



HOW MATE AVAILABILITY INFLUENCES FILIAL CANNIBALISM

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ABSTRACT

Parents sometimes eat their young to reduce the consequences of brood overcrowding, for nutritional gain, and/or to redirect investment toward future reproduction. It has been predicted that filial cannibalism should be more prevalent when mate availability is high as parents can more easily replace consumed young. Reviewing the available evidence—which comes almost exclusively from studies of paternal caring fish—we find support in some species, but not others. To explain this, we hypothesize that sexual selection against filial cannibalism and/or the tendency to acquire larger broods under conditions of high mate availability discourages filial cannibalism. Additionally, filial cannibalism might occur when mate availability is low to facilitate survival until access to mates improves. Since attractiveness can also influence remating opportunities, we review its effect on filial cannibalism, finding that attractive parents engage in less filial cannibalism. More research is needed to determine if this relationship is a result of individuals showing adaptive plasticity in filial cannibalism based on self-perceived attractiveness, or if the attractiveness of individuals is reduced by their propensity to commit filial cannibalism. More generally, to advance our understanding of how mate availability influences filial cannibalism, future studies should also focus on a wider range of taxa.

INTRODUCTION

KILLING one's own offspring appears to be the antithesis of a good reproductive strategy, yet such behavior is likely to be a significant—but poorly recognized—source of mortality among developing juveniles in many species (Mock 2004; Moreno

2012). One especially intriguing form of infanticide is filial cannibalism, which involves parents not only killing, but also eating their own offspring. This phenomenon has been reported in a wide range of taxa, including arthropods (Bartlett 1987; Mori and Chiba 2009), fish (FitzGerald 1992;

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Manica 2002b; Lindström and St. Mary 2008), amphibians (Okada et al. 2015), reptiles (Huang 2008), birds (Tortosa and Redondo 1992; Gilbert et al. 2005), and mammals (Bronson and Marsteller 1985; Beery and Zucker 2012).

There has been considerable effort focused on understanding why parents engage in filial cannibalism. In this respect, filial cannibalism is widely suspected to be adaptive, since it would otherwise be selected against if it did not confer fitness benefits to parents (see Lindström and St. Mary 2008 for a detailed discussion of this point). In particular, much work has focused on identifying the ways in which parents can benefit from eating their own young, and under what circumstances animals are compelled to do so (FitzGerald 1992; Manica 2002b). To this end, two broad classes of nonmutually exclusive benefits have been identified. First, eating offspring may provide cannibalistic parents with energy or nutrients (Bronson and Marsteller 1985; Schneider and Wade 1989; Hoelzer 1992; Kraak 1996; Lindström and Sargent 1997; Kvarnemo et al. 1998; Lindström 1998; Manica 2004; Okuda et al. 2004; Mehliis et al. 2009; Takeyama et al. 2013), which can enable the parent to produce or better care for other offspring (Rohwer 1978; Manica 2002b). Second, in common with other forms of infanticide (Mock and Forbes 1995), filial cannibalism could be beneficial in allowing parents to manage the size or composition of their broods (Payne et al. 2002, 2004; Creighton 2005; Klug et al. 2006; Beery and Zucker 2012). For example, reducing the number of young in the brood can be beneficial if offspring survivorship or quality are density-dependent (Payne et al. 2002, 2004; Klug et al. 2006). Parents that selectively consume low value offspring can also avoid wasting time or resources caring for them (Klug and Bonsall 2007; Klug and Lindström 2008).

Scientists recognize two forms of filial cannibalism: total filial cannibalism, where all of the young a parent currently has under its care are consumed, and partial filial cannibalism, where only a fraction of the brood is consumed (Rohwer 1978; Manica 2002b). Both of these forms of cannibalism

can offer nutritional benefits to parents (Candolin 2000a; Kume et al. 2000; Manica 2004; Okuda et al. 2004; Gomagano and Kohda 2008; Mehliis et al. 2009; Takeyama et al. 2013). Furthermore, both can function as brood management. For example, total filial cannibalism can enable parents to free up valuable space for larger more profitable broods, as seen in Egyptian mouthbrooders (*Pseudocrenilabrus multicolor*; Mrowka 1987) and fantail darters (*Etheostoma flabellare*; Lindström and Sargent 1997). Similarly, partial filial cannibalism can enable parents to remove slower developing offspring or ensure that the number of offspring in a brood does not exceed that which can be supported by parental provisioning, as shown, for instance, in burying beetles (*Nicrophorus tomentosus*; Trumbo 1990) and sand gobies (*Pomatoschistus minutus*; Klug and Lindström 2008). In the case of Syrian hamsters (*Mesocricetus auratus*), consumption of offspring may even enable parents to manipulate the sex ratio of their broods (Beery and Zucker 2012).

Regardless of how parents benefit from eating their young, whenever they do so, they are killing off progeny that they might otherwise have reared to directly contribute to their fitness. Hence, in order to gain a complete understanding of the circumstances under which animals should engage in filial cannibalism, we must not only consider the benefits of offspring consumption but also the costs. For parents, whenever the potential benefits derived from eating young outweigh the cost to replace them, filial cannibalism becomes an effective strategy. Therefore, the cost of filial cannibalism will largely be determined by what is required to produce offspring equivalent to those that were consumed. Included in this is the cost associated with parental effort as well as energetic, temporal, and survival costs of remating where necessary.

The costs associated with parental effort required to replace eaten offspring can help to predict the circumstances under which filial cannibalism occurs. For example, younger offspring are more likely to fall victim to filial cannibalism than older offspring, which corresponds to the parental

effort required to replace them (Schwanck 1986; Petersen and Marchetti 1989; Lavery and Keenleyside 1990; Petersen 1990; Manica 2002a). Furthermore, within biparental species, there is evidence to suggest that fathers have a greater inclination toward filial cannibalism than mothers, which can be partly explained by the greater expenditure required from females to produce gametes to replace eaten young (Lavery and Keenleyside 1990; Raadik et al. 1990). Similarly, the high incidence of filial cannibalism among teleost fish may, at least partly, be due to the prevalence of exclusive paternal care in this group, although detailed studies are required to verify the potential link between parent sex and filial cannibalism in uniparental species.

The mating effort required to replace offspring might also influence a parent's incentive to eat them. Here it is likely that the costs of remating are even more variable than those associated with parental effort. This is because an individual's opportunities to remate are dependent on environmental conditions—both physical and social. Furthermore, when filial cannibalism is performed to improve future offspring production or care (as opposed to benefit existing, uneaten young), the success of this strategy is entirely dependent on the outcome of remating attempts. For these reasons, the likelihood and costs of remating should be one of the principal factors mediating when individuals engage in filial cannibalism.

There are a number of factors that should influence the cost of remating for an individual. Principal among these is the presence of mature animals of the opposite sex and their willingness to breed with the individual, which should depend on the operational sex ratio (ratio of sexually active males to fertilizable females at any given time) and the cost of mate search (Emlen and Oring 1977; Clutton-Brock and Parker 1992; Kokko and Monaghan 2001), all of which can broadly be encompassed under the term "mate availability" (Kondoh and Okuda 2002). Thus, it has previously been predicted that animals experiencing high mate availability should, on average, commit

more filial cannibalism, as they can more easily replace young (Okuda and Yanagisawa 1996b; Manica 2002b). This possibility, which was raised as a key area for research in the last major review of the topic (Manica 2002b), was, at the time, based on a single study (Okuda and Yanagisawa 1996b). Since then, however, there have been several more empirical contributions investigating the role of mate availability on filial cannibalism (Table 1).

This review focuses on the prediction that filial cannibalism levels are mediated by mate availability. We begin by summarizing the empirical findings on the topic to illustrate that individuals have been observed to respond to changes in mate availability by increasing filial cannibalism rates in some species (Okuda and Yanagisawa 1996b; Okuda et al. 2004; Myint et al. 2011a; Takeyama et al. 2013), whereas in other species, filial cannibalism rates remain unchanged (Bjelvenmark and Forsgren 2003) or even decrease when prospective mates are made more accessible (Pampoulie et al. 2004; Klug et al. 2005). To explain this, we explore a range of potential mechanisms through which mate availability can influence cannibalism. In particular, we propose mechanisms to address the unexpected findings of reduced levels of filial cannibalism among animals experiencing high mate availability. These include: (1) the possibility that heightened mate availability leads to individuals having or expecting to have more young in their broods—and thus greater rewards from caring for such broods discourages filial cannibalism under these circumstances; (2) that individuals will commit filial cannibalism when mate availability is low to facilitate their survival until times of improved mate availability; and (3) that committing filial cannibalism can deter mates and thus is an inappropriate strategy when many potential mates are around.

Once we have outlined the possible mechanisms through which mate availability could influence filial cannibalism, we consider whether the different forms of filial cannibalism (partial and total) respond differently to mate availability. Since total

TABLE 1

Summary of the results of studies examining the relationship between the availability of mates to parental male fish and the filial cannibalism levels of these males

Study species	Form of care	Males capable of brooding multiple clutches simultaneously?	Experimental provisioning of food to males during parental care	Relationship between level of mate availability experienced by an individual and:		Reference
				Total filial cannibalism	Partial filial cannibalism	
Cardinalfish (<i>Apogon doederleini</i>)	Mouthbrooder	No	None	+	Unexamined	Okuda and Yanagisawa (1996b)
Two-spotted goby (<i>Gobiusculus flavescens</i>)	Nest-brooder	Yes	None	Not significant	Not significant	Bjelvenmark and Forsgren (2003)
Sand goby (<i>Pomatoschistus minutus</i>)	Nest-brooder	Yes	Daily	–	Not significant	Pampoulie et al. (2004)
Goby (<i>Rhinogobius</i> sp. OR)	Nest-brooder	Yes	None*		+**	Okuda et al. (2004)
Flagfish (<i>Jordanella floridae</i>)	Nest-brooder	Yes	Daily	–	Unexamined	Klug et al. (2005)
Lizard goby (<i>Rhinogobius flumineus</i>)	Nest-brooder	Yes***	None	Not significant	+	Myint et al. (2011a)
Lizard goby (<i>Rhinogobius flumineus</i>)	Nest-brooder	Yes***	None	Unexamined	+	Takeyama et al. (2013)

*Males were only left to care for their eggs for a small proportion of the brooding period, during which experimenters did not provide food. The effect of different prespawning feeding regimes was examined in this study.

**Due to dissection of males prior to the completion of brooding, it is uncertain whether this result applies to total filial cannibalism, partial filial cannibalism, or both.

***Typically, however, only single clutches are brooded.

filial cannibalism can only be seen as an investment into future reproduction, it might be expected that total filial cannibalism in particular should be favored by high mate availability. We discuss the empirical support, or lack thereof, for this hypothesis, as well as other possible mechanisms through which partial and total filial cannibalism might be affected differently by mate availability. From there, we address how key factors such as the timing of exposure to, and contact with, additional mates might influence filial cannibalism. We then broaden our consideration of how access to mates influences filial cannibalism by discussing how an individual's attractiveness could affect their propensity to devour their young. Following this, we examine the related question of how the quality of prospective mates influences filial cannibalism, an area that so far has received little attention. Finally, at the end of the review, we examine the relationship between filial cannibalism and mate availability at the macroevolutionary scale.

THE EFFECT OF MATE AVAILABILITY ON FILIAL CANNIBALISM AT THE LEVEL OF THE INDIVIDUAL

The orthodox view is that individuals will increase the amount of filial cannibalism they perform when mate availability is high (Okuda and Yanagisawa 1996b; Manica 2002b; Bjelvenmark and Forsgren 2003; Okuda et al. 2004; Myint et al. 2011a,b). The reasoning behind this is that an animal's expected future mating ease and success will be greater when many mates are available. The value of existing young will therefore be lower, since they are more easily replaced, and so the cost of losing young from filial cannibalism is lessened. Following from this, the greater ease and likelihood of remating that comes from elevated mate availability should mean that parents have the opportunity to reinvest energy gained from filial cannibalism into future young. Moreover, if the reproductive success of individuals is limited by access to food rather than mates, then filial cannibalism could provide a means of ac-

quiring the limiting resource. This might be especially important if increased levels of mate availability lead to the acquisition and consumption of young becoming a more viable means of attaining food than traditional foraging.

EMPIRICAL EVIDENCE

Although filial cannibalism is known to occur among all of the major vertebrate groups, and to be performed by both males and females showing various forms of parental care the only available evidence directly testing the effect of mate availability on filial cannibalism comes from studies of fish with exclusive paternal care (Table 1). The findings from these studies are nevertheless insightful and show that a diverse range of responses to altered mate availability can occur. Some studies support the orthodox prediction that heightened mate availability will facilitate greater rates of filial cannibalism (Okuda and Yanagisawa 1996b; Okuda et al. 2004; Myint et al. 2011a; Takeyama et al. 2013). For example, in their now classic study, Okuda and Yanagisawa (1996b) showed that male cardinalfish (*Apogon doederleini*) that had committed total filial cannibalism were able to remate more quickly than males that had their broods taken from them by the experimenters. This suggests that the cannibalistic males had above average access to mates when they ate their young. However, the causal relationship between access to mates and filial cannibalism is not entirely clear in this case. It is possible that, rather than access to mates having caused males to commit filial cannibalism, the act of eating eggs itself may have provisioned cannibalistic males with energy that helped them attain additional mates (Manica 2002b) or triggered changes in their physiology that lead to faster remating. Observations by Takeyama et al. (2002), however, show that only males with access to a female-biased operational sex ratio are able to remate quickly after filial cannibalism reinforcing the notion that male cardinalfish utilize surplus females to quickly replace cannibalized broods. An increase in filial cannibalism

among individuals with enhanced access to mates has also been reported in manipulative experiments on gobies (*Rhinogobius* sp. OR). Specifically, Okuda et al. (2004) found that male gobies paired with two gravid females consumed more eggs than males that were paired with a single gravid female. Because males offered an additional mate consumed more eggs, even when they succeeded in spawning with only one female, it is likely that mate availability itself, and not merely extra eggs from an additional mate, caused the increase in cannibalism.

Other studies, by contrast, have found no effect of mate availability on either total (Bjelvenmark and Forsgren 2003; Myint et al. 2011a) or partial filial cannibalism (Bjelvenmark and Forsgren 2003; Pampoulie et al. 2004). For instance, a study of two-spotted gobies (*Gobiusculus flavescens*), which created a high mate availability treatment (by exposing brooding males to gravid females) and low mate availability treatments (by exposing brooding males to other males or no other fish), found no effect of mate availability on filial cannibalism (Bjelvenmark and Forsgren 2003).

Indeed, several studies have found that heightened mate availability can even decrease the frequency of filial cannibalism. Specifically, in both sand gobies (*P. minutus*) and flagfish (*Jordanella floridae*), males that are exposed to females while brooding have been shown to completely consume their broods less often than brooding males that are not exposed to females (Pampoulie et al. 2004; Klug et al. 2005). Clearly, the orthodox prediction of heightened mate availability leading to increased filial cannibalism does not accord with cases where a greater access to potential suitors has been associated with unchanged or even reduced rates of filial cannibalism (Bjelvenmark and Forsgren 2003; Pampoulie et al. 2004; Klug et al. 2005). In the next section we outline some potential mechanisms through which heightened access to mates could elicit reduced levels of cannibalism.

MECHANISMS FAVORING A NEGATIVE ASSOCIATION BETWEEN MATE AVAILABILITY AND FILIAL CANNIBALISM

Increased Expectation of Brood Size with High Mate Availability Leads to Reduced Filial Cannibalism

In fish, it is well established through field correlates and brood size manipulations that individuals are often more likely to completely consume small broods than large broods (Kramer 1973; Schwanck 1986; Mrowka 1987; Petersen and Marchetti 1989; Lavery and Keenleyside 1990; Petersen 1990; Petersen and Hess 1991; Forsgren et al. 1996; Lindström and Sargent 1997; Manica 2002a; Pampoulie et al. 2004; Lissåker and Kvarnemo 2006; Myint et al. 2011a; but see Payne et al. 2003). This is because the care provided by most fish, usually egg guarding and fanning, is considered to be essentially “nondepreciable” (*sensu* Altmann et al. 1977; Blumer 1979; Clutton-Brock 1991; Smith and Wootton 1995; but see Klug et al. 2006). In other words, for each unit of parental expenditure, the benefit received by each member of the brood remains largely unchanged with increasing brood size. As a consequence, larger broods should offer a better payoff to the parent than smaller broods. Indeed, the expected number of young surviving from a small brood could be so low that the parent may actually be better off eating the entire brood rather than caring for the young and enduring the associated costs (Rohwer 1978; Petersen and Marchetti 1989; Manica 2002b). It is important to note, however, that strictly nondepreciable care is not a precondition for this brood size effect. However, cost per young raised in large broods should be less than that of smaller broods.

The tendency for parents to completely consume small broods might result in increased total filial cannibalism by individuals experiencing low mate availability. This is because, in species where males can care for the young of multiple females at once, low mate availability may result in males

acquiring smaller broods due to access to fewer females. Consequently, under such a scenario, total filial cannibalism may become more prevalent, as it tends to occur in response to small brood size. It should be noted, however, that this phenomenon should only occur if males can expect mate availability to increase in the future, since males should only commit total filial cannibalism of small broods if they can expect to attain larger broods in the future.

Although the effect of brood size might explain a negative association between filial cannibalism and mate availability in the field, it cannot explain experimental results that have explicitly controlled for brood size (e.g., Pampoulie et al. 2004; Klug et al. 2005; Lindström and St. Mary 2008). However, it is conceivable that even when brood size is controlled for, males may base their filial cannibalism decisions on their *expected* brood size. Consider that a male experiencing elevated mate availability may expect to have a greater number of clutches added to his brood. If males respond to the expectation of large brood size with a reduced tendency to engage in total filial cannibalism, as they do when they actually have large broods, then high mate availability should result in reduced levels of total filial cannibalism.

To recap, we have outlined two logical mechanisms through which the increase in expected future reproductive success that corresponds to high mate availability might influence filial cannibalism. From the orthodox position, animals should be more willing to commit filial cannibalism when future mating is likely, since consumed young are easily replaced. Paradoxically, an elevated likelihood of additional mating might also favor reduced total filial cannibalism, since the possibility of adding more young to a brood could increase the incentive to provide care. Differences between these two mechanisms do seem to accord with the available empirical evidence. For example, the expected brood size mechanism is only relevant for cases of total filial cannibalism, because it is total and not partial filial cannibalism that tends to be committed in response to small brood size (Manica 2002b;

Myint et al. 2011a). In accordance with this, we note that it is only total filial cannibalism that has been observed to decrease in response to elevated access to mates (Pampoulie et al. 2004; Klug et al. 2005). Moreover, the expected brood size mechanism relies on the assumption that males will avoid consuming small broods where additional mates are likely to add young to them. Therefore, this mechanism is only relevant for those species in which males brood the eggs of many females at once. Indeed, those species that decrease total filial cannibalism in response to mate availability do have males that care for the young of multiple females at once (Pampoulie et al. 2004; Klug et al. 2005). By contrast, among those species where males increase filial cannibalism in response to mate availability, males never or only rarely brood the young of multiple females at once (Okuda and Yanagisawa 1996b; Okuda et al. 2004; Myint et al. 2011a; Takeyama et al. 2013). This suggests that elevated mate availability might favor increased total filial cannibalism in species where males expect to care for the young of only one female at a time, whereas for species in which males often care for offspring from several females at once, elevated mate availability could promote males to continue to engage in brood care since the likelihood of obtaining a large brood is increased.

Filial Cannibalism as a Strategy to Survive Times of Low Mate Availability/Mating Success

Another mechanism that could favor a negative association between filial cannibalism levels and mate availability involves the use of filial cannibalism as a strategy to survive times of low mate availability. It has previously been suggested that eating young may provide crucial nutrition, and can also free a parent from the demands of engaging in costly parental behaviors (Petersen and Marchetti 1989; Smith and Wootton 1995). Filial cannibalism has the potential, therefore, to improve parental survival and should be employed to prolong survival where the expected increase

in fitness from surviving longer is greater than the fitness loss associated with consuming young. As a consequence, when access to mates varies over time, under some circumstances, it may befit an individual to perform filial cannibalism when mates are scarce. This strategy would facilitate the survival of the individual until mates become more abundant or accessible and should be favored if the fitness benefits of surviving longer are greater for those individuals experiencing low (rather than high) mate availability. Following this, when many mates are available, filial cannibalism may be reduced, so that animals can maximize reproductive gains during the time of peak mate availability. Importantly, this mechanism should only act where mate availability to individuals can increase with the passage of time. Such variation could be predictable, as might occur with breeding seasons, aging, and growth. Alternatively, variation could arise from stochastic events, such as the movements of mates into and out of an animal's territory.

Sexual Selection Against Filial Cannibals Facilitates Low Cannibalism Rates During Heightened Mate Availability

In some species, sexual selection may act against filial cannibalism. This may arise directly from potential mates avoiding mating with known filial cannibals or indirectly as a consequence of other forms of mate choice. For example, in the sand goby (*P. minutus*) it has been suggested that females might actively avoid males that appear to have eaten young (Lindström and Kangas 1996). It has further been theorized that, in some species, females might use "test eggs" to avoid mating with males with a predilection for offspring consumption (Manica 2010). Indeed, female scissortail sergeants (*Abudefduf sexfasciatus*) sometimes deposit small numbers of eggs within the nests of males, and return a short time later to assess the care provided to their eggs before deciding whether or not to commit a full clutch to the attendant male (Manica 2010).

Perhaps the most widespread phenomenon that could result in sexual selection

operating against filial cannibals is the preference of females to deposit their eggs in nests that already contain eggs. This preference has been reported in a number of taxa (e.g., assassin bug, *Rhynocoris tristis*, Thomas and Manica 2005; harvestman, *Pseudopucroliia* sp., Nazareth and Machado 2010), but is particularly well documented in fish (Ridley and Rechten 1981; Marconato and Bisazza 1986; Sikkell 1988; Unger and Sargent 1988; Knapp and Sargent 1989; Kraak and Videler 1991; Goldschmidt et al. 1993; Kraak and Groothuis 1994; Forsgren et al. 1996; Manica 2010; also reviewed in Reynolds and Jones 1999), where males sometimes steal or adopt eggs from other males to use to attract mates (Rohwer 1978; Unger and Sargent 1988; but see Östlund-Nilsson 2002). Intriguingly, it has been proposed that female preference to oviposit alongside other eggs may even be a counterstrategy to male filial cannibalism in some species, as it protects eggs via a dilution effect and since the likelihood of total filial cannibalism decreases as brood size grows (Rohwer 1978; Kraak 1996; Kraak and Weissing 1996; Lindström 2000). For example, female sand gobies (*P. minutus*) prefer egg-tending males and, as a result, gain direct benefits through reduced filial cannibalism (Forsgren et al. 1996), as do female Mediterranean blennies (*Aidablennius sphyinx*; Kraak and Videler 1991; Kraak and Groothuis 1994; Kraak 1996). Consequently, filial cannibalism may promote the evolution of this egg-laying strategy, thus potentially explaining why the two behaviors so commonly co-occur within species (Kraak and Weissing 1996; Lindström 2000). Females, of course, may choose egg-tending males for other reasons, including those benefits associated with mate choice copying (Gibson and Höglund 1992), as well as for protection from other egg predators through the dilution effect and because offspring in large broods may elicit greater parental effort from their fathers (Sargent 1988; Jamieson 1995). However, regardless of the female motivation for favoring egg-tending males, this phenomenon should result in males that engage in total filial cannibalism being less successful at attracting mates over the short term.

The likelihood that females directly or indirectly avoid mating with males that have committed filial cannibalism has implications for the patterns of filial cannibalism displayed in relation to mate availability. Specifically, since filial cannibalism may be aversive to females, it could be that males are reluctant to engage in this behavior unless their access to prospective mates is sufficiently high that, even after deterring some mates through offspring consumption, their reproductive success is not limited by access to females. This might be expected to occur in species such as the signal blenny (*Emblemaria hypacanthus*), where male reproductive success can be limited by the amount of space available for egg deposition within their gastropod shell nesting site (Hastings 1992).

Female aversion to mate with males engaging in filial cannibalism might also have the opposite effect: discouraging males from consuming their young when access to mates is high. Such a relationship might arise if males strategically engage in filial cannibalism most often when few females are around, either because this means that the number of mates that are deterred by cannibalism is minimized, or because males may be able to covertly engage in filial cannibalism with few females around to detect it.

Future investigations might also benefit from considering whether female choosiness varies with mate availability to males, and how this influences filial cannibalism. For instance, if the availability of mates to males is elevated as a result of a decrease in the operational sex ratio, then females may become less discriminating in their mate choice—and thus males might be permitted to engage in more filial cannibalism under such conditions. By contrast, if the availability of mates to males is elevated as a consequence of more frequent male-female encounters (as might occur when population density increases, or mate search becomes safer), instead of a change in the operation sex ratio, we could expect females to become more choosy (Pomiankowski 1987; Real 1990; Slagsvold and Dale 1991; Milinski and Bakker 1992). This, in

turn, should provide further disincentive for males to engage in filial cannibalism during times of high mate availability.

EFFECTS OF MATE AVAILABILITY ON TOTAL AND PARTIAL FILIAL CANNIBALISM

Considering studies of species with exclusive paternal care in which males can tend the clutches of multiple females simultaneously, there is an emerging pattern for total and partial filial cannibalism to respond differently to changes in mate availability (Table 1). For instance, experimental studies have shown that heightened mate availability increases the intensity of partial filial cannibalism in lizard gobies (*Rhinogobius flumineus*; Myint et al. 2011a; Takeyama et al. 2013) but decreases the incidence of total filial cannibalism in flagfish (*J. floridae*) and sand gobies (*P. minutus*; Pampoulie et al. 2004; Klug et al. 2005). The latter is surprising given that total filial cannibalism can only be a successful strategy when the parent is able to produce a new brood, the likelihood of which presumably increases (rather than decreases) with heightened access to mates. By contrast, partial filial cannibalism could be beneficial for an individual even if another brood is not produced (Payne et al. 2002, 2004; Creighton 2005; Klug et al. 2006; Beery and Zucker 2012).

So why might total filial cannibalism be negatively associated with mate availability while partial filial cannibalism shows a positive association? This observation, of course, may simply reflect the low number of studies on this topic. However, plausible biological explanations also exist. As previously discussed, it is total filial cannibalism (and not partial filial cannibalism) that parents might avoid during times of high mate availability since they expect more clutches to be added to their brood. Similarly, if, as previously suggested, males forego filial cannibalism at times of peak mate availability so as not to deter potential mates, then these males might benefit most from avoiding total filial cannibalism. This is because female mate choice strategies are likely to penalize total filial cannibalism more so than partial filial cannibalism.

Furthermore, if filial cannibalism is employed as a strategy to survive times of low mate availability, as we hypothesized earlier, then total filial cannibalism should probably be favored as it can provide nutrition and free the parent from the demands of brood care, whereas partial filial cannibalism only does the former.

A reduction in total filial cannibalism and increase in partial filial cannibalism might also be expected to follow a rise in mate availability if parents are able to gain enough energy through partial filial cannibalism that they no longer need to engage in total filial cannibalism under such conditions. Evidence for this is, however, currently weak, as no study has concurrently reported an increase in total filial cannibalism and a decrease in partial filial cannibalism as a result of heightened mate availability. Mathematical models that can isolate mechanisms through which mate availability affects filial cannibalism may be useful in determining which mechanisms are necessary to explain different effects of mate availability on total and partial filial cannibalism.

Interestingly, there is currently only one species, the cardinalfish *A. doederleini*, in which individuals have been reported to engage in total filial cannibalism more frequently when their access to mates is increased (Okuda and Yanagisawa 1996b). Perhaps the most important difference between this species and those that have so far been found to reduce total filial cannibalism in the face of elevated mate availability is the form of parental care. In the case of the latter, males typically have the ability to tend the young of multiple females simultaneously. By contrast, *A. doederleini* is a paternal mouthbrooder in which males are constrained to caring for the young of a single female at a time (Okuda et al. 1997). Thus, male *A. doederleini* must consume any eggs they are brooding before they can gain immediate access to others (Okuda and Yanagisawa 1996b). Clearly, further research on other mouthbrooders would help to redress the strong bias toward studies on nest brooders with simultaneous polygyny and confirm how brooding style interacts with the effect of mate availability on filial cannibalism.

EXPERIMENTAL CONSIDERATIONS

Timing of Presentation of Prospective Additional Mates

The timing of mate exposure can have important implications when trying to uncover the effects of mate availability on filial cannibalism. As highlighted recently by Myint et al. (2011a), studies that found an increase in filial cannibalism with heightened mate availability had additional mates presented prior to spawning (Okuda and Yanagisawa 1996b; Okuda et al. 2004; Takeyama et al. 2013). By contrast, when differences in mate availability between treatments were only manipulated after spawning, this effect was not observed (Bjelvenmark and Forsgren 2003; Pampoulie et al. 2004; Klug et al. 2005). Furthermore, Myint et al. (2011a) demonstrated that only exposure to additional females prior to spawning, and not after, elicited elevated levels of filial cannibalism in male lizard gobies (*R. flumineus*). The generality of these results, however, remains unclear because brooding male *R. flumineus* often close off their nest entrance after spawning (Myint et al. 2011a,b). Thus, in contrast to many other species that potentially could rely on postspawning mate availability cues, male *R. flumineus* may be adapted to respond only to prespawning cues (Myint et al. 2011a). Still, perhaps there is a more general theoretical explanation as to why prespawning (and not postspawning) mate availability cues trigger filial cannibalism. For example, maybe prespawning cues of mate availability more accurately reflect the level of mate availability an individual will experience after consuming their young because postspawning cues are misleading since the individual possesses young that might attract additional female attention (see discussion of female preferences for egg-tending males in the section, Sexual Selection Against filial Cannibals Facilitates Low Cannibalism Rates During Heightened Mate Availability). To further clarify the importance of prespawning cues, future studies are needed that examine the effects of prespawning mate availability in species that have previously been shown not to al-

ter their filial cannibalism in response to postspawning mate exposure.

Role of Physical Contact with Prospective Additional Mates

It has also been suggested that the failure of some studies to find a positive effect of mate availability on filial cannibalism could be due to experimental setups that prevent physical contact with any additional mates offered (Okuda et al. 2004). For example, Bjelvenmark and Forsgren (2003) and Pampoulie et al. (2004) found that the presence of females did not increase rates of filial cannibalism. However, in both studies, brooding males were physically isolated from stimulus females with transparent barriers. By contrast, males were found to display greater rates of filial cannibalism when they had the opportunity to physically spawn with additional females by Okuda et al. (2004). Similarly, in a study of the cardinalfish *A. doederleini*, where high mate availability was found to be associated with filial cannibalism, males were studied in the natural environment with no artificial separation from additional mates (Okuda and Yanagisawa 1996b). Recent work on the lizard goby (*R. flumineus*), however, has shown that physical contact is not always necessary to elicit an effect (Myint et al. 2011a; Takeyama et al. 2013). Furthermore, work on the flagfish (*J. floridae*) demonstrates that when direct mate contact is allowed, high mate availability can still be found to reduce filial cannibalism levels (Klug et al. 2005). It therefore seems unlikely that physical contact with mates is responsible for the failure of some studies to find high mate availability to increase filial cannibalism levels.

Food Availability

An additional component of experimental design worthy of consideration in future experiments is the provisioning of food to parents. As noted in the introduction, one important function of filial cannibalism can be the acquisition of nutrients or energy for parents. It is reasonable, therefore,

to propose that the effect of mate availability on filial cannibalism might interact with the effect of food availability. In this respect, filial cannibalism could potentially be more prevalent under conditions where potential mates are abundant, but food is scarce. In particular, if limited food supplies (rather than access to mates) restricts the number of young that can be acquired and reared, then the consumption of some offspring could provide parental males with a means to capitalize on abundant access to mates and acquire more food. Under such circumstances, extra nourishment provided to males by filial cannibalism might enable them to rear a greater number of young than would have been possible without engaging in cannibalism.

Examining experimental studies that have investigated the effect of mate availability on filial cannibalism, we see high mate availability is associated with inflated levels of filial cannibalism in studies where parental males were not fed during parental care (Table 1; but see Bjelvenmark and Forsgren 2003). By contrast, high mate availability is associated with decreased cannibalism rates in studies where food was provided to males during parental care (Table 1). If this pattern is borne out by further research, it could suggest that individuals respond differently to changes in mate availability according to their access to food. It should be noted, however, that the decisions by researchers about whether to provide males with food during parental care are probably related to whether the parental care behavior of their study species restricts parental feeding opportunities under natural conditions. Therefore, the apparent pattern in experimental findings might reflect interspecies differences rather than behavioral plasticity of individuals with respect to access to food (see the section, The Macroevolutionary Effect of Mate Availability on filial Cannibalism). In particular, species in which parental males have restricted access to food as a consequence of brood care (because males engage in mouthbrooding or hold themselves up inside their nest during parental care; see Okuda and Yanagisawa 1996b; Myint

et al. 2011a; Takeyama et al. 2013) could be more likely to respond to increased access to mates by engaging in greater levels of filial cannibalism.

Ideally, to investigate a potential interaction between the effect of food and mate availability on individual behavior, a crossed experimental design examining each of these factors in a single species would be employed. However, only a single study, conducted by Okuda et al. (2004), has so far taken this approach. Although they found that both poor condition (from being food restricted) and elevated access to mates are associated with increased levels of filial cannibalism in male gobies, no interaction between these two factors was detected. Nonetheless, further investigation of this potential interaction is needed, especially since the power to detect an interaction in the aforementioned study was low (Okuda et al. 2004).

RELATIONSHIP BETWEEN OFFSPRING CONSUMPTION AND ATTRACTIVENESS OF THE CANNIBAL

So far, we have examined studies that manipulate mate availability by altering the number of gravid females to which males are exposed. Yet, just as the physical presence of the opposite sex may influence the likelihood of an individual's future reproduction, so too should the willingness of potential suitors to mate with the individual. An individual's perceived attractiveness could therefore influence its tendency to commit filial cannibalism. Here, one possibility is that attractive parents could exploit their heightened access to mates by engaging in greater levels of cannibalism. Meanwhile, unattractive males might engage in less filial cannibalism since they have lower expected future reproductive opportunities on account of their low sex appeal. However, this does not appear to be supported by the literature, with evidence suggesting, in fact, that attractive males are less likely to eat their young. For example, males with preferred phenotypes have been shown to bring a greater proportion of eggs to hatching in both the sand goby (*P. minutus*; Fors-

gren 1997; Lehtonen and Lindström 2007) and the three-spined stickleback (*Gasterosteus aculeatus*; Candolin 2000a,b). Preferred males that engage in costly courtship displays have also been shown to cannibalize fewer eggs in the stream goby (*Rhinogobius brunneus*; Takahashi and Kohda 2004) and the bicolor damselfish (*Stegastes partitus*; Knapp and Kovach 1991). In the next section, we consider mechanisms that might explain the negative association between an individual's attractiveness and their propensity to engage in filial cannibalism.

WHY ARE ATTRACTIVE INDIVIDUALS LESS PRONE TO FILIAL CANNIBALISM

Several processes could underlie the negative association between filial cannibalism and attractiveness. The relationship could arise without any direct causal link between the two factors. For instance, poor body condition, foraging capabilities, or access to resources may lead to individuals becoming unattractive, while at the same time compelling them to commit filial cannibalism for nutritional gain. In terms of a causal relationship, it is plausible that the propensity of individuals to eat their young can directly influence their attractiveness. Thus, mate choice based on cues or signals that predict an individual's likelihood of engaging in cannibalism may explain why cannibals are less attractive. The best evidence for this involves male expression of epigamic behavior. For example, studies have shown that females often prefer males that court intensely, or in energetically demanding circumstances, because such males have superior energy reserves or efficient metabolisms—and are therefore less likely to eat their young (Knapp and Kovach 1991; Takahashi and Kohda 2004).

The reverse causality is also possible: attractiveness can potentially influence an individual's access to mates and, in so doing, affect their inclination to engage in cannibalism. For instance, already attractive males may avoid eating their young, as doing so may reduce their attractiveness in the short term and, thus, their competitive advantage over rivals. Unattractive males,

by contrast, might eat their offspring in anticipation of becoming more attractive in the future. Indeed, for such males, resources acquired from filial cannibalism could actually be used to directly improve their future attractiveness. This has been shown in the cardinalfish (*A. doederleini*), where younger males perform filial cannibalism to fuel growth to a larger size, which makes them more appealing to females in future mating attempts (Okuda et al. 1997; Takeyama et al. 2002).

It is currently unclear which direction of causality is most important in explaining the negative association between filial cannibalism and attractiveness. It is worth noting, however, that male signaling of egg hatching success appears to be particularly important among egg guarding ectotherms, suggesting that filial cannibalism propensity is likely to affect attractiveness (Møller and Jennions 2001). However, results of studies in which nest size has been manipulated suggest that males with small nests—which could be less attractive to females—commit greater rates of filial cannibalism (Okuda et al. 2004; Pampoulie et al. 2004; Klug et al. 2006; but see Björk and Kvarnemo 2012), thus indicating that males may alter their cannibalistic tendencies based on their self-perceived attractiveness. Other explanations, such as reduced ventilation or increased egg density, might also explain this observation, therefore further experiments examining the effect of attractiveness manipulation are needed.

EFFECT OF PROSPECTIVE MATE QUALITY ON AN INDIVIDUAL'S TENDENCY TO COMMIT FILIAL CANNIBALISM

Although there is a growing interest in how the presence of additional mates affects an individual's tendency to commit filial cannibalism, we know far less about how the quality of these mates might influence the cannibal's behavior. It seems reasonable to suppose that in some situations, when a brooding parent encounters extra mates, the quality of these mates could affect the likelihood and extent of filial cannibalism by the parent. If parents trade off

the cost of losing young from filial cannibalism against the benefits they can obtain from additional mating opportunities, this could encourage them to eat their young where doing so enables them to attract higher quality mates. For example, filial cannibalism could occur if it provides the cannibal with the resources needed to attract a better quality mate or to invest in their young. Here, a study of the lizard goby (*R. flumineus*) shows that males can indeed distinguish between potential mates, and engage in elevated levels of filial cannibalism only when exposed to gravid (as opposed to nongravid) females (Takeyama et al. 2013). However, the effects of other differences in mate quality are yet to be investigated.

There are several reasons why parents might be selective over which mates they will consume some or all of their young to gain access to. Certainly, for males, willingness to consume existing young could be contingent on the number of young that a prospective female mate would produce. In particular, in the absence of other benefits, we might expect that fathers will only commit filial cannibalism to gain access to an additional mate where the subsequent mating produces a greater number of young than were consumed. However, there are other reasons why parents (of either sex) might be choosy about which potential mates are worth consuming young for a chance to reproduce with. In particular, only high-quality mates may be acceptable as they produce either genetically superior or better resourced progeny. Similarly, it might be that parents base their decision on whether to cannibalize existing young on the genetic compatibility of a new prospective mate.

The behavior of potential suitors could also be influential in driving parents to commit filial cannibalism. In some species, prospective mates are known to kill the offspring of caring parents so as to coerce the parents into breeding with them (Hrdy 1974; Palombit 2015). A range of counterstrategies have evolved to help parents protect their young from this fate, or lessen the cost when it occurs (Palombit 2015).

One potential counterstrategy (the Bruce effect), well documented among a range of rodent species (among other mammals), involves female termination of pregnancy in response to encountering unfamiliar males (Bruce 1959; Labov 1981; Becker and Hurst 2008; Roberts et al. 2012). An analogous strategy available to parents caring for young after parturition or oviposition would involve parents eating their own young before infanticidal prospective mates are able to kill the young. This would allow the parent to recover some nutritional resources from their offspring before remating (Labov 1981). There is some evidence to suggest that this counterstrategy is employed by parental male sticklebacks (FitzGerald and van Havre 1987). However, as far as we are aware, it remains to be investigated whether such a strategy also exists in mammalian taxa, such as rodents, which display the Bruce effect (e.g., Bruce 1959; Heske and Nelson 1984; Hackländer and Arnold 1999; Pillay and Kinahan 2009; Marashi and Rüllicke 2012) and engage in high levels of filial cannibalism (Day and Galef 1977; Bronson and Marsteller 1985; but see Weber et al. 2013).

It may be difficult to differentiate between filial cannibalism as a counterstrategy to avoid infanticide and filial cannibalism that is a strategy to facilitate trading up to a higher quality mate (cf. Becker and Hurst 2008 for a similar discussion regarding the adaptive significance of the Bruce effect). In both cases, the value of the existing clutch relative to that of the expected clutch may influence the parent's choice to commit filial cannibalism. This is because the trading-up hypothesis relies on a more valuable brood being attained from the new clutch, while for the infanticide counterstrategy, parents may be willing to put themselves at greater risk to defend more valuable clutches, as seen for example in cichlids (*Aequidens coeruleopunctatus*) and bluegill sunfish (*Lepomis macrochirus*; Carlisle 1985; Coleman et al. 1985). One informative difference between filial cannibalism as a counterstrategy to infanticide, and that used to trade up, would be that only in the former would the capacity of the caring

parent to defend their brood from the new prospective mate influence the likelihood of cannibalism.

THE MACROEVOLUTIONARY EFFECT OF MATE AVAILABILITY ON FILIAL CANNIBALISM

So far, we have focused on how an individual's access to mates, and the quality of these mates, influences the amount and form of filial cannibalism they should commit; hereafter, we refer to this as the individual-level effect of mate availability. In this section, we discuss macroevolutionary patterns of filial cannibalism. Specifically, we consider how between-species differences in mate availability might modulate the relative rates of filial cannibalism of species. We refer to this as the species-level effect of mate availability. In other words, the individual-level effect of mate availability represents phenotypic plasticity, whereby the amount of filial cannibalism performed by an individual varies according to prevailing environmental conditions experienced by them, in particular their access to mates. By contrast, the species-level effect of mate availability refers the influence that the overall accessibility of mates to members of one sex within a species has on the average rate of filial cannibalism engaged in by that sex.

Some may argue that since the amount of filial cannibalism occurring within a species is merely the sum of the actions of all individuals in the species, then the species-level effects of mate availability should simply reflect the individual-level effect. However, it is possible that mate availability and filial cannibalism rates have different relationships at the species level and at the individual level. For instance, when comparing a group of species, it might be that the average level of access to mates and filial cannibalism are positively correlated. However, each of these species could conceivably be composed of individuals that are more likely to consume their young when they experience lulls in mate availability. Accordingly, we believe that future work will benefit from explicitly differentiating between

species- and individual-level effects of mate availability.

On a macroevolutionary scale, the current view is that within a sex, but between species, there will be a positive association between filial cannibalism levels displayed by the sex and mate availability experienced by the sex (Okuda 1999a, 2000; Kondoh and Okuda 2002). The currently accepted basis for this prediction is that organismal-level selection will favor greater rates of filial cannibalism by individuals of a given sex within species where that sex experiences relatively high mate availability. This would be because replacing eaten young should be less costly where mate availability is high. Therefore, with the effective cost of filial cannibalism lessened, it should become more common. Moreover, it can be argued that, as mate availability is increased to a given sex, access to mates could become less of a constraint on that sex's reproduction. Accordingly, other factors, including energetic demands, might begin to limit reproduction in that sex. Consequently, selection may favor an increased tendency toward performing filial cannibalism among the sex where access to mates is high, thereby allowing members of this sex to attain resources for more reproduction and exploit the availability of mates.

Field surveys of various species of paternal mouthbrooding cardinalfish of the genus *Apogon* provide evidence for mate availability having a species level effect on the incidence of filial cannibalism. It has been found that males of both *Apogon niger* (Okuda 1999a) and *Apogon notatus* (Okuda 2000) consume the clutches they are brooding less frequently than males of *A. doederleini* (Okuda and Yanagisawa 1996b; Okuda et al. 1997). Interestingly, *A. niger* (Okuda 1999a) and *A. notatus* (Okuda 1999b, 2000) both come from populations in which there is a male bias in the operational sex ratio and adult sex ratio, whereas these are both female biased for *A. doederleini* throughout most of the breeding season (Okuda and Yanagisawa 1996b). Thus, observations of *Apogon* cardinalfish support the prediction that high mate availability at the species level will result in high average rates of filial cannibalism. However, further

research on this genus would be desirable to elucidate more details about the mechanism through which high mate availability in *A. doederleini* favors its relatively high cannibalism rate. One possible mechanism is that filial cannibalism imposes minimal costs on *A. doederleini* males, as high mate availability means they are able to replace lost young easily. Another nonmutually exclusive mechanism is that male *A. doederleini* commit more filial cannibalism to compensate for the greater amounts of time and energy they spend mouthbrooding (Okuda and Yanagisawa 1996a; Okuda 1999a, 2000), with the increase in time spent mouthbrooding resulting from more frequent matings that accompanies increased access to mates.

Kondoh and Okuda (2002) developed the only model that sets out to determine how mate availability influences filial cannibalism at the species level. They modeled a population of exclusive paternal carers with filial cannibalistic males that care for a set number of clutches per brood. A game theoretic approach was used to determine an evolutionary stable strategy for the number of clutches cannibalized per brood. Consistent with empirical studies of *Apogon* cardinalfish, they found that, at the species level, high mate availability facilitates increased filial cannibalism. The value of this model to the development of the field cannot be underestimated. Nonetheless, as is nearly always the case with modeling, certain simplifying assumptions were made that could influence the results. Extension of this model could help determine if mechanisms that might influence the individual-level effects of mate availability (especially those listed in the section, Mechanisms Favoring a Negative Association Between Mate Availability and filial Cannibalism) also lead to species-level effects. At present, this remains a largely unresolved question. In particular, it would be instructive to develop models that include temporal and spatial fluctuations in mate availability, sexual selection against cannibals, and brood size effects on parental care and offspring survival. Furthermore, Kondoh and Okuda's (2002) model assumes that filial cannibalism is a genetic, fixed strategy without phenotypic

plasticity (Okuda et al. 2004). Developing filial cannibalism models in which animals can respond to their environment with a conditional strategy would be more realistic and, most importantly, provide insights into both species-level and individual-level effects of mate availability on cannibalism (Okuda et al. 1997, 2004; Takeyama et al. 2002). Although such models have been created (see, for example, Sargent 1992; Sargent et al. 1995), they have not yet been used to substantially investigate mate availability effects. Furthermore, models could be useful in gaining insight into whether partial and total filial cannibalism levels are each affected differently by changing mate availability at the species level; an area of particular interest as Kondoh and Okuda (2002) only addressed partial filial cannibalism in their model. Clearly, more investigations into the species-level effects of mate availability on filial cannibalism are needed to test the predictions of Kondoh and Okuda's (2002) model and verify the findings in a wider range of taxa. Experimental evolution with manipulations to mate availability should provide further insight into species-level effects. The challenge is to find a species that displays adequate levels of filial cannibalism and an appropriately short life cycle.

CONCLUSIONS

To date, all of the studies that have examined the effect of mate availability on filial cannibalism have been carried out on fish with exclusive paternal care. It is understandable why this bias in the literature exists, as fish with exclusive paternal care show relatively high levels of filial cannibalism, and because males are likely to experience greater variation in mate availability. Nonetheless, there is an obvious need for research on more varied study systems in regards to both phylogeny and life history. There are a number of invertebrate species that appear to show high enough levels of filial cannibalism to make studies feasible in species with maternal (e.g., maritime earwig, *Anisolabis maritime*; Miller and Zink 2012), paternal (e.g., assassin bug, *R. tristis*;

Thomas and Manica 2003), and biparental care (e.g., burying beetle, *Nicrophorus vespilloides*; Bartlett 1987). Furthermore, maternal (e.g., Egyptian mouthbrooder, *P. multicolor*; Mrowka 1987), biparental (e.g., convict cichlid, *Amatitlania nigrofasciata*; Lavery and Keenleyside 1990), and even noncaring (e.g., green razorfish, *Xyrichtys splendens*; Nemtzov and Clark 1994) fish species also offer opportunities to study filial cannibalism among species with more varied parental care systems. In addition to this, the significance of filial cannibalism in other vertebrate lineages requires greater attention. The consumption of offspring is increasingly being reported in birds (Parsons 1971; Bortolotti et al. 1991; Tortosa and Redondo 1992; Gilbert et al. 2005; Solaro and Sarasola 2012; Franke et al. 2013), and is also well documented in rodents and, to a lesser extent, other mammalian taxa (Day and Galef 1977; Bronson and Marsteller 1985; Braastad 1987; Cockburn 1994; but see Weber et al. 2013). In this respect, future studies involving a wider range of taxa will be important in providing robust tests of the existing interpretations of the relationships between mate availability and filial cannibalism.

The reduced cost of replacing young when many mates are available does seem to trigger elevated levels of filial cannibalism in some species (Okuda and Yanagisawa 1996b; Okuda et al. 2004; Myint et al. 2011a; Takeyama et al. 2013). However, in other species, there seems to be no effect of mate availability (Bjelvenmark and Forsgren 2003), or even a decrease in filial cannibalism in response to elevated mate availability (Pampoulie et al. 2004; Klug et al. 2005). To explain this, we suggest one or all of several alternative mechanisms may be involved. The first mechanism is that when the availability of mates is high, individuals are able to gain large numbers of young, or expect to do so. As a consequence of this, individuals may avoid committing total filial cannibalism, which is usually performed in response to having a small brood for which the cost of caring outweighs the reproductive gain. A second explanation for why some animals have an increased pro-

density for filial cannibalism when mate availability is low is that filial cannibalism may be used as a strategy by parents to facilitate their survival until times of higher mate availability. Finally, it could be that mate choice against individuals that have recently engaged in filial cannibalism encourages parents to avoid eating their own young when many potential mates are around as doing so could lead to large costs in lost mating opportunities. Future research testing the veracity of these mechanisms is needed.

One interesting emerging trend is that when a negative association between filial cannibalism and mate availability is reported, it involves total filial cannibalism (Pampoulie et al. 2004; Klug et al. 2005). Contrastingly, when a positive association is reported at the individual level, partial filial cannibalism is more often affected (Myint et al. 2011a; Takeyama et al. 2013). This pattern suggests that the aforementioned mechanisms, which drive reduced filial cannibalism when mate availability is high, may act more strongly on total filial cannibalism. Nonetheless, further research investigating how total and partial filial cannibalism are affected differently by mate availability is required.

Although researchers have focused largely on the role that physical access to additional mates plays in determining filial cannibalism, compelling areas for future studies involve investigating the role of parent attractiveness as well as the quality of potential future mates. Findings from studies that have measured attractiveness (or traits that confer it) suggest that attractive males commit the least filial cannibalism (Knapp and Kovach 1991; Forsgren 1997; Candolin 2000a,b; Takahashi and Kohda 2004; Lehtonen and Lindström 2007). Research

is needed to determine whether this is a consequence of females preferring males that are unlikely to commit filial cannibalism or whether attractive males avoid filial cannibalism as a consequence of increased access to mates. Similarly, future research should investigate whether parents take into account the quality of prospective mates when deciding to eat their young. Specifically, consideration should be given to the possibility that such behavior may represent parents attempting to trade up to higher quality mates or, alternatively, to avoid infanticide or offspring predation by potential mates.

Finally, it is important to distinguish the difference between the effect of mate availability at the level of the individual and at the level of the species. The former represents behavioral plasticity, which enables individual animals to alter their filial cannibalism levels according to their circumstances, and is not equivalent to the latter. The species-level effect describes macroevolutionary patterns where the evolution of the filial cannibalism rate of a species is influenced by availability of mates within that species. So far there have been very few studies investigating these phenomena and more are needed, especially because the species-level effect on partial filial cannibalism has not been empirically studied.

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REFERENCES

- Altmann S. A., Wagner S. S., Lenington S. 1977. Two models for the evolution of polygyny. *Behavioral Ecology and Sociobiology* 2:397–410.
- Bartlett J. 1987. Filial cannibalism in burying beetles. *Behavioral Ecology and Sociobiology* 21:179–183.
- Becker S. D., Hurst J. L. 2008. Pregnancy block from a female perspective. Pages 141–150 in *Chemical Signals in Vertebrates 11*, edited by J. L. Hurst, R. J. Beynon, S. C. Roberts, and T. D. Wyatt. New York: Springer.
- Beery A. K., Zucker I. 2012. Sex ratio adjustment by sex-specific maternal cannibalism in hamsters. *Physiology & Behavior* 107:271–276.
- Bjølvenmark J., Forsgren E. 2003. Effects of mate

- attraction and male-male competition on paternal care in a goby. *Behaviour* 140:55–69.
- Björk J. R., Kvamemo C. 2012. Mechanisms behind size-assortative nest choice by sand goby males in the absence of intrasexual competition. *Animal Behaviour* 83:55–62.
- Blumer L. S. 1979. Male parental care in the bony fishes. *Quarterly Review of Biology* 54:149–161.
- Bortolotti G. R., Wiebe K. L., Iko W. M. 1991. Cannibalism of nestling American kestrels by their parents and siblings. *Canadian Journal of Zoology* 69: 1447–1453.
- Braastad B. O. 1987. Abnormal behaviour in farmed silver fox vixens (*Vulpes vulpes* L.): tail-biting and infanticide. *Applied Animal Behaviour Science* 17: 376–377.
- Bronson F. H., Marsteller F. A. 1985. Effect of short-term food deprivation on reproduction in female mice. *Biology of Reproduction* 33:660–667.
- Bruce H. M. 1959. An exteroceptive block to pregnancy in the mouse. *Nature* 184:105.
- Candolin U. 2000a. Changes in expression and honesty of sexual signalling over the reproductive lifetime of sticklebacks. *Proceedings of the Royal Society B: Biological Sciences* 267:2425–2430.
- Candolin U. 2000b. Increased signalling effort when survival prospects decrease: male-male competition ensures honesty. *Animal Behaviour* 60:417–422.
- Carlisle T. R. 1985. Parental response to brood size in a cichlid fish. *Animal Behaviour* 33:234–238.
- Clutton-Brock T. H. 1991. *The Evolution of Parental Care*. Princeton (New Jersey): Princeton University Press.
- Clutton-Brock T. H., Parker G. A. 1992. Potential reproductive rates and the operation of sexual selection. *Quarterly Review of Biology* 67:437–456.
- Cockburn A. 1994. Adaptive sex allocation by brood reduction in antechinuses. *Behavioral Ecology and Sociobiology* 35:53–62.
- Coleman R. M., Gross M. R., Sargent R. C. 1985. Parental investment decision rules: a test in bluegill sunfish. *Behavioral Ecology and Sociobiology* 18:59–66.
- Creighton J. C. 2005. Population density, body size, and phenotypic plasticity of brood size in a burying beetle. *Behavioral Ecology* 16:1031–1036.
- Day C. S. D., Galef B. G., Jr. 1977. Pup cannibalism: one aspect of maternal behavior in golden hamsters. *Journal of Comparative and Physiological Psychology* 91:1179–1189.
- Emlen S. T., Oring L. W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215–223.
- FitzGerald G. J. 1992. Filial cannibalism in fishes: why do parents eat their offspring? *Trends in Ecology & Evolution* 7:7–10.
- FitzGerald G. J., van Havre N. 1987. The adaptive significance of cannibalism in sticklebacks (Gasterosteidae: Pisces). *Behavioral Ecology and Sociobiology* 20:125–128.
- Forsgren E. 1997. Female sand gobies prefer good fathers over dominant males. *Proceedings of the Royal Society B: Biological Sciences* 264:1283–1286.
- Forsgren E., Karlsson A., Kvamemo C. 1996. Female sand gobies gain direct benefits by choosing males with eggs in their nests. *Behavioral Ecology and Sociobiology* 39:91–96.
- Franke A., Galipeau P., Nikolaiczuk L. 2013. Brood reduction by infanticide in peregrine falcons. *Arctic* 66:226–229.
- Gibson R. M., Höglund J. 1992. Copying and sexual selection. *Trends in Ecology & Evolution* 7:229–232.
- Gilbert W. M., Nolan P. M., Stoehr A. M., Hil G. E. 2005. Filial cannibalism at a house finch nest. *Wilson Bulletin* 117:413–415.
- Goldschmidt T., Bakker T. C. M., Feuth-de Bruijn E. 1993. Selective copying in mate choice of female sticklebacks. *Animal Behaviour* 45:541–547.
- Gomagano D., Kohda M. 2008. Partial filial cannibalism enhances initial body condition and size in paternal care fish with strong male-male competition. *Annales Zoologici Fennici* 45:55–65.
- Hackländer K., Arnold W. 1999. Male-caused failure of female reproduction and its adaptive value in alpine marmots (*Marmota marmota*). *Behavioral Ecology* 10:592–597.
- Hastings P. A. 1992. Nest-site size as a short-term constraint on the reproductive success of paternal fishes. *Environmental Biology of Fishes* 34:213–218.
- Heske E. J., Nelson R. J. 1984. Pregnancy interruption in *Microtus ochrogaster*: laboratory artifact or field phenomenon? *Biology of Reproduction* 31:97–103.
- Hoelzer G. A. 1992. The ecology and evolution of partial-clutch cannibalism by paternal Cortez damselfish. *Oikos* 65:113–120.
- Hrdy S. B. 1974. Male-male competition and infanticide among the langurs (*Presbytis entellus*) of Abu, Rajasthan. *Folia Primatologica* 22:19–58.
- Huang W.-S. 2008. Predation risk of whole-clutch filial cannibalism in a tropical skink with maternal care. *Behavioral Ecology* 19:1069–1074.
- Jamieson I. 1995. Do female fish prefer to spawn in nests with eggs for reasons of mate choice copying or egg survival? *American Naturalist* 145:824–832.
- Klug H., Bonsall M. B. 2007. When to care for, abandon, or eat your offspring: the evolution of parental care and filial cannibalism. *American Naturalist* 170:886–901.
- Klug H., Lindström K. 2008. Hurry-up and hatch: selective filial cannibalism of slower developing eggs. *Biology Letters* 4:160–162.
- Klug H., Chin A., St. Mary C. M. 2005. The net effects of guarding on egg survivorship in the flagfish, *Jordanella floridae*. *Animal Behaviour* 69:661–668.

- Klug H., Lindström K., St. Mary C. M. 2006. Parents benefit from eating offspring: density-dependent egg survivorship compensates for filial cannibalism. *Evolution* 60:2087–2095.
- Knapp R. A., Kovach J. T. 1991. Courtship as an honest indicator of male parental quality in the bicolor damselfish, *Stegastes partitus*. *Behavioral Ecology* 2:295–300.
- Knapp R. A., Sargent R. C. 1989. Egg-mimicry as a mating strategy in the fantail darter, *Etheostoma flabellare*: females prefer males with eggs. *Behavioral Ecology and Sociobiology* 25:321–326.
- Kokko H., Monaghan P. 2001. Predicting the direction of sexual selection. *Ecology Letters* 4:159–165.
- Kondoh M., Okuda N. 2002. Mate availability influences filial cannibalism in fish with paternal care. *Animal Behaviour* 63:227–233.
- Kraak S. B. M. 1996. Female preference and filial cannibalism in *Aidablennius sphyinx* (Teleostei, Blenniidae); a combined field and laboratory study. *Behavioural Processes* 36:85–97.
- Kraak S. B. M., Groothuis T. G. G. 1994. Female preference for nests with eggs is based on the presence of the eggs themselves. *Behaviour* 131:189–206.
- Kraak S. B. M., Videler J. J. 1991. Mate choice in *Aidablennius sphyinx* (Teleostei, Blenniidae); females prefer nests containing more eggs. *Behaviour* 119:243–266.
- Kraak S. B. M., Weissing F. J. 1996. Female preference for nests with many eggs: a cost-benefit analysis of female choice in fish with paternal care. *Behavioral Ecology* 7:353–361.
- Kramer D. L. 1973. Parental behaviour in the blue gourami *Trichogaster trichopterus* (Pisces, Belontiidae) and its induction during exposure to varying numbers of conspecific eggs. *Behaviour* 47:14–32.
- Kume G., Yamaguchi A., Taniuchi T. 2000. Filial cannibalism in the paternal mouthbrooding cardinalfish *Apogon lineatus*: egg production by the female as the nutrition source for the mouthbrooding male. *Environmental Biology of fishes* 58:233–236.
- Kvarnemo C., Svensson O., Forsgren E. 1998. Parental behaviour in relation to food availability in the common goby. *Animal Behaviour* 56:1285–1290.
- Labov J. B. 1981. Pregnancy blocking in rodents: adaptive advantages for females. *American Naturalist* 118:361–371.
- Lavery R. J., Keenleyside M. H. A. 1990. Filial cannibalism in the biparental fish *Cichlasoma nigrofasciatum* (Pisces: Cichlidae) in response to early brood reductions. *Ethology* 86:326–338.
- Lehtonen T. K., Lindström K. 2007. Mate compatibility, parental allocation and fitness consequences of mate choice in the sand goby *Pomatoschistus minutus*. *Behavioral Ecology and Sociobiology* 61:1581–1588.
- Lindström K. 1998. Effects of costs and benefits of brood care on filial cannibalism in the sand goby. *Behavioral Ecology and Sociobiology* 42:101–106.
- Lindström K. 2000. The evolution of filial cannibalism and female mate choice strategies as resolutions to sexual conflict in fishes. *Evolution* 54:617–627.
- Lindström K., Kangas N. 1996. Egg presence, egg loss, and female mate preferences in the sand goby (*Pomatoschistus minutus*). *Behavioral Ecology* 7:213–217.
- Lindström K., Sargent R. C. 1997. Food access, brood size and filial cannibalism in the fantail darter, *Etheostoma flabellare*. *Behavioral Ecology and Sociobiology* 40:107–110.
- Lindström K., St. Mary C. M. 2008. Parental care and sexual selection. Pages 377–409 in *Fish Behaviour*, edited by C. Magnhagen, V. A. Braithwaite, E. Forsgren, and B. G. Kapoor. Enfield (New Hampshire): Science Publishers.
- Lissåker M., Kvarnemo C. 2006. Ventilation or nest defense—parental care trade-offs in a fish with male care. *Behavioral Ecology and Sociobiology* 60:864–873.
- Manica A. 2002a. Alternative strategies for a father with a small brood: mate, cannibalise or care. *Behavioral Ecology and Sociobiology* 51:319–323.
- Manica A. 2002b. Filial cannibalism in teleost fish. *Biological Reviews* 77:261–277.
- Manica A. 2004. Parental fish change their cannibalistic behaviour in response to the cost-to-benefit ratio of parental care. *Animal Behaviour* 67:1015–1021.
- Manica A. 2010. Female scissortail sergeants (Pisces: Pomacentridae) use test eggs to choose good fathers. *Animal Behaviour* 79:237–242.
- Marashi V., Rüllicke T. 2012. The Bruce effect in Norway rats. *Biology of Reproduction* 86:17, 1–5.
- Marconato A., Bisazza A. 1986. Males whose nests contain eggs are preferred by female *Cottus gobio* L. (Pisces, Cottidae). *Animal Behaviour* 34:1580–1582.
- Mehlis M., Bakker T. C. M., Frommen J. G. 2009. Nutritional benefits of filial cannibalism in three-spined sticklebacks (*Gasterosteus aculeatus*). *Naturwissenschaften* 96:399–403.
- Milinski M., Bakker T. C. M. 1992. Costs influence sequential mate choice in sticklebacks, *Gasterosteus aculeatus*. *Proceedings of the Royal Society B: Biological Sciences* 250:229–233.
- Miller J. S., Zink A. G. 2012. Parental care trade-offs and the role of filial cannibalism in the maritime earwig, *Anisolabis maritima*. *Animal Behaviour* 83:1387–1394.
- Mock D. W. 2004. *More than Kin and Less than Kind: The Evolution of Family Conflict*. Cambridge (Massachusetts): Belknap Press of Harvard University Press.
- Mock D. W., Forbes L. S. 1995. The evolution of parental optimism. *Trends in Ecology & Evolution* 10:130–134.
- Møller A. P., Jennions M. D. 2001. How important are

- direct fitness benefits of sexual selection? *Naturwissenschaften* 88:401–415.
- Moreno J. 2012. Parental infanticide in birds through early eviction from the nest: rare or under-reported? *Journal of Avian Biology* 43:43–49.
- Mori H., Chiba S. 2009. Sociality improves larval growth in the stag beetle *figulus binodulus* (Coleoptera: Lucanidae). *European Journal of Entomology* 106:379–383.
- Mrowka W. 1987. Filial cannibalism and reproductive success in the maternal mouthbrooding cichlid fish *Pseudocrenilabrus multicolor*. *Behavioral Ecology and Sociobiology* 21:257–265.
- Myint O., Takeyama T., Okuda N., Ohnishi N., Kohda M. 2011a. Mate availability facilitates cannibalistic behaviour in a nest brooding fish: effects of timing during the brood cycle. *Behaviour* 148:247–264.
- Myint O., Tsujimoto H., Ohnishi N., Takeyama T., Kohda M. 2011b. Mate availability affects female choice in a fish with paternal care: female counter-strategies against male filial cannibalism. *Journal of Ethology* 29:153–159.
- Nazareth T. M., Machado G. 2010. Mating system and exclusive postzygotic paternal care in a Neotropical harvestman (Arachnida: Opiliones). *Animal Behaviour* 79:547–554.
- Nemtsov S. C., Clark E. 1994. Intraspecific egg predation by male razorfishes (Labridae) during broadcast spawning: filial cannibalism or intra-pair parasitism? *Bulletin of Marine Science* 55:133–141.
- Okada S., Fukuda Y., Takahashi M. K. 2015. Paternal care behaviors of Japanese giant salamander *Andrias japonicus* in natural populations. *Journal of Ethology* 33:1–7.
- Okuda N. 1999a. Female mating strategy and male brood cannibalism in a sand-dwelling cardinalfish. *Animal Behaviour* 58:273–279.
- Okuda N. 1999b. Sex roles are not always reversed when the potential reproductive rate is higher in females. *American Naturalist* 153:540–548.
- Okuda N. 2000. Interspecific differences in male cannibalistic behavior between two sympatric cardinalfishes (Pisces: Apogonidae). *Journal of Ethology* 18:5–10.
- Okuda N., Yanagisawa Y. 1996a. Filial cannibalism by mouthbrooding males of the cardinal fish, *Apogon doederleini*, in relation to their physical condition. *Environmental Biology of Fishes* 45:397–404.
- Okuda N., Yanagisawa Y. 1996b. Filial cannibalism in a paternal mouthbrooding fish in relation to mate availability. *Animal Behaviour* 52:307–314.
- Okuda N., Takeyama T., Yanagisawa Y. 1997. Age-specific filial cannibalism in a paternal mouthbrooding fish. *Behavioral Ecology and Sociobiology* 41:363–369.
- Okuda N., Ito S., Iwao H. 2004. Mate availability and somatic condition affect filial cannibalism in a paternal brooding goby. *Behaviour* 141:279–296.
- Östlund-Nilsson S. 2002. Does paternity or paternal investment determine the level of paternal care and does female choice explain egg stealing in the fifteen-spined stickleback? *Behavioral Ecology* 13:188–192.
- Palombit R. A. 2015. Infanticide as sexual conflict: coevolution of male strategies and female counter-strategies. *Cold Spring Harbor Perspectives in Biology* 7:a017640.
- Pampoulie C., Lindström K., St. Mary C. M. 2004. Have your cake and eat it too: male sand gobies show more parental care in the presence of female partners. *Behavioral Ecology* 15:199–204.
- Parsons J. 1971. Cannibalism in herring gulls. *British Birds* 64:528–537.
- Payne A. G., Smith C., Campbell A. C. 2002. Filial cannibalism improves survival and development of beaugregory damselfish embryos. *Proceedings of the Royal Society B: Biological Sciences* 269:2095–2102.
- Payne A. G., Smith C., Campbell A. C. 2003. The effect of clutch size on whole clutch cannibalism in the beaugregory damselfish. *Journal of Fish Biology* 62:955–958.
- Payne A. G., Smith C., Campbell A. C. 2004. A model of oxygen-mediated filial cannibalism in fishes. *Ecological Modelling* 174:253–266.
- Petersen C. W. 1990. The occurrence and dynamics of clutch loss and filial cannibalism in two Caribbean damselfishes. *Journal of Experimental Marine Biology and Ecology* 135:117–133.
- Petersen C. W., Hess H. C. 1991. The adaptive significance of spawning synchronization in the Caribbean damselfish *Stegastes dorsopunicans* (Poey). *Journal of Experimental Marine Biology and Ecology* 151:155–167.
- Petersen C. W., Marchetti K. 1989. Filial cannibalism in the cortex damselfish *Stegastes rectifraenum*. *Evolution* 43:158–168.
- Pillay N., Kinahan A. A. 2009. Mating strategy predicts the occurrence of the Bruce effect in the vlei rat *Otomys irroratus*. *Behaviour* 146:139–151.
- Pomiankowski A. 1987. The costs of choice in sexual selection. *Journal of Theoretical Biology* 128:195–218.
- Raadik T. A., Bourke D. W., Clarke M. F., Martin A. A. 1990. Behaviour and reproductive success of pairs and lone parents in the convict cichlid *Heros nigrofasciatus*. *Animal Behaviour* 39:594–596.
- Real L. 1990. Search theory and mate choice. I. Models of single-sex discrimination. *American Naturalist* 136:376–405.
- Reynolds J. D., Jones J. C. 1999. Female preference for preferred males is reversed under low oxygen

- conditions in the common goby (*Pomatoschistus microps*). *Behavioral Ecology* 10:149–154.
- Ridley M., Rechten C. 1981. Female sticklebacks prefer to spawn with males whose nests contain eggs. *Behaviour* 76:152–161.
- Roberts E. K., Lu A., Bergman T. J., Beehner J. C. 2012. A Bruce effect in wild geladas. *Science* 335:1222–1225.
- Rohwer S. 1978. Parent cannibalism of offspring and egg raiding as a courtship strategy. *American Naturalist* 112:429–440.
- Sargent R. C. 1988. Paternal care and egg survival both increase with clutch size in the fathead minnow, *Pimephales promelas*. *Behavioral Ecology and Sociobiology* 23:33–37.
- Sargent R. C. 1992. Ecology of filial cannibalism in fish: theoretical perspectives. Pages 38–62 in *Cannibalism: Ecology and Evolution Among Diverse Taxa*, edited by M. A. Elgar and B. J. Crespi. Oxford (United Kingdom): Oxford University Press.
- Sargent R. C., Crowley P. H., Huang C., Lauer M., Neergaard D., Schmoetzer L. 1995. A dynamic program for male parental care in fishes: brood cycling and filial cannibalism. *Behaviour* 132:1059–1078.
- Schneider J. E., Wade G. N. 1989. Effects of maternal diet, body weight and body composition on infanticide in Syrian hamsters. *Physiology & Behavior* 46:815–821.
- Schwanck E. 1986. Filial cannibalism in *Tilapia mariae*. *Journal of Applied Ichthyology* 2:65–74.
- Sikkel P. C. 1988. Factors influencing spawning site choice by female garibaldi, *Hypsypops rubicundus* (Pisces, Pomacentridae). *Copeia* 1988:710–718.
- Slagsvold T., Dale S. 1991. Mate choice models: can cost of searching and cost of courtship explain mating patterns of female pied flycatchers? *Ornis Scandinavica* 22:319–326.
- Smith C., Wootton R. J. 1995. The costs of parental care in teleost fishes. *Reviews in Fish Biology and Fisheries* 5:7–22.
- Solaro C., Sarasola J. H. 2012. First observation of infanticide and cannibalism in nest of chimango caracara (*Milvago chimango*). *Journal of Raptor Research* 46:412–413.
- Takahashi D., Kohda M. 2004. Courtship in fast water currents by a male stream goby (*Rhinogobius brunneus*) communicates the parental quality honestly. *Behavioral Ecology and Sociobiology* 55:431–438.
- Takeyama T., Okuda N., Yanagisawa Y. 2002. Seasonal pattern of filial cannibalism by *Apogon doederleini* mouthbrooding males. *Journal of Fish Biology* 61:633–644.
- Takeyama T., Namizaki N., Kohda M. 2013. Mate availability accelerates male filial cannibalism in a nest brooding fish: effects of number and fecundity of females. *Behavioral Ecology and Sociobiology* 67:421–428.
- Thomas L. K., Manica A. 2003. Filial cannibalism in an assassin bug. *Animal Behaviour* 66:205–210.
- Thomas L. K., Manica A. 2005. Intrasexual competition and mate choice in assassin bugs with uniparental male and female care. *Animal Behaviour* 69:275–281.
- Tortosa F. S., Redondo T. 1992. Motives for parental infanticide in white storks *Ciconia ciconia*. *Ornis Scandinavica* 23:185–189.
- Trumbo S. T. 1990. Regulation of brood size in a burying beetle, *Nicrophorus tomentosus* (Silphidae). *Journal of Insect Behavior* 3:491–500.
- Unger L. M., Sargent R. C. 1988. Alloparental care in the fathead minnow, *Pimephales promelas*: females prefer males with eggs. *Behavioral Ecology and Sociobiology* 23:27–32.
- Weber E. M., Algers B., Hultgren J., Olsson I. A. S. 2013. Pup mortality in laboratory mice—infanticide or not? *Acta Veterinaria Scandinavica* 55:83.

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