An empiricists’ guide to sexual conflict over parental investment: a comment on Paquet and Smiseth

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Research on sexual conflict over parental investment is oddly out of step with analyses of other forms of this evolutionary conflict. Whereas other researchers focus on the never-ending evolutionary instability that ensues when the sexes have conflicting evolutionary interests (Arnvist and Rowe 2005), we persist in believing that conflict over parental investment has an evolutionarily stable outcome (Lessells 2012). Although others realize that proper analyses of evolutionary conflict must involve quantifying fitness (e.g., Mock and Forbes 1992; Holland and Rice 1998), we are often content to measure only behavior and to cross our fingers that it is a plausible proxy for fitness (even though it is commonly not: Sheldon 2002). And, although research on other aspects of sexual conflict has been led by incisive and elegant experimentation (Arnvist and Rowe 2005), theoretical analyses dominate research on sexual conflict over parental investment (Lessells 2012).

Paquet and Smiseth’s (2016) timely and stimulating review shows how empiricists can now lead the way in developing new thinking about sexual conflict over parental investment that brings it more into line with other research on conflict between the sexes (although, modestly, they stop short of saying this themselves). By calling our attention to the role that maternal effects might have on the outcome of sexual conflict over parental investment, they show how there might not be a stable outcome to sexual conflict over parental investment after all. The outcome might vary from pair to pair, according to the powers of manipulation shown by each individual breeding female. The outcome might also fluctuate in response to microecological conditions that influence the female’s capacity to manipulate her partner via a maternal effect. In fact, the capacity for individual variation in maternal effects to influence the outcome of sexual conflict is even greater than that described in Paquet and Smiseth (2016). Recent empirical work with burying beetles shows that parental effects can also influence sexual conflict not just within a generation, but by acting across generations too, to influence the provision of care when offspring mature into par-ents themselves (Kilner et al. 2015). The outcome of sexual conflict then varies according to the extent of mismatch in parental quality between breeding partners (Kilner et al. 2015).

A second empirical lesson to be learned from Paquet and Smiseth’s review is that sexual conflict cannot properly be analyzed without measuring the fitness consequences of parental behavior, separately for each parent and their young. This is essential because it is the only way to evaluate which partner has been manipulated into behaving in a way that is suboptimal for them. Measuring parental behavior alone will not suffice nor, in fact, is it even necessary for understanding the evolutionary conflict of interest here (De Gasperin and Kilner 2015). With more studies measuring the fitness consequences of sexual conflict over provisioning, the theoretical assumption that the outcome is evolutionarily stable will quickly become testable.

These 2 lessons, then, should form the benchmarks of quality for any future empirical work on sexual conflict over parental investment. It should start with the assumption that the outcome will vary from family to family and across generations and might proceed to determine why any such variation arises. It should also focus on measuring the fitness consequences of parental care for each member of the family, rather than quantifying parental behavior alone.

Studies that set out to test the specific hypotheses outlined in Paquet and Smiseth’s review must additionally be designed to experimentally eliminate closely related competing explanations for outcomes that might be observed. For example, they must show unambiguously that males are responding to the maternal effect alone, and not some correlate in the mother, the offspring, or the local environment. They must further demonstrate that changes in maternal effects function to be manipulative and are not simply a component of prenatal maternal investment that precipitates changes in the extent of paternal investment, in a division of labor that is to the mutual advantage of each sex (Lessells 2012). Finally, females must be shown to cause changes in male investment.

There should be no scope for reversing the causal arrow, with variation in male quality instead driving strategic changes in prenatal maternal investment (Sheldon 2000). Surprisingly, few of the existing studies that are claimed to show maternal effects manipulating fathers actually meet these exacting standards. Nevertheless, with carefully designed experiments, measuring effects on (correlates of) fitness, empiricists will be excitedly placed to lead the next generation of research on sexual conflict over parental investment.

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Expanding investigations of manipulation via maternal effects: a comment on Paquet and Smiseth

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In their invited review, Paquet and Smiseth (2016) provide a timely and stimulating overview of the potential avenues whereby females might attempt to manipulate male parental care behavior via maternal effects. From my perspective (as a herpetologist), their call to expand research in this area beyond birds to other taxa is particularly welcome, and their point that species with male-only parental care should be investigated in this regard is also well taken.

It seems to me that these kinds of maternal effects are particularly likely to be found in the poison frogs of South and Central America, especially those of the family Dendrobatidae. These frogs show elaborate parental care behaviors, and the most common form of parental care is uniparental male care. A number of studies have demonstrated that male parental care provides an important resource to females, one that they are willing to compete intensely to monopolize (Summers 1992). In Dendrobates auratus, the green and black poison frog, for example, some females will guard their mates intensively, aggressively driving off females that attempt to mate with that male (Summers 1989). This behavior is designed to prevent their mate from expending effort caring for the eggs and tadpoles of other females (and potentially depositing tadpoles of different females in the same pool, resulting in competition and cannibalism). Research on this and related species has demonstrated that females engage in deceptive strategies aimed at ensuring that the male does not care for the eggs of other females, although these are not always successful (see Summers 2014 for a review).

At this point, we do not know if the kinds of effects that Paquet and Smiseth (2016) highlight are relevant to the poison frogs, but it is not hard to imagine that such effects might be common. For example, in D. auratus, tadpole survival depends crucially on being the first into a pool. These tadpoles are highly cannibalistic, and tadpoles deposited later (typically at a smaller size than the earlier deposited tadpole) are usually cannibalized by the larger resident tadpole. A female could provide her eggs with growth and development promoting hormones and other factors designed to ensure that if the male is caring for the eggs of several females, hers will be the ones to mature first and be transported to the pool first. Whether females are actually using this kind of strategy is unknown at this time, but it is a fascinating possibility that deserves to be investigated.

A few species of poison frogs (e.g., Ranitomeya imitator) have biparental care, which also offers opportunities for maternal manipulation of offspring in the interests of maximizing male contributions. For example, maternal contributions to eggs might increase egg size or egg color, potentially making those offspring a more attractive target for male investment. Although R. imitator is largely monogamous (and represents the only documented case of social and genetic monogamy in amphibians [Brown et al. 2010; Tumulty et al. 2014]), one case of polygyny has been identified (Brown et al. 2010). Hence, it may be valuable to females to maximize the size and healthy appearance of offspring in order to stimulate and maintain male devotion of parental care to her offspring (note that this could apply to species with male-only care as well).

This brief commentary provides only a glimpse of the many ways in which females might employ maternal effects to manipulate male behavior in the context of parental care in poison frogs, but hopefully one that will stimulate further research in this area.

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Maternal effects likely coevolve with plasticity in male care: a comment on Paquet and Smiseth

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Parental care is in many ways the quintessential example of conflict between the sexes. Paquet and Smiseth (2016) suggest that maternal effects may affect this conflict by allowing females to induce males to provide more care. This represents a promising generalization of the more specific hypothesis that females adjust the androgens in their eggs to increase male care. The strength of this review is that it not only examines the empirical evidence for this specific hypothesis but it also gives concrete suggestions for future research. Here, I highlight some promising insights this research could provide, but question whether it is useful to frame these maternal effects as female manipulation of male care.