

Parent–offspring cannibalism throughout the animal kingdom: a review of adaptive hypotheses

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ABSTRACT

Parents that kill and consume their offspring often appear to be acting against their own reproductive interests. Yet parent–offspring cannibalism is common and taxonomically widespread across the animal kingdom. In this review, I provide an overview of our current understanding of parent–offspring cannibalism, which has seen a proliferation in adaptive hypotheses over the past 20 years for why parents consume their own young. I review over four decades of research into this perplexing behaviour, drawing from work conducted on fishes, reptiles, insects, birds, and mammals among other taxa. Many factors have been hypothesised to explain parent–offspring cannibalism in nature, including poor parental energy reserves, small or large brood sizes, low or uncertain parentage, and high brood densities, and additional factors are still being uncovered. Parent–offspring cannibalism does not appear to have a single predominant explanation; rather, the factor, or set of factors, that govern its expression is largely taxon specific. Parents may either consume all offspring under their care (full-brood cannibalism) or consume a fraction of their offspring (partial brood cannibalism). These forms of cannibalism are thought to provide adaptive benefits to cannibals under a range of circumstances, primarily by allowing parents to allocate parental efforts more optimally – energy from eating (some of) one’s current offspring can be redirected to other offspring, or to parental growth, survival, and ultimately to other future reproductive endeavours. Thus, parent–offspring cannibalism is a phenotypically plastic trait that responds to changing environmental, social, and physiological conditions. The expression of parent–offspring cannibalism in any given system is intimately linked to the reproductive value of current young relative to parents’ expectations for future reproduction, and also to whether parental care is predominantly depreciable or non-depreciable. Furthermore, parent–offspring cannibalism has the potential to generate conflict between the sexes, and I briefly discuss some consequences of this conflict on patterns of mate choice. Finally, there still remain many aspects of this behaviour where our understanding is poor, and I highlight these topics to help guide future research.

Key words: filial cannibalism, kronism, infanticide, parental care, parental investment, sexual selection, reproductive strategy, mate choice, review.

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I. INTRODUCTION

Humans generally regard cannibalism as an ‘evil’ or a ‘reprehensible’ act. But, in nature, such views are meaningless because selection simply favours, and makes more prevalent, traits that improve mating and survival prospects. Irrespective of its human cultural notoriety, cannibalism is extremely common and taxonomically widespread in the animal kingdom (Fox, 1975; Polis, 1981; Smith & Reay, 1991; Elgar & Crespi, 1992; Soulsby, 2013). It is not difficult to envision how cannibalism could sometimes afford adaptive benefits, for example, by using conspecifics as a food source or by removing potential competitors. More puzzling, however, is the observation that parents of many species readily cannibalise offspring under their care (Klug & Bonsall, 2007). Parental care is a means for individuals to increase the survival and/or quality of their offspring (Clutton-Brock, 1991; Royle, Smiseth & Kolliker, 2012), which makes the killing and consumption of young by their parents surprising as it seemingly counteracts this goal. This apparent juxtaposition led early researchers to consider parent–offspring cannibalism to be a maladaptive behaviour or an abnormal laboratory artefact (e.g. Hauschka, 1952; Chardine & Morris, 1983). Yet over the past 40 years, parent–offspring cannibalism has been increasingly reported in a range of taxa including fishes [e.g. common goby, *Pomatoschistus microps* (Kvarnemo, Svensson & Forsgren, 1998); bluegill sunfish, *Lepomis macrochirus* (Neff, 2003)], amphibians (e.g. Japanese giant salamander, *Andrias japonicus*; Okada, Fukuda & Takahashi, 2015), reptiles (e.g. long-tailed skink, *Mabuya longicaudata*; Huang, 2008),

birds (e.g. peregrine falcon, *Falco peregrinus tundrius*; Franke, Galipeau & Nikolaiczuk, 2013), mammals (e.g. mouse, *Mus musculus*; Weber & Olsson, 2008), and insects [e.g. assassin bug, *Rhynocoris tristis* (Thomas & Manica, 2003); maritime earwig, *Anisolabis maritima* (Miller & Zink, 2012)]. Despite having been documented in numerous taxa, many aspects of our understanding of parent–offspring cannibalism are still in their infancy. The last major review was published approximately 20 years ago by Manica (2002) and focused only on fishes, and a more recent review by Deal & Wong (2016) focused only on one particular adaptive hypothesis for this behaviour.

The aim of this review is to provide a broad synthesis of research on parent–offspring cannibalism, specifically focusing on species that provide parental care. I begin by providing a brief conceptual and theoretical summary of parent–offspring cannibalism. I then present an overview of the adaptive hypotheses that have been investigated or proposed to date. Next, I briefly review how individuals choose among potential mating partners when those partners could be offspring cannibals. Finally, I pinpoint areas where research is currently lacking to provide a guide for future research to understand parent–offspring cannibalism more comprehensively.

II. CONCEPTS AND THEORY

For the purposes of this review, I consider parent–offspring cannibalism to be the consumption of offspring by an

individual that is simultaneously the offspring's caregiver. Parent–offspring cannibalism can therefore be thought of as part of a parent's broader reproductive strategy, yielding the parent adaptive benefits under certain scenarios. I begin by describing the concept of energetic reinvestment and how such reinvestments allow parents to respond adaptively to changing conditions. I then provide an overview of previous theoretical models that have been employed to explore adaptive hypotheses and evolutionary drivers of parent–offspring cannibalism.

(1) Energetic reinvestments

Parent–offspring cannibalism can be viewed as a phenotypically plastic trait, where parents modulate its expression in response to changing ecological, social, and physiological conditions (Manica, 2002; Deal & Wong, 2016). In a sense, parent–offspring cannibalism is a special case of infanticide, with the notable difference being that while both infanticide and parent–offspring cannibalism save parents energy because fewer offspring subsequently require care, consuming young after they are killed yields additional caloric benefits to the killer. These energetic benefits can be reinvested in various ways to affect the parent's current or future reproductive prospects. How much energetic benefit parents receive from offspring cannibalism depends crucially on whether they primarily provide depreciable or non-depreciable care (Hoelzer, 1995). In depreciable care, the expenditures made by parents cannot be shared among offspring (Clutton-Brock, 1991; e.g. offspring provisioning or offspring grooming). This means that larger broods are more costly to rear, as additional offspring require parents to expend more effort caring. Non-depreciable care on the other hand benefits all offspring in the brood simultaneously, and thus costs do not scale with brood size (e.g. nest or brood defence). This makes large broods more profitable for parents to rear than small broods. If parents provide depreciable care, then the energetic benefits that offspring cannibalism provides can be divided into direct *energy gains* from the consumption itself and indirect *energy savings* from the reduced parental effort needed to raise the remainder of the brood, if any (Hoelzer, 1995). However, if parents provide non-depreciable care, then they can still receive energy gains from offspring consumption, but cannibalism will provide fewer energy savings; in this case parents must either terminate all their current offspring or just their slowest developing ones to shorten the overall time that they spend providing care in order to accrue energy savings (Klug & Lindström, 2008). The energetic benefits (i.e. gains and savings) from offspring cannibalism can then be reinvested elsewhere, and here, two types of parent–offspring cannibalism are recognised. Parents may commit full-brood cannibalism, whereby they consume all the offspring under their care and this can be considered an investment into future reproductive opportunities. Or parents may commit partial brood cannibalism, in which only a fraction of the offspring are eaten and this can be considered an investment into either future

reproduction or into the continued care for the remaining young (FitzGerald, 1992; Sargent, 1992; Hoelzer, 1995; Manica, 2002). Here, I use the term 'brood' to refer to all offspring currently under the care of a parent (sometimes synonymous with 'clutch' or 'litter' depending on taxon).

Whether the optimal parental response is to cannibalise a brood completely, partially, or not at all should depend on the net effects of *per offspring* cannibalism on two fitness components (*sensu* Williams, 1966): (i) the value of the current reproductive attempt; and (ii) the parent's residual reproductive value. A parent can improve the value of the current reproductive attempt by sacrificing some offspring to increase the survival and/or quality of other offspring in the brood. A parent can also improve their own residual reproductive value by investing the energetic benefits they receive from cannibalism into parental survival, somatic growth, or alternative mate attraction (Hoelzer, 1995; Manica, 2002). With each offspring consumed, the net effect of these two fitness components is altered. Thus, for some parents, full-brood cannibalism may be the optimal choice that maximises the sum of these two components, while for other parents it might be partial brood cannibalism, or no cannibalism at all. Parent–offspring cannibalism is therefore thought to provide adaptive benefits under certain circumstances, in part by permitting individuals to allocate their parental efforts more optimally *via* energetic reinvestment.

(2) Theoretical models

Theoretical models have yielded important insights into the adaptive potential of parent–offspring cannibalism. In general, two types of modelling approaches have been used. First, there are models that treat cannibalism as a phenotypically plastic trait and ask whether it can be adaptive under different environmental or physical conditions. These models investigate the utility of cannibalism across behavioural timescales. Rohwer (1978) was the first to suggest an adaptive model for parent–offspring cannibalism and used it to explain mating patterns seen in three-spined sticklebacks, *Gasterosteus aculeatus*. Rohwer's (1978) verbal model inspired several early mathematical models (e.g. Sargent, 1992; Sargent *et al.*, 1995). Together, this work predicted that parents should be more likely to (i) cannibalise young offspring; (ii) cannibalise when their parental energy reserves are low; (iii) fully cannibalise broods that are small; and (iv) partially cannibalise broods that are large. The rationale behind these predictions was that (i) older offspring require less further parental investment to rear to independence and therefore have higher value than younger offspring (Dawkins & Carlisle, 1976); (ii) parental care often restricts foraging opportunities for caregivers (Clutton-Brock, 1991; Zięba *et al.*, 2018), and low parental energy reserves can threaten the survival of offspring and parent alike (Smith & Wootton, 1995; Alonso-Alvarez & Velando, 2012); (iii) smaller broods yield lower fitness benefits than larger broods (Manica, 2002), primarily when parental care is non-depreciable (see Section II.1); and (iv) the *per offspring* costs of

consuming young from a large brood are lower than doing so from a small brood (see Section III.2). Since then, several other models have highlighted the putatively adaptive role of parent–offspring cannibalism for individuals in conditions of high mate availability (Kondoh & Okuda, 2002; see Section III.4) or when offspring mortality is exacerbated by high offspring densities (Payne, Smith & Campbell, 2004; see Section III.5).

The second type of modelling approach entails (co)evolutionary models that have been inspired by observations of offspring cannibalism and parental care co-occurring in the wild. Unlike the previous models, these models focus on cannibalism over evolutionary timescales. They examine which factors promote the evolution of parent–offspring cannibalism and whether cannibalism can facilitate the evolution and maintenance of parental care. For example, Klug & Bonsall (2007) showed that rare mutants expressing both parental care and filial cannibalism (i.e. the cannibalism of their own genetic offspring) can sometimes invade a resident population that provides care but does not cannibalise. Specifically, invasion success occurred when cannibalism was associated with energetic benefits, when parents could selectively consume low-quality offspring, when cannibalism increased the maturation rate of the remaining offspring, and when cannibalism increased the parent's reproductive rates (Klug & Bonsall, 2007). Klug & Bonsall (2019)'s model also showed how the energetic benefits of filial cannibalism can allow parental care and cannibalism to evolve and persist together across a wider range of life-history parameters than care in the absence of filial cannibalism. In a similar vein, Davenport, Bonsall & Klug (2019) presented a model that came to a similar conclusion, especially when offspring cannibalism not only provided energetic benefits, but also alleviated density-dependent offspring mortality. Taken together, both modelling approaches have been instrumental in testing or generating predictions for which factors are likely to unlock the adaptive potential of parent–offspring cannibalism.

III. ADAPTIVE HYPOTHESES

The theory discussed above has guided much empirical research on a variety of ecological, social, and physiological factors hypothesised to affect parent–offspring cannibalism (Table 1), and I review each of these hypotheses below. However, I first broadly explore the relevant literature to identify which taxonomic classes of organisms and which adaptive hypotheses have been given the most research attention. I performed a search of the *Web of Science* Core Collection using the query (cannibal*) AND (filial OR parent* OR maternal OR paternal OR egg* OR offspring* OR young* OR litter* OR brood* OR pup* OR nestl* OR chick* OR hatchl* OR *infant* OR embryo OR juvenile* or larva*) in the 'TS' field, which searches all titles, abstracts, and key words. This search yielded 4055 articles of which 200 were deemed relevant (see online Supporting Information, Appendix S1, for

details of article-screening steps and inclusion/exclusion criteria). Overall, the vast majority of empirical research conducted to date has focused on fishes (Fig. 1) and certain hypotheses have received far more attention than others (Fig. 2). Clearly, greater representation across taxonomic boundaries and hypotheses will be beneficial for clarifying the broader patterns of parent–offspring cannibalism throughout the animal kingdom. From the available data, no single factor can be associated with parent–offspring cannibalism across all species (Table 1). Rather, different factors, or combinations of factors, likely operate in different systems to modulate parent–offspring cannibalism (Table 1).

(1) Parental energy reserves hypotheses

Parental care can be an energetically demanding task that reduces a parent's ability to produce future offspring (Williams, 1966; Trivers, 1972; Clutton-Brock, 1991; Alonso-Alvarez & Velando, 2012). These energetic costs can come from elevated metabolic demand during parental care and/or reductions in foraging opportunities (Clutton-Brock, 1991; Smith & Wootton, 1995; Zięba *et al.*, 2018). It is not uncommon for parental body condition to deteriorate across care periods to the point where parental survival is compromised. For example, in the plainfin midshipman fish, *Porichthys notatus*, parental males care for eggs and embryos for up to 3 months during which time they feed only on the limited prey items found within their nests (Cogliati *et al.*, 2015). Over this period, the males' endogenous energy reserves diminish to the extent that near the end of the care period they rely on muscle protein catabolism for energy production (Bose, McClelland & Balshine, 2015). One well-studied hypothesis for why parents cannibalise offspring is that offspring can represent a food source when alternative sources are unavailable or insufficient (Rohwer, 1978; Sargent, 1992), with the prediction that parents with lower energy reserves are more likely to cannibalise offspring, both for full-brood and partial brood cannibalism (Rohwer, 1978; Sargent, 1992; Sargent *et al.*, 1995; Manica, 2002).

Relative to parents in good condition, parents in poor condition can experience higher costs of care while tending a brood (Alonso-Alvarez & Velando, 2012). Parents with low energy reserves will therefore sometimes encounter cost–benefit ratios where their best option is to cannibalise the brood completely. In these cases, they should cannibalise as early as possible to avoid investment into offspring that will eventually be killed (Manica, 2002). However, when the best option is to partially cannibalise a brood, it is not always obvious when parents should do so, nor how many offspring to eat. Here, the energy reserves hypothesis can be rephrased in three subtly different ways (Fig. 3). First, a parent may cannibalise some of their offspring when their energy reserves become so depleted that they cannot otherwise finish caring for their brood, or when their energy reserves need supplementing to ensure their survival and success in subsequent breeding attempts. This can be seen as a 'last-resort' form of energy recoupment *via* partial brood cannibalism (Form

Table 1. Overview of adaptive hypotheses for parent–offspring cannibalism and their predictions. Parents can make offspring cannibalism decisions based on general sources of information and either consume all offspring in their brood (full-brood cannibalism, FBC), or consume only a portion of their brood (partial brood cannibalism, PBC). In these cases, the cannibalism of offspring is assumed to be indiscriminate. However, parents can also make cannibalism decisions based on offspring-specific information. Here, offspring that express specific features or phenotypes can be selectively consumed. Therefore, each hypothesis can have a general prediction and/or a narrower prediction based on offspring-specific cues (dashes indicate when there is no corresponding prediction). Note that these hypotheses are not mutually exclusive.

Adaptive hypothesis	Description	General prediction	Prediction for offspring-specific cannibalism	Example publications
Parental energy reserves	Parents use cannibalism to manage their onboard energy reserves	Low energy reserves: ↑ FBC and PBC	—	Rohwer (1978); Sargent (1992); Sargent <i>et al.</i> (1995); Manica (2002)
Brood size	Small broods may not be worth the parental effort to raise them. Individual offspring from large broods are less costly to consume	Small brood size: ↑ FBC Large brood size: ↑ PBC	—	Rohwer (1978); Sargent (1992); Sargent <i>et al.</i> (1995); Manica (2002)
Brood parentage	Broods containing non-kin offspring may not be worth the parental effort to raise them. Consuming non-kin offspring incurs fewer inclusive fitness costs	Low/uncertain parentage: ↑ FBC and PBC	Non-kin offspring should be selectively consumed based on perceived parentage cues	Neff & Sherman (2002); Neff (2003); Manica (2004)
Mate availability	Costs of cannibalism are lower when offspring can be replaced quickly and efficiently	High re-mating probability: ↑ FBC and PBC	—	Okuda & Yanagisawa (1996b); Kondoh & Okuda (2002); but see Deal & Wong (2016)
Brood density	Cannibalism is used to reduce offspring overcrowding	High offspring density: ↑ FBC and PBC	—	Payne, Smith & Campbell (2002); Klug, Lindström & St Mary (2006)
Brood survival prospects	Cannibalism is used to remove offspring with low odds of survival	Low survival probability: ↑ FBC and PBC	Weakest offspring should be selectively consumed	Forbes & Mock (1998); Huang (2008); Chin-Baarstad, Klug & Lindström (2009)
Non-viable offspring and brood hygiene	Consuming dead offspring incurs no inclusive fitness costs. Cannibalism is used to remove offspring that are likely to spread disease in a brood	Presence of non-viable (dead) offspring: ↑ FBC and PBC	Dead or diseased offspring should be selectively consumed	Kraak (1996); Lehtonen & Kvarnemo (2015a, b); Okada <i>et al.</i> (2015)
Offspring age	Younger offspring have lower reproductive value than older offspring	Old offspring (relative to young offspring): ↓ FBC and PBC	Youngest offspring should be selectively consumed	Sargent (1992); Manica (2002); Vallon & Heubel (2016)
Parental stress	Cannibalism is a result of parental stress	Parental stress: ↑ FBC and PBC	—	Burn & Mason (2008); Butler & Maruska (2021)
Brood sex ratio	Cannibalism is used to manipulate offspring sex ratios	—	Offspring of less-valuable sex should be selectively consumed	Beery & Zucker (2012)
Parental micronutrients	Cannibalism is used to obtain essential micronutrients (e.g. carotenoids)	Low parental micronutrients: ↑ FBC and PBC	Offspring yielding greater amounts of required micronutrients should be selectively consumed	Pike <i>et al.</i> (2007)
Parental care duration	Cannibalism of certain offspring shortens parental care period and allows parents to re-enter the mating pool sooner	—	Offspring that are slowest developing should be selectively consumed	Klug & Lindström (2008)
Parasitic infections	Cannibalism is a result of parasites	Parental parasite load: ↑ FBC and PBC	—	Stott & Pulin (1996); Sasal (2006)

1, Fig. 3). Here, parental behaviour is expected to be governed primarily by current energetic status, e.g. glycogen, lipid, or protein reserves. Second, parents may cannibalise because their endogenous fuel reserves will become insufficient in the future to complete the ongoing bout of care or to succeed in subsequent breeding attempts. In this case, parents could cannibalise earlier in the care period relative to

parents that wait until their reserves are critically low. This can be seen as a ‘pre-emptive’ form of energy recoupment *via* partial brood cannibalism (Form 2, Fig. 3). Cannibalising earlier in the care bout could be beneficial as younger eggs are potentially more nutritious due to changes in lipid and protein composition across development (FitzGerald, 1991; Manica, 2002). Thus, parents may need to consume fewer offspring overall under Form 2 compared to Form 1. Under Form 2, parental behaviour is expected to be governed both by current energetic status and by parental expectations of future energetic costs. A third form of the energy reserves hypothesis is that parents may cannibalise regularly to maintain their reserves at a stable level. This would lead to a more constant rate of cannibalism across the care period (Form 3, Fig. 3).

In all three forms of this hypothesis, parents should ensure that they end their care period with sufficient reserves to survive until and succeed in any future breeding attempts. Each form also makes the same general prediction: parental caregivers in worse condition should be more cannibalistic. The important differences among the three forms lie in parents’ abilities to predict their future care costs reliably. Therefore, cannibalism following Form 1 would be expected to occur more often in stochastic or unpredictable environments, with parents cannibalising only when their energy reserves are nearly depleted. This strategy would allow some parents to benefit from chance periods of favourable conditions during which their energy reserves are diminished less. Importantly, Form 1 is not expected to occur in systems where parents must maintain high reserves across the entire care period, for example if they must continuously defend their nest or territory from takeover attempts. Cannibalism following Form 2 would be expected to occur in stable or predictable

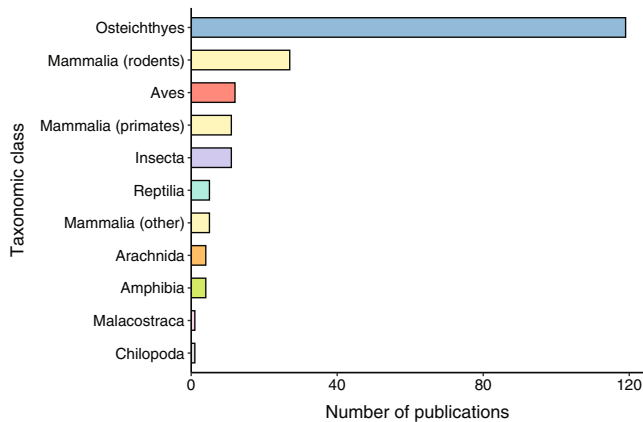


Fig. 1. Taxonomic representation within the primary empirical literature examining parent–offspring cannibalism. Osteichthyes (bony fishes) constitute by far the most studied group of organisms to date. The literature on mammals is dominated by studies on rodents held in artificial laboratory conditions. There are multiple reports of parent–offspring cannibalism in birds and primates, but these reports tend to be case studies that focus on only one or a few cannibalism observations each. Only a limited number of arthropod studies are available to date.

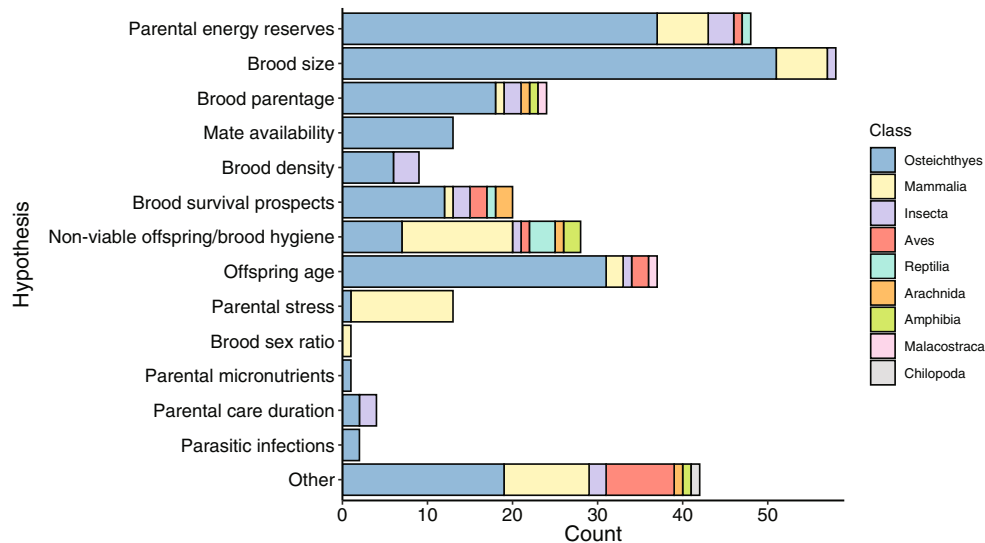


Fig. 2. Parent–offspring cannibalism hypotheses that have been investigated in the primary empirical literature. The x-axis shows the number of publications containing data that relate to each hypothesis, broken down by major taxonomic class. Note that some publications address more than one hypothesis. The category ‘Other’ indicates studies where other hypotheses were investigated or where no particular hypothesis was tested.

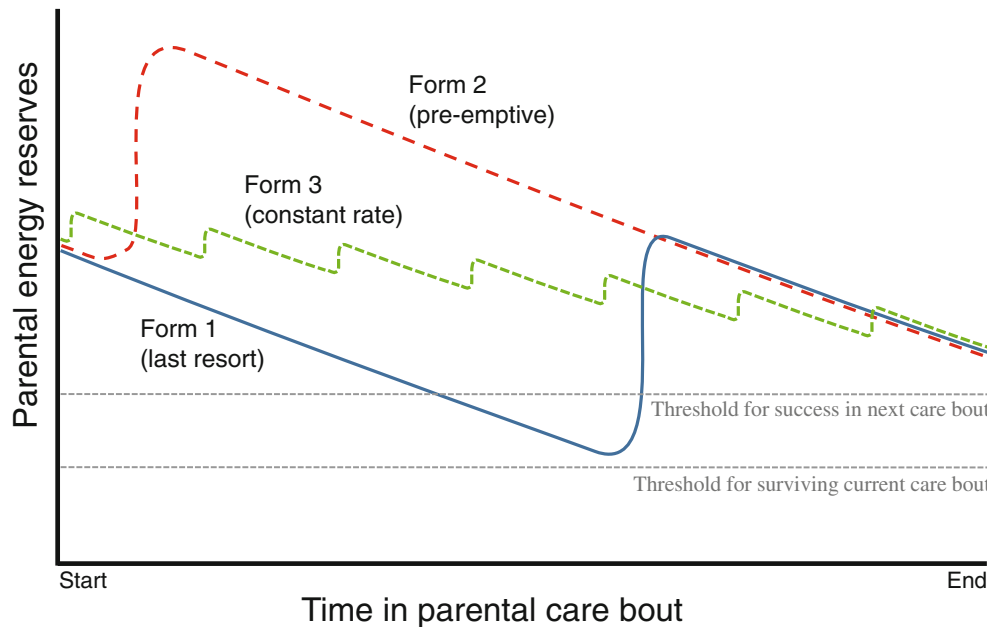


Fig. 3. Graphical illustration of three forms of the energy reserves hypothesis for partial brood cannibalism. Each line represents a different (identical) parent caring for a brood of offspring. Under Form 1 (blue solid line), the parent waits until their energy reserves are extremely low before cannibalising heavily, denoted by the tall spike in parental energy reserves. Under Form 2 (red dashed line), the parent cannibalises heavily and pre-emptively before their energy reserves are low. Under Form 3 (green dotted line), the parent cannibalises more frequently across the care bout, but consumes fewer offspring per meal. In all three forms, parental energy reserves are assumed to decrease over the parental care bout and end at levels that exceed thresholds for survival and success in the next care bout (e.g. a subsequent breeding season). All parents start and end care with the same energy reserves.

environments, where parents can accurately gauge the optimal level of cannibalism needed to bring their care bout to fruition. Cannibalism following Form 3 may be expected in environments of intermediate predictability, where parents can engage in small amounts of cannibalism to capitalise on prior information, but then make updated decisions as care progresses. Form 3 might also be expected when care durations are particularly long relative to parents' starvation tolerance, such that more periodic meals are needed. It is also conceivable that parents adopt Form 1 at first, but then transition to Form 3 to maintain their reserves until the end of their care bout.

In general, the empirical and theoretical research on partial brood cannibalism to date has not clearly differentiated among these three forms of the energy reserves hypothesis. Among fishes, it is not uncommon for studies to uncover temporal patterns in parent–offspring cannibalism, with offspring in some taxa being consumed early in the care period or breeding season (e.g. male Cortez damselfish, *Stegastes rectifraenum*; Hoelzer, 1988) and others being consumed later (e.g. mouthbrooding male cardinalfish, *Apogon doederleini*; Okuda & Yanagisawa, 1996a). Whether these temporal patterns relate to different forms of the energy reserves hypothesis or to variation in other environmental conditions would be a fruitful area for future research.

The general predictions that parents should be more cannibalistic when in poorer condition or with limited access to food have been studied in a range of different taxa, yielding

support in some systems but with a notable absence of support in others. In general, researchers have either correlated a parent's propensity to cannibalise against their body condition or food availability, or the researchers have experimentally manipulated parental access to food resources and monitored for differences in offspring cannibalism. Among fishes, some correlational studies have uncovered the predicted negative relationship between cannibalism and body condition or food availability [e.g. male river bullhead, *Cottus gobio* (Marconato *et al.*, 1993); mouthbrooding male cardinalfish (Okuda & Yanagisawa, 1996a); male bluegill sunfish (Neff, 2003)], and some diet-manipulation experiments have also shown that parents with access to less food cannibalise more [e.g. male Cortez damselfish (Hoelzer, 1992); male Mediterranean blenny, *Aidablennius sphynx* (Kraak, 1996); male common goby (Kvarnemo *et al.*, 1998); male scissortail sergeant, *Abudefduf sexfasciatus* (Manica, 2004); male freshwater goby, *Rhinogobius* sp. (Okuda, Ito & Iwao, 2004)]. In rodents, food deprivation during early lactation can lead mothers to consume more of their young [e.g. mice (Bronson & Marsteller, 1985); Syrian hamsters, *Mesocricetus auratus* (Schneider & Wade, 1989)]. And in reptiles such as the southern grass skink, *Pseudemoia entrecasteauxii*, pregnant mothers experiencing food shortages are more likely to abort and cannibalise their offspring (Van Dyke, Griffith & Thompson, 2014). Parents of some species have also been suggested to use cannibalism to maintain their body condition across the care period [e.g. male assassin bugs

(Thomas & Manica, 2003); male three-spined stickleback (Mehlis, Bakker & Frommen, 2009)], or even to increase their body condition (long-snout clingfish, *Diademichthys lineatus*; Gomagano & Kohda, 2008). Parallels can even be drawn with social insects such as honeybees, *Apis mellifera carnica*, and paper wasps, *Polistes chinensis antennalis*, as food deprivation can lead to the cannibalism of larvae by nurse bees (Schmickl & Crailsheim, 2001) or by colony foundresses (Kudô & Shirai, 2012).

Some correlational studies have found inconclusive or even opposing evidence for the energy reserves hypothesis [e.g. male sand goby, *Pomatoschistus minutus* (Klug *et al.*, 2006); male plainfin midshipman fish (Bose *et al.*, 2015); male Lusitanian toadfish, *Halobatrachus didactylus* (Félix *et al.*, 2016)], and some experimental diet manipulations have also failed to influence parent–offspring cannibalism [e.g. male three-spined stickleback (Belles-Isles & Fitzgerald, 1991); male fantail darter, *Eltheostoma flabellare* (Lindström & Sargent, 1997); male sand goby (Kvarnemo, 1997); male beaugregory damselfish, *Stegastes leucostictus* (Payne *et al.*, 2002)]. Matsumoto *et al.* (2018) conducted egg-removal experiments with an intertidal blenny, *Rhabdoblennius midius*, and found that full-brood cannibalism was unrelated to the cannibal male's body condition. Interestingly, Klug & St Mary (2005) even found that in flagfish, *Jordanella floridae*, male parents subjected to a restricted diet actually cannibalised *less* than males given a supplemented diet. Taken together, the above results imply that the management of parental energy reserves is a prominent explanation for parent–offspring cannibalism, but many study systems also appear to engage in offspring cannibalism for other reasons.

A salient pattern that has emerged from investigations into the energy reserves hypothesis is the focus on within-species studies. Therefore, a natural avenue for future research would be to conduct cross-species comparisons, either *via* direct empirical studies or synthesis approaches (e.g. phylogenetically controlled comparative analyses, meta-analyses). Such studies could search for factors, or combinations of factors, that are consistently associated with parent–offspring cannibalism within and across phylogenetic clades. A useful starting point would be to compare capital breeders and income breeders (Jönsson, 1997), which represent ends of a prominent life-history continuum. Species at one end of the continuum fuel their reproductive bouts using existing energy reserves (capital breeders), while species at the other end rely on immediately accessible food sources (income breeders). A particularly striking example of capital breeders are mouthbrooding fishes, such as *A. doederleini* (Okuda & Yanagisawa, 1996a,b), where parents hold offspring within their buccal cavities for the duration of care and are therefore severely limited in their ability to forage. Relative to income breeders, capital breeders may be less likely to cannibalise for energetic reasons due to their greater starvation tolerances. Alternatively, capital breeders may be more likely to cannibalise for energetic reasons due to the foraging limitations that they typically endure during care – foraging limitations which co selected for their capital

breeding strategy in the first place. Relative to income breeders, however, capital breeders should be less likely to cannibalise offspring in response to short-term fluctuations in local food abundance because of their reliance on stored energy.

(2) Brood size hypotheses

In many species brood size is not fixed and the number of offspring that a parent cares for can vary from individual to individual and across reproductive bouts. This has generated a considerable amount of research into the relationship between parent–offspring cannibalism and brood size. In particular, two hypotheses have been evaluated. First, small broods may not be worth the parental effort needed to rear them – a situation that is more likely to arise in systems with predominantly non-depreciable care (Rohwer, 1978; Sargent, 1992; Sargent *et al.*, 1995; Manica, 2002). Parents are therefore predicted to use full-brood cannibalism to terminate small broods, allowing them to re-enter the mating pool and to reallocate resources to future larger broods. Second, larger brood sizes necessarily imply that each offspring constitutes a smaller proportion of the parent's lifetime reproductive success, which reduces the *per offspring* cost of consuming them. All else being equal, partial brood cannibalism is therefore predicted to increase with brood size (Sargent, 1992; Sargent *et al.*, 1995; Manica, 2002). However, as we will see below, while the empirical relationships between brood size and full-brood cannibalism are rather clear, the patterns with respect to partial brood cannibalism are far less so.

The vast majority of parent–offspring cannibalism research to date has focused on paternal caregiving fishes, which tend to display tremendous variation in brood size and provide non-depreciable care for their offspring (Perrone & Zaret, 1979). The termination of small broods *via* full-brood cannibalism has also been observed consistently across studies with fish [e.g. male *Tilapia mariae* (Schwanck, 1986); male and female convict cichlids, *Cichlasoma nigrofasciatum* (Lavery & Keenleyside, 1990); male common goby (Kvarnemo *et al.*, 1998; Vallon *et al.*, 2016b); male bluegill sunfish (Neff, 2003); male stream goby, *Rhinogobius* spp. (Ito *et al.*, 2016); male sand goby (Deal *et al.*, 2017); male and female *Neolamprologus caudopunctatus* (Cunha-Saraiva *et al.*, 2018)]. Of note here is the prevalence of species that engage in brood cycling; that is, parents alternate between periods of courtship and periods of parental care (Van Jersel, 1953; Matsumoto *et al.*, 2012). In brood cyclers, the termination of small broods can allow parents to abandon care and re-enter the courtship phase to potentially acquire or produce a more profitable brood sooner. By contrast, non-brood cyclers often have longer care periods, and may spend their entire breeding season caring for a single brood or multiple overlapping broods. Critically, non-brood cyclers can also court and mate multiple times even after initiating care, increasing the size of their brood with each mating. Thus, non-brood-cycling parents do not need to eliminate existing offspring to mate again. For example, parental males

of the plainfin midshipman fish care for broods consisting of overlapping age cohorts of offspring that each take ~60 days to reach independence (Bose *et al.*, 2018). Their breeding season, however, lasts ~90 days, precluding males from raising separate non-overlapping broods. Consistently, plainfin midshipman males cannibalise partially, never fully, from their broods, allowing eggs from multiple females to accumulate in their nests throughout the season (Bose *et al.*, 2014). Fewer studies exist on parent–offspring cannibalism in non-brood cyclers (but see Hoelzer, 1988; Kraak, 1996; Payne, Smith & Campbell, 2003; Klug, Chin & St Mary, 2005), and so this is an area where additional empirical research would be valuable. Although not yet explicitly studied, full-brood cannibalism might still occur in non-brood cyclers, for example if polygynous male caregivers cannibalise very early in the season when their broods are still so small that even a little cannibalism would remove the brood; however, in this case selection for female counterstrategies would also be expected to be high. Alternatively, full-brood cannibalism in a non-brood cycler might be used to forgo reproduction entirely or to cut a parental care period short to invest in survival until the next breeding season.

Unlike full-brood cannibalism, partial brood cannibalism does not show a consistent pattern in relation to brood size. In fact, the most prevalent finding in fishes so far is a lack of a significant relationship between brood size and the quantity of offspring consumed [e.g. male fantail darters (Lindström & Sargent, 1997); male scissortail sergeant (Manica, 2003); male bluegill sunfish (Neff, 2003); male Lusitanian toadfish (Félix *et al.*, 2016); male plainfin midshipman fish (Bose *et al.*, 2019)]. Work with the common goby and sand goby has yielded particularly mixed results, with some studies detecting no relationship between brood size and partial cannibalism (Kvarnemo *et al.*, 1998; Lissåker, Kvarnemo & Svensson, 2003), while others report the predicted pattern of elevated partial cannibalism from larger broods (Pampoulic, Lindström & St. Mary, 2004), and yet others have found that parents even reduce partial cannibalism when caring for a large brood (Forsgren, Karlsson & Kvarnemo, 1996; Svensson *et al.*, 1998). Ito & Yanagisawa (2000) and Okuda *et al.* (2004) provide some evidence in favour of a positive relationship between brood size and partial brood cannibalism by males in a stream goby, *Rhinogobius* sp.; in assassin bugs, *Rhinocoris tristis*, male parents cannibalise more eggs from larger broods (Thomas & Manica, 2003).

Clearly, only a fraction of the empirical data support the theoretical prediction of increased partial brood cannibalism from larger broods. There are several potential reasons for this. First, for the sacrifice of offspring to be adaptive, the young that are eaten must be translated into at least as many offspring equivalents in terms of future reproduction. This will be easier to achieve when the cannibal not only receives the energy gain from offspring consumption, but also the energy savings from avoiding their care. This latter benefit is primarily associated with depreciable care, whereas most studies to date have been conducted on fishes with

predominantly non-depreciable, male care (Smith & Wootton, 1995). For example, in golden hamsters and mice, where care is depreciable, mothers cannibalise more from large litters than from small litters, likely to match the resulting number of pups to the prevailing environmental conditions and to their own energetic status (Day & Galef, 1977; Hood, 2012). Therefore, the relationship between partial cannibalism and brood size should be stronger in systems with depreciable care than non-depreciable care. A second reason is that parents are expected to receive diminishing marginal returns from consuming greater numbers of offspring. Therefore, at very large brood sizes, it may no longer pay parents to consume proportionately larger numbers of young (Manica, 2002). Third, when parents are faced with a large brood, they may increase their effort into non-depreciable forms of care (Clutton-Brock, 1991; Klug, Alonzo & Bonsall, 2012). This is because as brood size increases the benefits of non-depreciable care become higher per unit of parental expenditure (as the care is received by more offspring overall). Partial cannibalism would reduce these benefits. Fourth, while consuming individual offspring from large broods may seem less costly in terms of the proportion of lifetime offspring that are lost, these offspring may also contribute fewer caloric benefits if there is a life-history trade-off between offspring number and offspring size (Smith & Fretwell, 1974; Fischer, Taborsky & Kokko, 2011). Lastly, the prediction of increased partial cannibalism from larger broods, particularly by male caregivers, was originally generated without considering co-evolutionary implications with female choice. That is, if larger broods are indeed more susceptible to partial cannibalism, then this may select for females to *avoid* contributing to already-large broods. Therefore, moving forward, it would be valuable for the theory behind the relationship between partial brood cannibalism and brood size to be reassessed.

(3) Brood parentage hypothesis

In many species, parents rarely have certainty regarding their relatedness to the offspring under their care. In numerous situations, e.g. cuckoldry, intra-specific brood parasitism, or communal breeding, parents may be rearing mixed broods composed of both their own and foreign offspring. When parentage is low or uncertain, parents are expected to reduce care to preserve resources for more certain reproduction in the future (Alonzo & Klug, 2012). In particular, parental investment should co-vary with parentage when (i) parental care is costly such that investing into current offspring diminishes the ability to invest in future reproduction; (ii) relatedness to offspring varies among reproductive attempts; and (iii) caregivers have access to reliable information to assess their relatedness to offspring (Westneat & Sherman, 1993). If these conditions are satisfied, then parent–offspring cannibalism may also vary with parentage (Manica, 2002, 2004). This can lead to full-brood cannibalism of low-parentage broods if they do not provide the fitness benefits necessary to outweigh their care costs (Manica, 2002). Partial

cannibalism from low-parentage broods will also incur fewer inclusive fitness costs on average than cannibalism from high-parentage broods (Svensson *et al.*, 1998; Manica, 2002). The ability of parents to recognise kin and distinguish their own from foreign offspring could conceivably allow parents to selectively remove unrelated offspring ('heterocannibalism', *sensu* Rohwer, 1978) and avoid eating related offspring ('filial cannibalism', *sensu* Rohwer, 1978). However, it is unlikely that such selective cannibalism could be committed with perfect accuracy, as co-evolutionary dynamics between the 'parasites' and 'hosts' would presumably make it difficult for a situation to arise in which foreign young (parasites) enter a brood where the parent (host) consistently identifies and removes them (Dawkins & Krebs, 1979; Davies, Brooke & Kacelnik, 1996). Accordingly, studies have tended to report whether the likelihood and degree of parent-offspring cannibalism varies with overall brood parentage or with some putative cue of parentage (see 'proximate cue' from Neff & Sherman, 2002).

The strongest support for the brood parentage hypothesis comes from studies that have related the intensity of cannibalism by caregiving individuals to their parentage within a brood [e.g. male bluegill sunfish (Neff, 2003); male three-spined stickleback (Frommen, Brendler & Bakker, 2007; Mehlis *et al.*, 2010); male fathead minnow, *Pimephales promelas* (Green, Mirza & Pyle, 2008); female rock-pool amphipod, *Apherusa jurinei* (Patterson, Dick & Elwood, 2008); male and female stag beetle, *Figulus binodulus* (Mori & Chiba, 2009)], or to simulated cuckold activity in the vicinity of their nest or territory (e.g. male scissortail sergeant; Manica, 2004). However, numerous studies have not detected any relationship between cannibalism and brood parentage or cuckold pressure [e.g. male common goby (Svensson *et al.*, 1998; Vallon & Heubel, 2016); male spottail darter, *Etheostoma squamiceps* (Bandoli, 2006); male sand goby (Svensson & Kvarnemo, 2007; Lissåker & Svensson, 2008); male Lusitanian toadfish (Félix *et al.*, 2016); male and female *Neolamprologus caudopunctatus* (Cunha-Saraiva *et al.*, 2018)].

Clearly, tests of the brood parentage hypothesis have revealed mixed results. This hypothesis is, however, particularly challenging to test observationally in an unconfounded manner [see Sheldon (2002) for discussion of the challenges relating brood parentage to parental care]. Even experimental tests of the brood parentage hypothesis require special precautions. This is because before a test can be run, an appropriate study system must be selected that satisfies the three aforementioned criteria: care must be costly, parentage must be variable, and reliable cues must be accessible (Westneat & Sherman, 1993). Indeed, a meta-analysis by Griffin, Alonzo & Cornwallis (2013) suggests that reductions in parental investment do not necessarily occur unless the costs of care and risk of parentage loss are both sufficiently high. A system in which care is only mildly costly and/or parentage is relatively invariable would therefore be unlikely to show a detectable relationship between cannibalism and parentage. Furthermore, experimenters must carefully choose a relevant cue of parentage to manipulate in their study. In

some species, parents use offspring odours as a reliable cue to estimate their relatedness towards a brood (e.g. male bluegill sunfish; Neff & Sherman, 2003), while in others the presence of cuckolders in the nearby environment is sufficient (e.g. male scissortail sergeant; Manica, 2004). However, such cues are not generalisable across species; indeed, the presentation of single cuckolders has been shown to be ineffective in some species where they each pose little paternity threat on average (Svensson & Kvarnemo, 2007; Bose *et al.*, 2020). Therefore, while the brood parentage hypothesis holds promise, it would be beneficial for future studies to make *a priori* predictions about the strength of covariation that can be expected between parental investment and brood parentage in their study systems.

(4) Mate availability hypothesis

Cannibalism decisions of parents should be strongly influenced by the probability that eaten offspring can be replaced quickly and efficiently. In their review on how mate availability influences filial cannibalism, Deal & Wong (2016) consider mate availability in detail. The mate availability hypothesis was originally proposed by Okuda & Yanagisawa (1996b), after observing mouthbrooding male cardinalfish cannibalising their entire broods and then re-mating very quickly. A game theoretical model by Kondoh & Okuda (2002) subsequently emphasised how mate availability can facilitate parent-offspring cannibalism, for example when mate searching is efficient, when population density is high, and when the population operational sex ratio is biased towards the non-caring sex. In essence, when the potential for replacing sacrificed offspring is high, the costs of cannibalism are reduced, which should in turn increase its prevalence. However, an alternative scenario is also conceivable in which offspring cannibalism is upregulated under conditions of low mate availability in order to ensure parental survival until conditions improve (Deal & Wong, 2016), although this alternative may partially fall under the purview of the energy reserves hypothesis. Further complexities arise when one considers how cannibalism can either elevate or diminish the attractiveness of individuals or indeed how the attractiveness of potential mates influences individuals' cannibalistic proclivities (Deal & Wong, 2016). With relatively few studies published to date on this topic, readers are referred to Deal & Wong (2016) for a thorough synthesis and outline of future research directions.

Support for the mate availability hypothesis is provided by studies investigating the relationship between re-mating likelihoods and full-brood cannibalism [e.g. mouthbrooding male cardinalfishes, *Apogon doederleini*, *A. notatus*, and *A. niger* (Okuda & Yanagisawa, 1996b; Okuda, 1999, 2000)] as well as partial brood cannibalism [male freshwater goby, *Rhinogobius* sp. (Okuda *et al.*, 2004); male lizard goby, *Rhinogobius flumineus* (Myint *et al.*, 2011a,b; Takeyama, Namizaki & Kohda, 2013)]. Interestingly, this body of work suggests that species may respond to mate availabilities in different ways depending on whether they engage in brood cycling. That

is, brood cyclers cannot capitalise on extra mating opportunities until they terminate their current brood *via* full-brood cannibalism, whereas non-brood cyclers are not so constrained, and may instead only commit partial brood cannibalism in response to alternative mates. Other studies, however, have found no significant relationship between parent–offspring cannibalism and mate availability (male two-spotted goby, *Gobiusculus flavescens*; Bjelvenmark & Forsgren, 2003). In the sand goby, male parents actually commit more full-brood cannibalism when apparent mating opportunities are scarce (Pampoulie *et al.*, 2004), and in flagfish caregiving males commit less full-brood cannibalism in the presence of females (Klug *et al.*, 2005). Altogether, this suggests that mate availability can interact with various aspects of a species' life history and ecological or social circumstances to produce complex cannibalistic outcomes.

(5) Brood density hypothesis

Offspring can be raised in a variety of microhabitats, including nests, burrows, dens, or even in the mouths of their parents (e.g. in mouthbrooding fishes). A consistent feature of all these locations is that offspring tend to be packed tightly together into a confined space, which can sometimes be detrimental to their survival and development. Density-dependent effects on offspring survival can become apparent under suboptimal environmental conditions or can arise when offspring are overcrowded, leading to resource competition. Thus, by partially cannibalising a brood, the development of the remaining offspring can potentially be improved (Klug & Bonsall, 2007). For example, in burying beetles, *Nicrophorus orbicollis*, male and female parents reduce their broods through cannibalism to match the size of the small vertebrate carcass on which the young are raised, suggesting that for a given set of environmental conditions, there exists an optimal brood density (Creighton, 2005). In mouthbrooding cardinalfish, males care for young by brooding them in their mouths but may partially cannibalise their female partner's brood according to the size of their buccal cavity (Okuda, 2001). In fishes, parents often 'fan' eggs or embryos to oxygenate them (Smith & Wootton, 1995). Fanning behaviour becomes more important, and also more energy and time demanding, when concentrations of dissolved oxygen in the water deteriorate. A number of empirical and theoretical studies based on fishes suggest that partial brood cannibalism can reduce offspring density and improve the survival of the remaining offspring when oxygen conditions are low [e.g. male beaugregory damselfish (Payne *et al.*, 2002, 2004; but see Olsson *et al.*, 2016)]. When experimenters artificially simulated partial cannibalism by haphazardly removing eggs from broods to reduce density, survival of the remaining offspring was improved in sand gobies, raising the possibility that partial cannibalism alleviates density effects in this system (Klug *et al.*, 2006). Surprisingly, however, Vallon & Heubel (2017) found that common goby

cannibalised more offspring when brood densities were low rather than high. Taken together, this suggests that in some, but not all, systems, partial brood cannibalism can act to improve the survival of the remaining young, which is consistent with cannibalism itself being a parental care behaviour (see Davenport *et al.*, 2019).

(6) Brood survival prospects hypothesis

The chances that offspring will survive to reproduce themselves are expected to affect strongly how much care a parent should provide (Klug *et al.*, 2012). Some offspring may be consigned to have lower prospects than others due to genetic variability, environmental circumstances, sibling competition, or even the selective actions of parents themselves (Forbes & Mock, 1998). In such cases, it can pay parents to cannibalise some offspring and redirect the energy to the remainder of the brood for whom parental effort can be better translated into fitness benefits, or to future reproduction when conditions may be less hostile to the young. Many different approaches have been used to investigate this idea. In some experiments, researchers have attempted to manipulate parents' perceptions of the risk of egg predation in their environment. Huang (2008) demonstrated in the long-tailed skink that frequent intrusions by egg-eating predators can cause mothers to consume all the eggs under their care, presumably because the energetic demands of defence became too high or because ultimate offspring survival was perceived to be low. Similarly, sand goby males will engage in more full-brood cannibalism when exposed to egg-predator cues from brown shrimp, *Crangon crangon* (Chin-Baarstad *et al.*, 2009), but not from shore crabs, *Carcinus maenas* (Lindström, 1998; Olsson *et al.*, 2016). Other studies have shown that parents may join other individuals in cannibalising their own offspring when they are unable to stop them from attacking their brood (e.g. female *Neolamprologus pulcher*; Jindal *et al.*, 2017). Male common goby are also more likely to cannibalise from their broods under low-salinity conditions, when fungal infections that threaten offspring survival strike more commonly (Vallon & Heubel, 2017). Extreme weather events such as intense rainfall can damage nests and lead to poor offspring survival prospects, triggering parents to cannibalise their young, as is suspected to have occurred in a case study on peregrine falcons (Franke *et al.*, 2013). Furthermore, infanticide and offspring cannibalism in moustached tamarins, *Saguinus mystax*, can sometimes occur when the number of helpers in a social group is low, which diminishes the survival probability of dependent young (Culot *et al.*, 2011). Finally, parents might also selectively consume offspring from their broods that are least likely to survive to adulthood. For example, abnormally developed or weak offspring can be cannibalised preferentially by their parents, as seen in laboratory rat, *Rattus norvegicus domestica*, mothers during the pre-weaning period (DeSantis & Schmaltz, 1984) and in female Oriental pied hornbills, *Anthracoceros albirostris convexus* (Ng *et al.*, 2011).

(7) Non-viable offspring and brood hygiene hypothesis

The consumption of non-viable or already-dead offspring may be particularly common and widespread. For example, this form of parent–offspring cannibalism has been observed in female Colombian rainbow boas, *Epicrates cenchria maurus* (Lourdais *et al.*, 2005), and in female laboratory mice (Brajon *et al.*, 2021), sometimes for considerable energetic gains. Although parent–offspring cannibalism is considered to be very rare in primates, maternal consumption of the bodies of their dead infants has been recorded multiple times (Watson & Matsuzawa, 2018). This form of cannibalism differs from the others described in this review because the adaptive significance of removing non-viable offspring is very conspicuous: non-viable offspring no longer offer direct fitness benefits to the parent, significantly reducing the costs of cannibalising them. At the same time, leaving non-viable offspring untouched can be costly in terms of disease transmission (Hoelzer, 1988; Kraak, 1996). Thus, parent–offspring cannibalism that targets non-viable or sick offspring to help prevent disease transmission has been termed ‘hygienic cannibalism’ (*sensu* Okada *et al.*, 2015), and is conceptually related to both the brood density hypothesis (Section III.5) and the brood survival prospects hypothesis (Section III.6). This is because disease transmission can be amplified under high-density conditions (Paull *et al.*, 2012), which can threaten the survival of the entire brood. In the sphynx blenny, *Aidublenius sphynx*, male parents recognise and eat dead or non-developing eggs (Kraak, 1996), and in Japanese giant salamanders, male parents, also called ‘den-masters’, selectively consume eggs that appear dead or infected with water mould (Okada *et al.*, 2015). Male spottail darter, *Etheostoma squamiceps*, and common goby also consume eggs infected with *Saprolegnia* fungus at higher rates than healthy eggs (Bandoli, 2016; Vallon, Anthes & Heubel, 2016a). Interestingly, recent work has suggested that parents may use partial brood cannibalism pre-emptively, consuming healthy offspring to reduce their brood’s general risk of infection. For example, parents may cannibalise to reduce offspring densities, thereby hindering disease transmission between offspring, but will do so primarily under environmental conditions that are more prone to outbreaks [e.g. low-salinity conditions which are conducive to fungal infections in sand goby (Lehtonen & Kvarnemo, 2015a,b)]. Thus, in a number of systems, cannibalism is used to remove (or recover energy from) non-viable offspring, which can reduce the likelihood of disease outbreaks, or cannibalism may act as a prophylactic measure to reduce density-dependent disease transmission more generally.

(8) Offspring age hypothesis

In systems where parent–offspring cannibalism has already evolved, younger offspring are expected to be cannibalised more often than older offspring because of their lower reproductive value (Dawkins & Carlisle, 1976; Rohwer, 1978; Sargent, 1992; Sargent *et al.*, 1995). By consuming offspring

as early as possible, parents can avoid expending energy on young that will eventually be consumed (Sargent, 1992; Manica, 2002). A preference for cannibalising younger offspring has been found in terms of both full-brood cannibalism (e.g. male damselfish, *Stegastes dorsopunicans*; Petersen, 1990), and partial brood cannibalism [e.g. female golden hamster (Day & Galef, 1977); male common goby (Vallon & Heubel, 2016)]. Even in honeybees, pollen shortages can stimulate nurse bees to cannibalise larvae starting with the youngest (Schmickl & Crailsheim, 2001). Some studies, however, have failed to detect a relationship between parent–offspring cannibalism and offspring age [e.g. male scissortail sergeant (Manica, 2003); male barred-chin blenny, *Rhabdoblennius ellipes* (Takegaki, Yoshimoto & Matsumoto, 2011)], although in these cases the authors argued that the age differences among offspring in their broods were too small to convey meaningful differences in reproductive value or energy savings to the parents. Interestingly, the predictions of the offspring age hypothesis can sometimes be reversed due to female choice. For example, in garibaldi damselfish, *Hypsypops rubicundus*, females prefer to lay their eggs next to young eggs in a male’s nest. This means that males will selectively eat old eggs that happen to be situated next to young eggs. Doing so clears space for new eggs to be laid next to the young eggs and enhances the males’ attractiveness to prospecting females (Sikkel, 1994).

(9) Parental stress hypothesis

Parent–offspring cannibalism has also been examined in non-evolutionary research domains (e.g. medical, veterinary, animal welfare, and commercial animal breeding) where captive, domesticated, or laboratory animals are used as study organisms. In laboratory mice, maternal cannibalism of pups can be quite common and is often attributed to stress or disturbances in their holding environments (Weber & Olsson, 2008). Frequent cage cleaning in laboratory rats leads to increased cannibalism of pups by their mothers (Burn & Mason, 2008). Furthermore, high-fat diets administered to female laboratory mice during pregnancy are associated with maternal stress, impaired fetal intrauterine growth, and elevated pup cannibalism along with other ‘aberrant’ maternal behaviours (Bellisario *et al.*, 2015; Powell & Choudhury, 2019). In cage-held rabbits, handling stress or other local disturbances have been implicated in mother–offspring cannibalism, which has also been labelled as a ‘disorder’ and a ‘failure of maternal behavioural development’ (González-Redondo & Zamora-Lozano, 2008, p. 283). Tartabini (1991) discusses two cases of mother–offspring neglect followed by cannibalism in thick-tailed bushbabies, *Galago crassicaudatus umbrosus*, as being pathological and attributes them to artificial laboratory holding conditions which elevated maternal stress levels. In the mouthbrooding cichlid *Astatotilapia burtoni*, exposure to anthropogenic noise elevates maternal cortisol levels and dramatically increases their likelihood of cannibalising the young being brooded in their mouths (Butler & Maruska, 2021). The general theme from this literature is that parent–offspring cannibalism can be

induced by stress or disturbance. However, many of these cases might also be consistent with one or more of the alternative factors discussed in this review (e.g. low parental energy reserves, poor offspring survival prospects, non-viable offspring, etc.). Cannibalism might allow parents that are facing unfavourable and stressful conditions in the present to redirect investments to potentially more favourable opportunities in the future. However, since parent–offspring cannibalism evolved under natural conditions, its expression under highly artificial settings should not always be expected to coincide with the predictions of adaptive hypotheses.

(10) Maladaptive cannibalism

It is possible that some instances of parent–offspring cannibalism are maladaptive, although this is unlikely to be a general explanation given that this behaviour is so widespread in nature (Manica, 2002). For example, the accidental consumption of the ‘wrong’ offspring can occur from time to time (Munehara & Miura, 1995). Females of the mouth-brooding cichlid *Pseudocrenilabrus multicolor*, may accidentally swallow some live eggs while attempting selectively to eat unfertilised eggs (Mrowka, 1987). Furthermore, small numbers of live eggs might become dislodged from the nest surface and eaten during routine nest cleaning in plainfin midshipman fish (Bose *et al.*, 2019). However, it remains difficult to argue that a behaviour is maladaptive, when many alternative adaptive hypotheses remain untested.

(11) Other hypotheses

In addition to the above-discussed hypotheses, several others have been proposed to influence the expression of parent–offspring cannibalism, although each has been studied very scantily to date. The generality of these hypotheses therefore remains unclear but they warrant further attention.

(a) Brood sex ratio

Partial brood cannibalism has been shown to allow parents to adjust the sex ratio of their broods and thereby invest more heavily into care for one sex over the other (e.g. female Syrian hamsters; Beery & Zucker, 2012).

(b) Parental micronutrients

Parent–offspring cannibalism has also been suggested to allow parents to obtain important micronutrients that are lacking in their diets (e.g. offspring as a source of carotenoids in three-spined stickleback; Pike *et al.*, 2007).

(c) Parental care duration

Partial brood cannibalism can allow parents to shorten their care period. For example, by preferentially consuming the slowest-developing eggs laid later in a brood cycle, male sand goby can shorten their duration of care, allowing them to re-enter the mating pool sooner and potentially to increase their

reproductive rates (Klug & Lindström, 2008). Miller & Zink (2012) also tested this idea in the maritime earwig, but did not find support.

(d) Parasitic infections

Parents that are infected with parasites may cannibalise offspring at different rates than uninfected parents. In damselfish, *Stegastes planifrons*, male parents infected with monogenean parasites exhibit increased partial brood cannibalism, potentially to offset the energetic costs of their infection (Sasal, 2006). Stott & Pulin (1996) also tested for a relationship between parental parasite load and cannibalistic behaviour in male upland bullies, *Gobiomorphus breviceps*, but failed to find a correlation.

IV. MATE CHOICE, SEXUAL SELECTION, AND PARENT–OFFSPRING CANNIBALISM

How should individuals choose their mates when those mates could also be offspring cannibals? A simplified prediction would be that all individuals should prefer mating with partners who are least likely to cannibalise their offspring. Individuals are expected to choose mating partners based on the potential mates’ phenotypic traits and/or resources that indicate the fitness benefits of mating with them (Andersson, 1994) – and this could include traits that predict the likelihood of cannibalism. However, when parent–offspring cannibalism functions to improve the survival and development of the current offspring, then the potential for cannibalism should not be a deterrent in mate choice (Lindström, 2000). However, as outlined above, where parent–offspring cannibalism functions to improve the cannibal’s own future reproductive prospects, it could generate sexual conflict because it will be unlikely also to benefit the chooser (Lindström, 2000). Parent–offspring cannibalism has primarily been studied in fishes to date, which mostly provide paternal care. In these systems, mate choice is the main strategy for females to minimise the number of offspring that they lose to investments into the male caregivers’ future reproduction (Manica, 2002).

One female preference that frequently co-occurs with father–offspring cannibalism in fishes is for females to lay eggs with males that are already caring for eggs (Jamieson, 1995; Forsgren *et al.*, 1996; Lindström, 2000). By laying eggs alongside others, females benefit from dilution effects that reduce the proportion of their broods lost to cannibalism or predation (Rohwer, 1978; Lindström, 2000; Matsumoto, Tawa & Takegaki, 2011). In some cases, choosing to lay eggs alongside others allows females to contribute to broods that ultimately become large enough to ensure male care, surpassing the male caregiver’s threshold for full-brood cannibalism or abandonment (Forsgren *et al.*, 1996). In a surprising female counterstrategy, Kume, Yamaguchi & Aoki (2002) suggest that female cardinalfish lay broods that are surreptitiously supplemented with

yolkless eggs to deceive the mouthbrooding male into thinking the brood is larger than it is, thereby reducing his odds of committing full-brood cannibalism. Females should also prefer to lay eggs with males that are caring for younger (rather than older) offspring. This is because, when given the choice, parents are predicted to consume the youngest offspring in a brood preferentially, as they require the largest additional parental expenditure to raise to independence (Rohwer, 1978; Manica, 2002; Matsumoto *et al.*, 2011). Furthermore, a female preference to mate with high-condition males would be expected if these males are able to provide care without consuming offspring for energetic supplements (Lindström, 2000). While direct assessment of the endogenous fuel reserves of a potential mate may not be possible, assessment of coarse body condition, or secondary sexual characteristics and courtship behaviours that are condition dependent could provide reliable information (Andersson, 1994; e.g. Takahashi & Kohda, 2004). Finally, females should prefer to mate in the absence of sperm competitors if low paternity assurance is linked to decreased paternal care and increased offspring cannibalism (but see Reichard, Le Comber & Smith, 2007).

Females may also employ post-mating strategies to reduce the number of offspring lost to male cannibalism. In some fish species, females remain with a male or near to him after spawning. This can allow her to monitor the male's behaviour and she may retaliate against males that cannibalise at her expense (e.g. cardinalfish; Okuda & Yanagisawa, 1996b). Furthermore, in biparental systems, females may actively police their male partners should they have cannibalistic proclivities, keeping them away from the brood while tending to it [e.g. convict cichlid (Lavery & Keenleyside, 1990); *Neolamprologus caudopunctatus* (Cunha-Saraiva *et al.*, 2018)].

Individual variation will also exist in the propensity for parents to cannibalise their offspring (Vallon *et al.*, 2016b), and this is likely to influence their attractiveness to prospective mates. Deal & Wong (2016) provide a discussion on how the propensity to commit offspring cannibalism could affect individual attractiveness and/or be a function of their self-perceived attractiveness.

V. FUTURE DIRECTIONS

(1) Need for greater taxonomic representation

The majority of research on parent–offspring cannibalism to date has been conducted on fishes (Fig. 1), and this presents a hurdle to our general understanding across the animal kingdom. Questions naturally arise as to whether and why certain taxonomic groups show more parent–offspring cannibalism than others. The survey of animal taxa presented in Figs. 1 and 2 reveals that in addition to Osteichthyes fishes, parent–offspring cannibalism is also present in some mammals and insects. One salient pattern is that cannibalism appears to be most common in species that display large brood sizes and have rapid reproductive cycles. For example,

among the studied mammals, considerable attention has been given to rodents, which reproduce quickly and are notorious parent–offspring cannibals. Thus, it seems possible that parent–offspring cannibalism may be most common in species where individual offspring constitute a relatively small proportion of their parents' lifetime reproductive success so that small, rather than large, sacrifices can be translated into future benefits. This is also supported by the fact that while parent–offspring cannibalism has been studied in taxa that typically produce small broods over longer time intervals, such as primates and birds, the behaviour is thought to be relatively rare (Stanback & Koenig, 1992; Watson & Matsuzawa, 2018). Among birds, parent–offspring cannibalism is notably better represented in predators, such as owls and raptors (Stanback & Koenig, 1992), which hints at a more general pattern that carnivorous (or omnivorous) species are more likely to display parent–offspring cannibalism than herbivores. Thus, dietary specialisations will likely preclude cannibalism in certain taxa constraining parents to express brood abandonment or infanticide instead. Finally, the taxonomic groups that have been studied to date tend to differ with respect to their dominant care strategies. That is, most investigated fishes provide sole paternal care, while most mammals provide maternal care, and many birds provide biparental care. Increasing the representation of different care strategies within the various taxa will ultimately be important to disentangle these potentially confounding factors. As future research expands to include a greater variety of taxa, we will undoubtedly learn more about why parents in some taxa are more cannibalistic than others.

(2) Parent–offspring cannibalism and the four pillars of behavioural ecology

Parent–offspring cannibalism can be framed in terms of Tinbergen's four pillars of behavioural ecology (Tinbergen, 1963; Bateson & Laland, 2013), and doing so can help identify gaps in our current understanding and directions for future research.

(a) Adaptive significance and current utility

Most empirical and theoretical research to date has been concerned with understanding the adaptive significance and current utility of parent–offspring cannibalism. Studies tend to ask under what circumstances the behaviour is expressed, and then speculate on how it could translate to increased lifetime reproductive success. This work has given rise to the hypotheses considered in Section III, and as additional taxa are investigated, future research may uncover new reasons for why parents commit offspring cannibalism.

(b) Evolutionary history

How many times parent–offspring cannibalism has independently evolved and what trajectories it has taken in various lineages are still open questions. Mapping its occurrence onto

high-quality molecular phylogenies will make it possible to answer these questions as more data become available for a greater number of species. Understandably, most work to date has focused on species that show high rates of parent–offspring cannibalism, leaving gaps in our understanding of what features are shared among species that do *not* express cannibalism. Some studies have shown that adults do not cannibalise, or inhibit their cannibalistic tendencies, during periods of reproduction and care [e.g. female wolf spiders, *Schizocosa ocreata* (Wagner, 1995); male pipefish, *Syngnathus abaster* (Cunha *et al.*, 2016)], and these would provide good starting points for populating phylogenies with the behavioural variation needed to answer such evolutionary questions.

(c) *Ontogeny*

One ontogenetic approach to studying parent–offspring cannibalism would involve long-term monitoring to track how individuals change their expression of cannibalism across broods and over their lifetimes [see Takeyama, Okuda & Yanagisawa, 2002 and Okuda, Takeyama & Yanagisawa, 1997 for differences in cannibalism exhibited by young and old parents]. Here, theoretical expectations should mirror those for how parental effort is predicted to change as individuals age and should include the possibility of terminal investment (Clutton-Brock, 1984). Furthermore, one could ask how early-life experiences, for example parental effects, affect the expression of cannibalism as a caregiver later in life. Early-life experiences and social learning might shape cannibalism propensity later in life, and this may be particularly relevant in group-living species in which juveniles remain with their parents through several brood cycles. These all represent open areas of research.

(d) *Mechanisms of control*

Besides tests of the energy reserves hypothesis that have focused on endogenous energy stores, the genetic, physiological, and neuronal mechanisms that underlie parent–offspring cannibalism are still poorly understood. Some evidence of a genetic basis for cannibalism exists: different genetic strains of livebearing fish, *Poeciliopsis* spp. (Lima & Vrijenhoek, 1996) and laboratory mice (Weber & Olsson, 2008) are more (or less) prone to infanticide and cannibalism. Thus far, we know very little about the patterns of hormone expression that either inhibit cannibalism or predispose parents to cannibalise offspring. Transition from a pre-breeding phase to a parental care phase are known to be associated with a myriad of hormonal shifts (e.g. in fishes, Sikkell, 1993; Magee, Neff & Knapp, 2006), and Takegaki, Nakatake & Amiya (2020) implicated prolactin-releasing peptide 2 (PrRP2) and its receptors as a possible mechanism by which feeding and egg cannibalism are inhibited during parental care in the intertidal blenny. In this species, the presence of eggs in a nest suppresses androgen (testosterone and 11-ketotestosterone) secretion in the male caregiver, compromising his ability to perform subsequent courtship

behaviours. In the event of receiving a small brood, males that resort to full-brood cannibalism can once again produce the androgens necessary to resume courtship and re-mating (Matsumoto *et al.*, 2018). Butler *et al.* (2020) showed that activation of galanin neurons in the lateral tuberal nucleus of the brain is associated with feeding and offspring cannibalism in mouthbrooding female cichlids *Astatotilapia burtoni*. Serum oxytocin levels are known to be lower in female dogs that have cannibalised their pups relative to females that have not (Kockaya *et al.*, 2018). Overall, only a few studies have begun to explore the mechanisms underlying parent–offspring cannibalism and future studies should attempt to clarify the molecular processes that modulate the expression of this behaviour.

VI. CONCLUSIONS

(1) Although parent–offspring cannibalism appears superficially counterintuitive, it is now widely understood to be a phenotypically plastic behaviour that confers adaptive benefits under a variety of circumstances. In particular, it allows parents to invest their time and energy more optimally, redirecting investments from current offspring to alternative or future reproductive opportunities (Rohwer, 1978; Sargent, 1992; Manica, 2002).

(2) Energy-based arguments are frequently offered to explain observations of parent–offspring cannibalism, but research over the past several decades has systematically uncovered a variety of explanations that are not directly related to parental body condition or energetic state. It is evident that the expression of parent–offspring cannibalism can be driven by numerous non-mutually exclusive factors (Klug & Bonsall, 2007).

(3) The probability that a parent will engage in offspring cannibalism in any given system will depend on the reproductive value of the offspring relative to the parent's residual reproductive value, the physiological condition of the parent and their re-mating prospects, the environmental circumstances surrounding the current reproductive attempt relative to future attempts, and specific life-history characteristics of the species. Together, these factors will determine the relative costs and benefits of either continuing to care for offspring or terminating them and reinvesting energy elsewhere.

(4) Diversifying studies across additional taxa will allow hypotheses to be tested in association with novel combinations of mating systems (e.g. lifelong genetic monogamy, polygyny, polyandry), life-history characteristics (e.g. income *versus* capital breeding, brood sizes and reproductive rates, reproductive lifespans), reproductive modes (e.g. internal *versus* external fertilisation), and parental care strategies (e.g. depreciable *versus* non-depreciable, maternal, paternal, biparental, cooperative, communal). Future research should include species from more diverse taxonomic groups, mating systems, and parental care strategies, which will undoubtedly lead to new insights into this puzzling parental behaviour.

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IX. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Details of literature search and article screening process generating the data to produce Figs. 1 and 2.

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