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Reproductive Strategies: Eat Your Kids to Restart Your Sex Life

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A recent study shows that filial cannibalism is not merely a desperate survival tactic for hungry fathers. Rather, brood destruction triggers sexual physiology, enabling males to restart courtship with new partners. Like abandonment and infanticide by males and females across taxa, cannibalism generates evolutionary conflict between fathers, mothers, and offspring.

One of European art's most shocking images is Goya's depiction of the Titan Cronos devouring his children (Figure 1). The term 'filial cannibalism' conjures something so desperate and beyond the moral pale as to defy explanation. Animal behavior is interesting in no small part because it holds up a mirror to human experience, but giving technical meaning to fraught terms — choice, rape, cuckoldry, divorce — makes for what Bateson [1] called "unconscious punning" and a tendency to seek special explanations for behaviors that evoke abhorrence.

Infanticide is a case in point: until Sarah Blaffer Hrdy's [2] seminal papers in the late 1970s, scientists strove to explain away the killing of dependent offspring as a rare, pathological behavior. Hrdy proposed a classic set of testable hypotheses for the adaptive benefits of infanticide; for genetic parents, it pays to kill (or abandon) young offspring and restart reproduction if the costs associated with offspring care exceed the benefits. Filial cannibalism — eating one's genetic progeny — is a form of infanticide found across taxa, and is particularly well-documented in fishes with male parental care. In many species, individual males defend nests or spawning sites. One or more females spawn with the male in his territory, leaving him to care for the young. Parental care often involves little more than keeping intruders away from the nest, particularly other fish species likely to eat eggs [3].

Yet Dad is often the worst predator of his own eggs. Partial filial cannibalism, like parental infanticide in birds [4], may be beneficial for both parents if thinning the brood increases average offspring fitness, for example, by increasing oxygen availability [5] or skewing sex ratios [4]. But what about total filial cannibalism, in which a male consumes the whole brood? There is abundant evidence that less-valuable clutches — those that are smaller, earlier in development [6], or of mixed paternity [7] — are more likely to be cannibalized.

Why do males eat these eggs instead of just soliciting matings from more females? The consensus until now has been that cannibalism is driven by the direct benefit of eating eggs: a caviar snack serves as an alternative food source for hungry males. Total filial cannibalism is adaptive if the nutritional benefit of eating eggs, applied to future courting and guarding, has a greater fitness benefit than guarding the current clutch. It therefore pays a father to reap the energy benefit from the eggs, at the expense of mother and progeny [6]. The unique prediction of the so-called energy-based hypothesis is that cannibalism will be sensitive to nutritional state and food availability: hungrier males will be more likely to cannibalize, and cannibalism will confer a nutritional benefit. This prediction is poorly supported by empirical data [8].

In this issue of *Current Biology*, Matsumoto and colleagues [9] suggest that filial cannibalism may primarily serve to trigger a behavioral return to bachelor ways. In barred-chin blennies, adult male behavior cycles between a 'mating phase' when males are courting females and a 'parental phase' when they are guarding their young. As in humans [10] and other vertebrates, blenny courtship is androgen dependent [11], and androgen levels decline during parental care. In female mammals, termination of parental care speeds a return to the reproductive state [2]. Similarly, Matsumoto *et al.* [9] argue that filial cannibalism accomplishes an ''endocrinological reset'' — in this case, a return of androgen titers and courtship efforts to levels observed during the mating phase. When stuck with an unprofitable clutch, males eat their offspring to restart courtship.

By adding and removing eggs from nests in the wild, Matsumoto and colleagues [9] show that the presence or absence of eggs acts to rapidly modulate androgen levels and therefore courtship. Males with eggs in the nest have low androgen levels and infrequently perform courtship behaviors; but androgen and courtship levels rise dramatically after egg removal, with most males remating by the following day. Adding eggs to a courting male's nest has the reverse effect. In contrast, nutrition seems to play a small role at best: leaner males are no more likely to cannibalize eggs, and eggs are often spit out rather than eaten. Eating eggs, therefore, is mainly a byproduct of the process of removing them from the nest. When a male has a bad clutch of eggs, cannibalism increases fitness through its effects on reproductive physiology rather than nutritional state.

But why cannibalize instead of keeping the eggs on the nest and continuing to court females? Males continue to court, albeit at a lower rate, during the parental phase, and females will sometimes oviposit on existing nests. The answer seems to be that reproductive physiology imposes hard trade-offs on male behavior. High androgen levels compromise parental care because, as the authors mention, they reduce immunocompetence and increase the risk of pathogen transmission to progeny. Studies in other fish suggest that androgen-pumped males make lousy fathers, diverting time and energy away from caregiving and towards intrasexual-selection aggression [12]. Behaviorally and physiologically, the mating phase and the parental phase have different demands.

Filial cannibalism therefore joins a variety of mechanisms that accelerate a return to a reproductive state, generally benefiting one parent at the expense of the offspring and the other parent. As the authors suggest, the term 'cannibalism' is not the best descriptor for the destruction of fertilized eggs. Indeed, sensationalistic terms like cannibalism and infanticide not only conjure Goya-esque images of depravity, they also create spurious divisions that obscure the general problem of how resources are allocated across the reproductive cycle and of the coevolutionary conflict that allocation generates between fathers, mothers, and offspring.

Sexual reproduction involves finding and choosing mates, fertilizing gametes, and then fostering the survival of some zygotes to adulthood. Intersexual differences and interspecific variation run the gamut in terms of how individuals invest in each of these stages. For example, most male mammals invest largely in the mating phase, while females invest in the parental phase [13]. For blennies, and other vertebrates with male care, androgens modulate the switch between the two.

Infanticide and filial cannibalism are the extreme cases of adults treating their offspring unequally, usually for reasons that are advantageous to at least one parent. Starting from the zygote stage, some embryos get more yolk protein, some are aborted, and some become food for their siblings [14]. Discrimination continues after birth, when some young are fed less or abandoned outright. From the point of view of an individual caregiver's fitness, the same economic logic applies for blennies destroying a clutch as for female mice aborting embryos when a new, infanticidal male enters their social group — the so-called Bruce effect [14] — or for monogamous seabirds abandoning their brood in an El Niño year [15]. In all these cases, it pays an individual to terminate care because the expected fitness return from the current brood is less than that gained from terminating care.

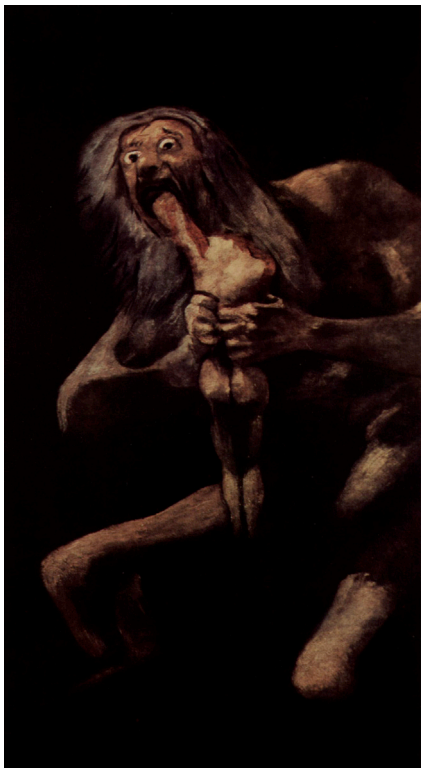

Figure 1. ***Saturno devorando a su hijo.***
Painting by Francisco Goya, ca. 1819–1823. Museo del Prado, Madrid. Photo provided by the Yorck Project.

The differences among these systems lie in how they shape sexual conflict between the parents [16]. In the seabirds, terminating investment in offspring has similar returns for both male and female, since they both provide care and return to mate with each other the next year. But in the other two cases the caregiver is increasing its fitness at the expense of not only the unfortunate offspring but also the other parent. In the case of the Bruce effect, it pays a novel male to hasten the return to receptivity of the females he can access. The Bruce effect therefore has similar coevolutionary dynamics to the widespread phenomenon of males killing unrelated young to trigger females' return to a reproductive state [17]. Further, by terminating pregnancy early, the Bruce effect mitigates the cost to females of bearing progeny doomed to be killed by the novel male.

Clutch destruction by a male fish similarly increases the male's fitness at the mother's expense. Since males cannibalize the offspring of some females but not others, it is instructive to think of

clutch destruction as a form of post-mating mate choice, with males choosing to defend or consume offspring based on clutch size and perhaps other factors. What role do females play in inhibiting or encouraging 'filial cannibalism', and what mechanisms are involved in a father's switch from protector to predator? Selection plainly favors females that lay large clutches, but there may also be an opportunity for females to manipulate male behavior through egg chemistry — both in terms of suppressing androgens and discouraging destruction.

Selection also should favor females that can anticipate the probability of clutch destruction. While early studies suggested that females could use courtship vigor as a reliable cue of male nutritional state, and therefore risk of cannibalism [18], Matsumoto *et al.*'s work [9] suggests that vigorous courtship may, if anything, signal a male who's recently devoured his progeny. The importance of clutch size for male decisions suggests a tough choice for females: perhaps they maximize clutch survival by entrusting most of their reproductive output to one male, rather than hedging their bets across fathers [19].

Blennies show mutual mate choice: females by selecting males with whom to oviposit, and males by clutch destruction. Biological market theory [20] may prove useful in elucidating how mating outcomes are distributed in systems with male parental care. We gain a much richer picture of behavioral evolution when we consider underlying mechanisms in all parties involved, and when we emancipate these mechanisms from semantic stereotypes.

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Spindle Assembly: Two Spindles for Two Genomes in a Mammalian Zygote

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A single bipolar spindle was thought to form around both parental genomes in zygotes initiating the first division. A recent study challenges this predominant view by showing that two independent spindles assemble to prevent parental genome mixing in mouse zygotes.

The one-cell embryo, or zygote, results from the fusion of male and female haploid gametes. It is a unique state in the life of an organism, as the subsequent encounter of the two parental genomes within this single cell enables the recovery of a diploid genome. In many model systems, the process starts with the migration of the two pronuclei, each containing a single parental genome, to