

Akademisk avhandling för Filosofie Doktorsexamen
Thesis for the degree of Doctor of Philosophy

EGG SIZE EVOLUTION AND PATERNAL CARE IN PIPEFISHES

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Avhandlingen kommer att försvaras offentligt fredagen den 17 september
2010 kl 10:00, på Zoologiska Institutionen, Medicinargatan 18, Göteborg.

Opponent är Professor Ian Fleming från Memorial University,
Ocean Sciences Centre, Newfoundland, Kanada.

The oral defence of this thesis will take place at 10:00 a.m. on Friday September 17th
2010 at the Department of Zoology, Medicinargatan 18, Göteborg, Sweden.

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Braga Gonçalves, Inês 2010.

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SUMMARY

In this thesis I explore how sexual selection, sexual conflicts, coevolution with parental care and an environmental selective agent (hypoxia) affect the evolution of different egg characteristics and embryo survival and size in pipefishes (Syngnathidae).

In the broad-nosed pipefish, *Syngnathus typhle* Linnaeus, both sexes prefer to mate with large partners; large females produce more and larger eggs and large males can care for more young, and, as shown in this thesis, invest more per embryo and provide better oxygenation during brooding. However, if given time to assess their partners prior to mating, females deposit significantly more proteins into eggs when they mate with non-preferred (smaller) males. This result suggests that females are able to improve offspring fitness by compensating for small males' lower paternal care quality, thus reducing effects of differences in care between small and large males.

The spherical shape common to fish eggs minimizes the ratio between surface area and volume. As embryo respiration is assumed to be proportional to egg volume and oxygen availability to be restricted by the surface of the egg, this shape may be unfavourable for larger eggs. In *S. typhle*, both small eggs and hypoxia (low ambient oxygen levels) during brooding resulted in smaller embryos, but the negative effect of hypoxia on embryo size was similar for small and large eggs. In brooding males, within-pouch oxygen levels were found to be consistently lower than those of the surrounding environment, both in high and low ambient oxygen conditions indicating a limited paternal ability to maintain high levels of oxygenation to the embryos.

When comparing pipefish species with and without brood pouches, the species with pouches were found to suffer, on average, greater embryo mortalities during brooding. However, under hypoxia embryo survival and size were negatively affected both in species with and without brood pouches. Between species, large egg size resulted in significantly larger offspring, but had a negative effect on embryo survival, compared to species that produce small eggs.

This thesis contributes to the understanding of egg size evolution in relation to hypoxia and paternal care in syngnathids. The studies presented here suggest that the evolution of brood pouches carries costs in terms of embryo oxygenation. Furthermore, the evolution of more complex types of brooding has potentially enabled phenotypic variation to arise in the quality of male care, in turn selecting for flexible female reproductive investment with stronger selection on egg size evolution in species with brood pouches, and greater female control of egg quality.

Keywords: Egg size, embryo development, embryo survival, hypoxia, male quality, mate choice, mating constraints, oxygen, parental care, parental effects, paternal care, reproductive compensation, sex-role reversal, sexual conflict, Syngnathidae, *Syngnathus typhle*.