance. Studying individuals born and raised under standard conditions could provide further insight.

Examination of all measured characteristics of egg capsules and juvenile shell characteristics revealed that capsule width more strongly predicted both hatchling shell length ($r^2=0.311$) and shell width ($r^2= 0.324$). At a certain size pre-emergent individuals begin moving within their capsules, reorienting their position frequently, perhaps to enhance the diffusion of gas into and out of their capsules. This movement when so close to their full hatchling size may be why size is limited by, and therefore more closely associated with the smallest diameter of their capsule rather than another measurement or the total volume.

All of the individuals that survived the removal of capsular materials survived to hatching, indicating that up to 67% of capsular fluid can be removed without affecting viability. Despite an inability to draw conclusions about any directional effect of juvenile size based on a change in capsule size, the fact that such a large volume of intracapsular fluid could be removed and still result in viability is striking. As some parents invest more than twice the nutrients required for viable birth, there may be a yet hidden benefit to this excess energy, such as increased shell thickness.

Refrences

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