

Evidence for male allocation in pipefish?

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Sexual differences in the extent and type of parental care lie at the heart of sexual selection theory¹, and evolution resulting from parental conflict has produced some striking behavioural and morphological adaptations. In a study of male pregnancy in Gulf pipefish, Paczolt and Jones² showed that more eggs were transferred to the male's brood pouch and more offspring survived following mating with large females (preferred by males) than with small (less preferred) females. Although the authors conclude that the lower survival of embryos from small females is most consistent with males actively removing resources from these offspring^{2–4}, no data are presented to directly support this hypothesis (ref. 2, and Supplementary Information therein) and the data do not refute the alternative explanation that differential egg survival is caused by female effects mediated by variation in fecundity and egg size or quality. We argue that only by experimentally manipulating female attractiveness separately from the quality of eggs deposited in the brood pouch can the extent of sexual conflict in this role-reversed system be assessed.

Smaller female fishes are known to produce fewer and smaller eggs⁵ that also have “exceptionally low viability” (ref. 2 Supplementary Information: Egg quality and female-mediated effects). Thus, the exclusion of extremely small females from the experiment does not suggest that low intrinsic egg viability is an inadequate explanation (ref. 2 Supplementary Information). Moreover, the negative correlation between brood survivorship and offspring length at birth is consistent with an intrinsic female effect if only the largest eggs transferred by small females are capable of surviving until birth.

The paper concludes that interactions between the male's placenta and his brood explain the findings because an initial brooding bout with a large clutch decreases fecundity and offspring viability in a subsequent brood (ref. 2, and Supplementary Information therein). However, as the authors state, such an interaction simply indicates a trade-off between current and future reproduction (a core prediction of life history theory). Furthermore, the trade-off does not explain the overall differences in viability of the embryos of large and small females evident in both prior and current broods. Even if the costs are a result of nutrient allocation to offspring in the first brood (see refs in ref. 2) they may represent the total costs of being pregnant with a large brood rather than differential allocation to the eggs of different sized females².

The syngnathid male-pregnancy system is an intriguing one in which to examine role-reversed sexual conflict and male post-copulatory choice. However, we suggest that correlations² cannot distinguish

between the effects of male differential allocation and intrinsic female quality on offspring viability. These two hypotheses could be tested by manipulating male perception of females in the population (see, for example, ref. 6). Male pipefish would experience either large or small females. Within each experience group (AB and CD in Table 1) males would then be mated with females of either size. Both hypotheses predict that offspring viability for broods from large and small females will be higher and lower, respectively, because male pipefish are attracted to larger females⁷ and larger females have greater offspring viability^{2–5}. However, predictions exclusive to Paczolt and Jones' model (ref. 2 Supplementary Information) are first, that males experiencing large females but then mated to a small one (B in Table 1) selectively abort more offspring than expected from low female quality alone as males conserve resources for future matings with higher quality (large) females. Second, males with a reversal in these experience and mating types (C in Table 1) should invest more in their current brood compared to that expected from intrinsic female quality alone because their past experience predicts that a subsequent mate is likely to be of poor quality.

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Table 1 | Predictions of embryo survival

Experience group	Males experience, but do not mate with:	Males mate with a:	Predictions about embryo survival	
			Differential allocation	Female quality
A	Large females	Large female	+	+
B	Large females	Small female	– –	–
C	Small females	Large female	++	+
D	Small females	Small female	–	–

Table shows an experiment separating the effects of intrinsic female quality and male differential allocation on the survival of offspring in the male brood pouch. Greater- and lesser-than-average embryo survival are indicated respectively by + and –; doubled symbols indicate further increased or decreased embryo survival.

Paczolt & Jones reply

Replying to: D. T. Gwynne, K. A. Judge & C. D. Kelly *Nature* 466, doi:10.1038/nature09275 (2010)

Our recent study of pre- and post-copulatory sexual selection in the sex-role-reversed Gulf pipefish indicates that males prefer to mate with larger females compared to smaller females, that larger females transfer more eggs per copulation than smaller females, that the eggs from larger females are more likely to result in viable offspring than eggs from smaller females, and that males experience fitness trade-offs between broods¹. We suggest that the most likely explanation for this suite of results is that males exert choice before and after copulation in a way that favours larger females over smaller females during every phase of pre- and post-copulatory sexual selection. Gwynne *et al.*² have challenged the interpretation of one facet of our results by suggesting that males do not differentially allocate resources to offspring originating from different females. Rather, they suggest that our results can be explained entirely by differences among females in fecundity, egg size and egg quality².

Under the Gwynne *et al.* model, smaller females produce smaller eggs than larger females and these smaller eggs are less likely to result in viable progeny². However, Gwynne *et al.* go on to explain that this model alone is inadequate, because it does not predict a trade-off between offspring survivorship in subsequent broods, one of our key findings. Thus, they add a second layer to their model, which posits that the “total costs of being pregnant with a larger brood” are higher than those for a smaller brood², without specifying how these costs may arise. In fact, if the total cost of being pregnant reduces future reproductive opportunities, then this total cost is clearly a form of parental investment³. Under the Gwynne *et al.* model, then, males experience an increase in parental investment for larger broods originating from larger females. As we discuss in the paper, this increase in parental investment must either be a consequence of males using a strategy in which they increase investment in broods from larger females, or a female (or offspring) strategy in which the broods of larger females somehow take resources from the male¹. As we indicate in the paper, only the former strategy is consistent with all of our observations¹.

Further support for the idea that the male is playing an important role in post-copulatory sexual selection in Gulf pipefish can be seen in our path diagram (figure 3 in ref. 1), which indicates what appears to be a counterintuitive negative relationship between male size and brood size¹. This observation, which cannot be explained easily by a female-mediated strategy, is easily explained by a male-mediated strategy of cryptic choice. We paired males with females at random with respect to male body size. Consequently, a larger male was more likely than a smaller male to be paired with a female smaller than

himself. If males assess female attractiveness relative to their own body size, as our data indicate (figure 2 in ref. 1), then the larger males should have been the least attracted to their assigned mates, which would explain a reluctance to accept eggs. Female control of egg transfer would predict either a positive relationship between male length and brood size or no relationship, but not a negative relationship. Hence, males appear to control brood size, which is the key variable in the Gwynne *et al.* model² and must be controlled by females to successfully dismiss a role for males in post-copulatory sexual selection.

In summary, the Gwynne *et al.* model still requires a mechanism for trade-offs between broods, and our data indicate that the most likely explanation in Gulf pipefish is that males adjust parental investment¹. Observations by other scientists documenting nutrient transfer from pregnant male to brood^{4–6} and from brood to pregnant male⁷ lend additional credence to this interpretation. However, we agree with Gwynne *et al.* that further research is warranted. Moreover, we would be surprised if intrinsic egg quality and female-mediated effects play no role in determining egg or offspring survivorship within male pregnancies. Nevertheless, our results strongly support the conclusion that male-mediated processes play a significant role in post-copulatory sexual selection in pipefish.

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