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Filial cannibalism in teleost fish

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ABSTRACT

This review summarizes information on filial cannibalism (the act of eating one's own offspring) in teleost fish. Cannibalistic parents can either consume their whole brood (total filial cannibalism), or eat only some of the eggs in the nest (partial filial cannibalism). Offspring consumption has been argued to be adaptive under the assumption that offspring survival is traded against feeding, and that offspring can act as an alternative food source for the parents. The evidence supporting the basic predictions formulated under these assumptions is summarized for both total and partial filial cannibalism. These two forms of cannibalism differ significantly since the former represents an investment only in future reproductive success, whereas the latter can affect both present and future reproductive success. Despite a few inconsistencies in the data from laboratory and field studies, the energy-based explanation appears valid for both forms of cannibalism. Alternative non-energy-based explanations are considered, but they are unable to account for the wide distribution of this behaviour in teleosts. The intersexual conflict arising from attempts of the non-cannibal sex to minimize the cost of filial cannibalism is also discussed, together with the potential effect of this behaviour on the operational sex ratio at a population level.

Key words: filial cannibalism, parental care, teleost fish, reproductive strategies, energetics, sexual selection.

CONTENTS

I. INTRODUCTION

Filial cannibalism, the act of eating one's own offspring, is hardly the most obvious example of a successful reproductive strategy. However, this behaviour is extremely common in teleost fish (e.g. Dominey & Blumer, 1984; Smith & Reay, 1991; FitzGerald & Whoriskey, 1992), having been recorded in 17 families (Table 1), and it occurs in a wide range of other taxa (Polis, 1981).

Until two decades ago, any form of filial cannibalism was considered an abnormal behaviour or a laboratory artefact. Based on Trivers' analysis of parental investment (Trivers, 1974) and parent–offspring conflict (Trivers, 1972), Rowher (1978) was the first to consider the possibility that offspring consumption might be an adaptive strategy to maximize lifetime reproductive success. Rowher's (1978) argument is based on the assumption that offspring survival is traded against feeding, and that parents can use their offspring as an alternative food source. Sargent (1992) and Sargent *et al.* (1995) developed dynamic models to formalize Rowher's (1978) verbal approach.

Cannibalistic parents might eat the whole clutch (a clutch being defined as a batch of eggs laid by a female) or brood (all eggs present in the nest) (total filial cannibalism), or consume only a few eggs (partial filial cannibalism). These two forms of filial cannibalism are conceptually different when we consider the fitness component that is maximized. Total filial cannibalism can only be an investment in future reproductive success, whereas partial filial cannibalism can influence current as well as future reproductive output (Sargent, 1992). Total filial cannibalism has been widely accepted as an optimal reproductive strategy, but several authors (e.g. Belles-Isles & Fitzgerald, 1991; Smith, 1992) have questioned the adaptiveness of partial filial cannibalism.

Table 1. *Families of teleost fish in which filial cannibalism has been reported*

Family	Example of species	Reference
Ictaluridae	*Ictalurus punctatus* Rafinesque	Brown (1942)
Cyprinodontidae	*Cyprinodon pecosensis* Echelle & Echelle	Kodric-Brown (1983)
Gasterosteidae	*Gasterosteus aculeatus* L.	van den Assem (1967)
Hexagrammidae	*Oxylebius pictus* Gill	DeMartini (1987)
Cottidae	*Cottus gobius* L.	Marconato & Bisazza (1988)
Centrarchidae	*Lepomis macrochirus* Rafinesque	Dominey & Blumer (1984)
Nandidae	*Badis badis* (Hamilton)	Barlow (1964)
Cichlidae	*Pseudocrenilabrus multicolor* (Schoeller)	Mrowka (1987)
Pomacentridae	*Chromis notata* (Temminck & Schlegel)	Ochi (1985)
Tripterygidae	*Enneapterygius etheostomus* Jordan & Snyder	Ohta & Nakazono (1988)
Blenniidae	*Blennius pholis* L.	Qasim (1957)
Belontidae	*Trichogaster trichopterus* (Pallas)	Kramer & Liley (1971)
Gobiidae	*Pomatoschistus minutus* (Pallas)	Lindström (1998)
Labridae	*Xyrichtys splendens* Castelnau	Nemtzov & Clark (1994)
Apogonidae	*Apogon doederleini* Jordan & Snyder	Okuda & Yanagisawa (1996*a*)
Poeciliidae	*Poeciliopsis monacha* Miller	Lima & Vrijenhoek (1996)
Percidae	*Etheostoma flabellare* Rafinesque	Lindström & Sargent (1997)

II. TOTAL FILIAL CANNIBALISM

(1) Theory and predictions

Total filial cannibalism, the consumption of the whole brood or clutch by the parent (for simplicity, from here onwards, I refer only to broods), can be seen as a form of brood termination. Termination of care is expected when the cost of caring is higher than the benefit (Clutton-Brock, 1991), and it has been recorded in a wide variety of taxa (Hrdy, 1979). By not providing care, the parent can reallocate time and energy into increasing its survival and growth, and into finding a new mate sooner. If the survival of offspring without care is low (as is often the case in fish, e.g. Barash, 1980; Itzkowitz & Mackie, 1986; Tyler, 1995), it might be adaptive for the parent to cannibalize the brood, and thus recover some energy from the aborted breeding attempt. Improved body condition following filial cannibalism has been recorded in several studies (e.g. Lavery & Keenleyside, 1990*a*; Lindström & Sargent, 1997).

Many factors can influence the cost to benefit ratio of parental care. The most studied factor in the literature is brood size. Parental care in fish has been shown to be mostly non-depreciable (*sensu* Clutton-Brock, 1991), meaning that each unit of care is enjoyed by all of the offspring irrespective of their number (Williams, 1975; Perrone & Zaret, 1979). If this is the case, the *per capita* cost of care is inversely proportional to the number of offspring. Thus, cannibalism of the whole brood is expected when brood size is small (Prediction A, Section II.2*a*; Rowher, 1978; Sargent, 1992). By terminating a small brood, the parent can reallocate time and energy to future broods, which are likely to be larger and thus have a better *per capita* cost to benefit ratio. This prediction might be less applicable to species that actively oxygenate eggs, as this form of parental care is non-sharable and the cost of care increases with brood size (e.g. Perrin, 1995).

Parents are also expected to cannibalize their offspring as early as possible (Prediction B, Section II.2*b*), to minimize the loss of resources in caring for the aborted brood (Petersen & Marchetti, 1989; Sargent, 1992). A further incentive for early cannibalism is that younger eggs are more nutritious than older ones (Gilbert, 1985).

Parental energy resources are also important in determining the cost of parental care (Sargent, 1992). Both in substrate guarders (fish that care for eggs that have been laid on a substrate) and mouthbrooders (fish that care for the eggs by holding them in their mouths), parents have been shown to have higher energetic requirements and fewer foraging opportunities than non-caring individuals (reviewed in Smith & Wootton, 1995*a*). Thus, the cost of care is especially high for parents with limited energy reserves. Parents in low body condition are more likely to cannibalize the brood (Prediction C, Section II.2*c*).

Availability of mates can also influence the occurrence of total filial cannibalism (Okuda & Yanagisawa, 1996*b*). If the likelihood of finding another mate is low, cannibalism is expected to be rare as the value of the current brood is high. On the other hand, if a cannibal is likely to find another mate promptly (especially in the case of males, whose energy investment in gametes is low), brood termination should be relatively common (Prediction D, Section II.2*d*).

The different investment in gamete production by males and females predicts that the two sexes should exhibit differences in the incidence of cannibalism (FitzGerald, 1992). A female can never fully recover the energy invested in the brood by cannibalizing her eggs, whereas the male can actually gain energy by eating eggs. Thus, one would predict filial cannibalism by males to be more common than cannibalism by females. An interspecific test of this prediction is difficult without an extensive data set and an accurate phylogeny, since male-only parental care is the predominant form of care in fish (Blumer, 1982; Sargent & Gross, 1986, 1993). A more practical, if slightly simplistic, hypothesis to test is that males should usually be more cannibalistic than females in species with biparental care (Prediction E, Section II.2*e*; FitzGerald, 1992). However, it should be noted that a proper game-theoretical approach would be required to predict under which conditions this hypothesis is correct.

Another factor that will affect the value of the brood is certainty of paternity. Total filial cannibalism is predicted to become more frequent when parents have a low certainty of paternity (Prediction F, Section II.2*f*).

(2) Empirical evidence

(*a*) *Brood size*

Brood size is arguably the most studied factor potentially influencing filial cannibalism. Several studies have uncovered an inverse relationship between brood size and the natural occurrence of total filial

Table 2. *Reports of total filial cannibalism in small broods or clutches*

Species	Notes	Reference
Badis badis (pat)	(lab)	Barlow (1964)
Gasterosteus aculeatus (pat)	(lab)	van den Assem (1967)
Lepomis macrochirus (pat)	(field)	Dominey & Blumer (1984)
Chromis notata (pat)	Deserted broods smaller than those cared for (lab)	Ochi (1985)
Tilapia mariae Boulenger (bip)	Broods of less than 100 eggs are eaten; males preferentially eat broods from females smaller than themselves (lab)	Schwank (1986)
Oxylebius pictus (pat)	Small single clutches most likely to be cannibalized (field)	DeMartini (1987)
Hypsypops rubicundus (Girard) (pat)	Small single clutches most likely to be cannibalized (field)	Sikkel (1988); unpublished results cited in Sikkel (1994)
Stegastes rectifraneum (Gill) (pat)	Cannibalized clutches smaller than those cared for (field)	Petersen & Marchetti (1989)
Stegastes dorsopunicans (Poey) (pat) and *Microsphatodon chrysurus* (Cuvier) (pat)	Cannibalized clutches smaller than those cared for (field)	Petersen (1990)
Apogon doederleini (pat)	Males preferentially eat broods from females smaller than themselves (field)	Okuda & Yanagisawa (1996*b*)
Pomatoschistus minutus (pat)	Smaller broods cannibalized (lab)	Forsgren *et al.* (1996)
Etheostoma flabellare (pat)	Small broods fully consumed	Lindström & Sargent (1997)
Pomatoschistus microps (Krøyer) (pat)	Cannibalized broods smaller than cared for (lab)	Unpublished results cited in Kvarnemo *et al.* (1998)
Abudefduf sexfasciatus (Lacépède) (pat)	Cannibalized broods smaller than cared for (field)	Manica (2002)

lab, studies undertaken in the laboratory; field, field observations; pat, paternal care; bip, biparental care.

cannibalism (Table 2). However, this correlation could be explained in terms of parent quality. Low-quality individuals only manage to produce (in the case of females) or acquire (for males) relatively small broods. Following Prediction C, inferior individuals are the most likely to cannibalize.

Experimental brood reduction clearly demonstrates that the parent is able to estimate the value of the brood based on the number of eggs, as already suggested by several studies which show a correlation between parental effort and brood size (e.g. Carlisle, 1985; Coleman, Gross & Sargent, 1985; Sargent, 1988; Ukegbu & Huntingford, 1988; Lavery & Keenleyside, 1990*b*). When the brood, and thus the benefit of caring, is experimentally reduced, parents become more likely to cannibalize (Table 3).

(*b*) *Timing of cannibalism*

Total filial cannibalism at a relatively early stage of paternal care has been reported in several species (see Table 4). However, the relationship between brood age and total filial cannibalism has been experimentally tested only by Lavery and Keenleyside (1990*b*) and Manica (2002). Lavery and Keenleyside (1990*b*) experimentally reduced the brood of convict cichlid *Cichlasoma nigrofasciatum* pairs in the laboratory at the wriggler stage (post-hatching but pre-free-swimming) and showed that pairs with an experimentally reduced brood cannibalized their eggs more often than did control pairs and pairs with an augmented brood. Experimental brood reduction at a later stage of parental care did not elicit filial cannibalism but only lower levels of parental effort. Manica (2002) performed a similar experiment in the field on the scissor-tail sergeant *Abudefduf sexfasciatus*, a tropical damselfish with male-only parental care, and found a significant decrease in the incidence of cannibalism with increasing egg age during the parental phase.

(*c*) *Parent physical condition*

Indirect evidence for a relationship between parent

Table 3. *Reports involving experimental brood reduction showing a relationship between total filial cannibalism and brood or clutch size*

Species	Notes	Reference
Trichogaster trichopterus (pat)	A minimum number of eggs is needed to elicit care (lab)	Kramer (1973)
Pseudocrenilabrus multicolor (mat)	Brood cannibalized if it falls below 80 % of original size at spawning (lab)	Mrowka (1987)
Stegastes rectifraneum (pat)	Clutch reduction by 50 % increases cannibalism (field)	Petersen & Marchetti (1989)
Stegastes dorsopunicans (pat) and *Microsphatodon chrysurus* (pat)	Clutch reduction increases the likelihood of cannibalism (field)	Petersen (1990)
Cichlasoma nigrofasciatum (Günther) (bip)	Brood reduction by 66 % leads to increased cannibalism (lab)	Lavery & Keenleyside (1990*b*)
Abudefduf sexfasciatus (pat)	Brood reduction by 75 % leads to increased cannibalism (field)	Manica (2002)

lab, studies undertaken in the laboratory; field, field observations; pat, paternal care; bip, biparental care; mat, maternal care.

Table 4. *Reports of early total filial cannibalism*

Species	Notes	Reference
Tilapia mariae (bip)	Cannibalism only at egg stage, but not wrigglers or fry (lab)	Schwank (1986)
Cichlasoma nigrofasciatum (bip)	Total filial cannibalism only occurs in wriggler stage but not later stage broods (lab)	Lavery & Keenleyside (1990*b*)
Stegastes rectifraneum (pat)	The probability of cannibalism significantly decreases with egg age (field)	Petersen & Marchetti (1989)
Stegastes dorsopunicans (pat) and *Microsphatodon chrysurus* (pat)	Cannibalism is most likely when eggs are young (field)	Petersen (1990)
Pomatoschistus minutus (pat)	Broods fully cannibalized within the first few days of parental care (lab)	Forsgren *et al.* (1996)
Apogon doederleini (pat)	Cannibalism always on the first day of mouthbrooding (field)	Okuda & Yanagisawa (1996*a*, *b*)
Etheostoma flabellare (pat)	Broods fully cannibalized within the first few days of parental care (lab)	Lindström & Sargent (1997)
Abudefduf sexfasciatus (pat)	Total cannibalism always on the first day of parental phase (field)	Manica (2002)

lab, studies undertaken in the laboratory; field, field observations; pat, paternal care; bip, biparental care.

physical condition and total filial cannibalism is provided by the seasonal changes in the incidence of cannibalism. Okuda and Yanagisawa (1996*a*) detected a correlation of both total filial cannibalism and male physical condition with season in the cardinal fish *Apogon doederleini*: as the season advanced, the frequency of cannibalism increased while male condition decreased. Similarly, male yellowtail damsels *Microspathodon chrysurus* are more likely to consume their clutch late in the monthly reproductive cycle (Petersen, 1990), but in this study body condition was not monitored.

However, manipulative investigations have failed to support the prediction that well-fed parents should cannibalize less than starved ones. In a feeding experiment on the fantail darter *Etheostoma flabellare*, Lindström and Sargent (1997) did not find an effect of ration on total cannibalism. Brood size was the best predictor of whether a male would cannibalize or not, and fed males diverted the additional energy input into somatic growth. Similarly, Kvarnemo, Svensson and Forsgren (1998) found no relationship between feeding treatment and total filial cannibalism in an experiment that revealed a link between energy reserves and partial filial cannibalism in the common goby *Pomatoschistus microps* (see Section III.2*b*). The consumed broods were significantly smaller than those that were cared for, independent of the feeding regime. However, only two out of 26 males used in the experiment consumed their whole brood, and the statistical power of the test was consequently low ($\beta < 0.2$).

(*d*) *Availability of mates*

Okuda and Yanagisawa (1996*b*) provide circumstantial evidence that *Apogon doederleini* practises total filial cannibalism in relation to mate availability. In their study, cannibalistic males always re-mated within a shorter period than males whose brood had been removed on the first day of care, to coincide with the timing of cannibalism. The possibility that the longer re-mating time was due to the artificial manipulation was excluded by showing that males whose brood was reduced just before hatching took the same time to re-spawn as males whose brood hatched normally. Furthermore, males always changed their mate after cannibalism. However, the results could also be explained in terms of energetics. Cannibalistic males increase their physical condition by eating their brood and could thus be more attractive to females, thereby implying a shorter mate searching time (Smith & Wootton, 1995*b*). To my knowledge, there is no study that has addressed directly the effect of the operational sex ratio (OSR, defined as the number of males ready to mate to that of females ready to mate, *sensu* Emlen & Oring, 1977) on filial cannibalism.

(*e*) *Sex of cannibals*

The prediction that males should be more cannibalistic than females receives support from work on two species with biparental care. In the spotted tilapia *Tilapia mariae*, intrapair aggression is frequent and the male is more likely to cannibalize the clutch than the female (Schwank, 1986). Lavery and Keenleyside (1990*a*) argue that male convict cichlids are most likely to initiate brood termination as cannibalism is only registered at the wriggler stage, when the male is allowed close to the young. The male does not perform any active care of the eggs and is kept at a distance from the brood by the female until hatching. In another study on this species, FitzGerald (1976, cited in FitzGerald & Whoriskey, 1992) only observed males, but never females, to consume their own eggs.

(*f*) *Certainty of paternity*

The prediction that total filial cannibalism should be common in broods with low certainty of paternity has not been tested as yet.

(3) Discussion

Much evidence has been accumulated to support the basic predictions of an increase in the incidence of total cannibalism with decreasing brood size and brood age. Thus, it can be convincingly argued that total cannibalism is an adaptive form of brood termination. However, the underlying assumption that total cannibalism is energy related has received only limited support. The inconsistency between field correlates and laboratory experiments is confusing and it questions whether the experimental approach adopted to date is appropriate. Feeding schedules as well as the quality of food items used in the laboratory are often very different from those experienced by fish in the field. Our understanding of fish energetics, especially during parental care, is still very fragmentary (Sargent, 1997), and it is difficult to detect laboratory artefacts. Another important issue is that the ability to re-mate might influence decisions. Isolated individuals in the laboratory might perceive a highly male-biased OSR (i.e. a shortage of potential mates) and might thus tend to avoid cannibalism. This reluctance to abort the brood unless it is extremely small might limit the effect of food ration, thus making it undetectable with the usual small sample sizes adopted in such experiments. As the effect of OSR on total filial cannibalism has yet to be explored, it is difficult to assess the magnitude of this factor. Field experiments are needed to understand whether the lack of a link between energetics and cannibalism in the laboratory is simply an artefact of the experimental procedures, or whether some of the assumptions behind the theory of total filial cannibalism might need to be reconsidered.

The effects of intersexual and intrasexual interactions (mate availability, sex of the cannibal, paternity certainty) have only received very little attention in the literature, and the evidence is at best circumstantial. As discussed above, the interaction between mate availability and filial cannibalism could have fundamental consequences on the interpretation of laboratory studies. There is a strong need for manipulative experiments, rather than correlates, to investigate explicitly this possibility. The prevalence of male cannibalism in species with biparental care is suggestive, but a much more thorough theoretical approach based on game theory is necessary to assess the validity of this trend. Interspecific comparisons, appropriately controlled for phylogenetic interactions, could clarify this issue.

III. PARTIAL FILIAL CANNIBALISM

(1) Theory and predictions

Partial filial cannibalism can be interpreted as an investment in current as well as future reproductive success (Sargent, 1992; Fig. 1). By eating some of their eggs, parents can minimize the deterioration of body condition due to the loss of foraging opportunities and the high energetic cost of care (Rowher, 1978; Sargent, 1992). Parents might be able in this way to provide better care to the remaining offspring (Fig. 2). Furthermore, cannibal parents might improve their own survival and might be able to re-enter the actively breeding population at a much faster rate than non-cannibals.

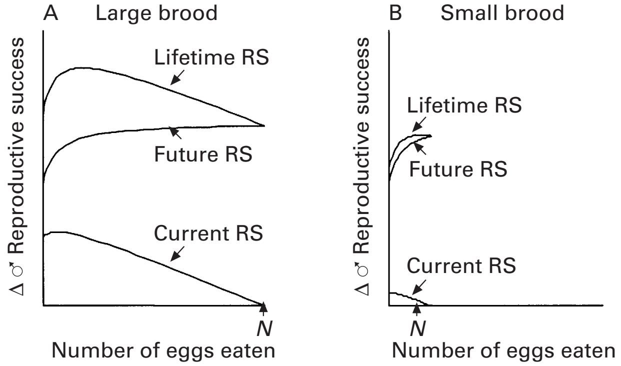

Fig. 1. Effect of filial cannibalism on the components of male reproductive success (RS). The current reproductive success peaks when a few eggs are eaten (see Fig. 2 for a full explanation); the future reproductive success is assumed to show a diminishing marginal return. Total brood size is indicated by N. (A) For a large brood, optimal lifetime reproductive success is achieved when only some of the eggs are eaten. The optimal level of cannibalism is higher than when only current reproductive success is considered. (B) Within this framework, total filial cannibalism is expected in small broods. Current reproductive success is low, but the effect of cannibalism on future reproductive success is the same as with a large brood. Lifetime reproductive success increases monotonically and it is maximized when the whole brood is cannibalized (i.e. when future reproductive success is maximized). Redrawn after Hoelzer (1995), modified to include the beneficial effect of filial cannibalism on current reproductive success.

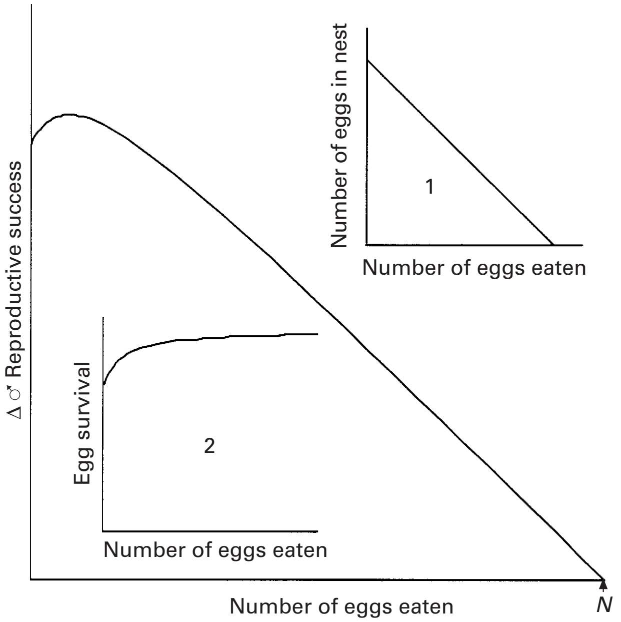

Fig. 2. The effect of filial cannibalism on current reproductive success. The curve is the product between (1) the number of eggs left in the nest after cannibalism and (2) the probability of hatching. (1) The number of eggs in the nest declines linearly as the male cannibalizes them. (2) The survival of the eggs, a function of parental effort and thus of the male physical condition, is assumed to show a diminishing marginal return with increasing cannibalism.

The relationship between brood size and partial filial cannibalism (Fig. 3) is profoundly different from that with whole-clutch cannibalism. The number of cannibalized eggs is expected to increase with brood size, as the cost of eating one egg decreases proportionally as brood size increases, but it should level off and become independent of size above a threshold number of eggs (Prediction A, Section III.2*a*). The asymptotic value is due to the diminishing marginal return of eating more eggs; beyond a given ration, the male is simply satiated.

If parents eat some of their eggs to counteract the loss of foraging opportunities experienced during brood care, the number of eggs cannibalized should depend on the physical condition of the parent

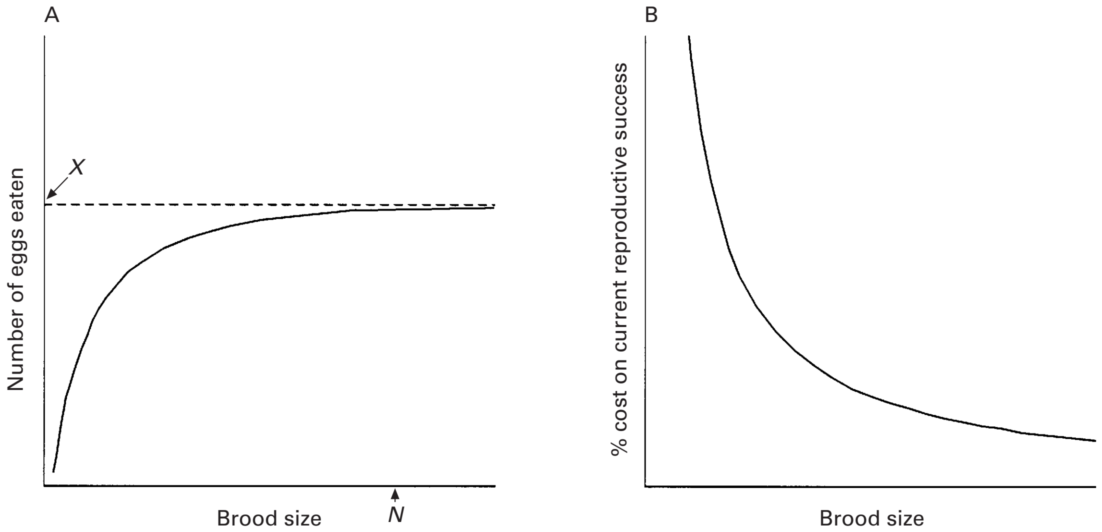

Fig. 3. (A) The relationship between brood size and filial cannibalism. At brood sizes above *N*, the number of eggs eaten reaches an asymptotic value (*X*) due to the diminishing marginal return of consuming eggs. (B) The effect of brood size on the relative cost of partial filial cannibalism assuming the relationship between brood size and cannibalism shown in (A). Cannibalism of a constant number of eggs irrespective of brood size gives a qualitatively similar graph, but the slope of the right-hand side of the curve is less steep.

(Prediction B, Section III.2*b*; Rowher, 1978; Sargent, 1992). As a corollary, we would also expect larger males to eat more eggs than smaller males (Prediction C, Section III.2*c*), as their energy requirements are higher (Rowher, 1978; FitzGerald, 1992).

When given a choice, males are also predicted preferentially to cannibalize eggs with a lower reproductive value (Rowher, 1978; Pressley, 1981; Sargent, 1992). Thus, if differently aged eggs are present in the nest, males are expected to cannibalize the youngest eggs in the brood (Prediction D, Section III.2*d*). As a further bonus, younger eggs have a higher nutritional value than older ones (Gilbert, 1985).

Rowher (1978) argued that the value of eggs changes during the breeding season. Early in the season, males should show high levels of cannibalism because of the high expected future reproductive success (Prediction E, Section III.2*e*). Conversely, at the end of the breeding season, the reproductive value of eggs is maximal, as the male is unlikely to get another brood. However, following Prediction C, a loss in body condition over the breeding season would tend to produce the opposite trend.

The value of the eggs should also depend on the certainty of paternity (Svensson *et al.*, 1998). The incidence of partial filial cannibalism is expected to increase as sneaking (defined as opportunistic males interfering with a spawning pair to attempt to fertilize some of the eggs) becomes more frequent (Prediction F, Section III.2*f*).

(2) Empirical evidence

(*a*) *Brood size*

Sargent (1988) found no correlation between brood size and the number of eggs eaten by parental males in the fathead minnow *Pimephales promelas* Rafinesque in aquaria, leading to a significant increase in clutch survivorship with clutch size. Analogous results were found in the laboratory for *Etheostoma flabellare* (Lindström & Sargent, 1997), in the field for the dusky damselfish *Stegastes dorsopunicans* (Petersen & Hess, 1991), and both in the field and in the laboratory for the Mediterranean blenny *Aidablennius sphynx* (Valenciennes) (Kraak, 1996). Forsgren, Karlsson and Kvarnemo (1996) also describe an increase in hatching success with brood size in the sand goby *Pomatoschistus minutus*, but the relationship loses significance when the episodes of total cannibalism are removed from the data set ($P = 0.06$).

Svensson *et al.* (1998) found a relationship opposite to that expected in the common goby *Pomatoschistus microps*, as parental males that ate some of their eggs had smaller broods than non-cannibals. Svensson *et al.* (1998) suggest either an increase in paternal effort with brood size or a threshold number of eggs above which males do not cannibalize. The trend is unlikely to be explained in terms of male quality (i.e. better males receive more eggs and cannibalize less) as males were randomly assigned a female to spawn with.

(*b*) *Parent physical condition*

Marconato, Bisazza and Fabris (1993) found a correlation between parental energy reserves and the incidence of partial cannibalism in the river bullhead *Cottus gobio* in the field. They observed an increasing number of eggs being eaten as the breeding season advanced while male condition deteriorated. The authors argue that, since this species only shows one brood cycle per reproductive season, partial cannibalism is the only option for the male to avoid dying of starvation while caring and it can only be interpreted as an investment in current reproductive success. However, they fail to consider that maintaining a higher fitness might also improve overwinter survival, and thus enhance future reproductive success as well. Similarly, partial filial cannibalism increases towards the end of the breeding season in the shanny *Blennius polis* (Qasim, 1956, 1957) and late in the monthly reproductive cycle in *Microspathodon chrysurus* (Petersen & Hess, 1991).

Belles and Isles (1991) found contradictory results in different species of sticklebacks. Filial cannibalism by male threespine sticklebacks *Gasterosteus aculeatus* was more common late in the breeding season both in the laboratory and in the field, but no seasonal trend was found for field-breeding *Gasterosteus wheatlandi* Putnam. Significant differences were also detected between the two years included in the survey.

In a manipulative field experiment, Hoelzer (1992) investigated the effect of supplementary feeding on partial filial cannibalism in the Cortez damselfish, *Stegastes rectifraenum*. Parental males of this species have two major food sources: the algal mats grown in their territories and the eggs in their nests. Hoelzer offered conspecific eggs to guarding males and observed a decrease in cannibalism compared to control males without supplementary feeding. However, supplementary feeding was never observed fully to inhibit partial filial cannibalism, but only to reduce it. Kraak (1996) obtained similar results with *Aidablennius sphynx* in the field. She experimentally fed one male, and the male reduced cannibalism while guarding a small brood, but filial cannibalism was not fully inhibited.

The results from laboratory feeding experiments are contradictory. A feeding experiment on *Gasterosteus aculeatus* showed no effect of ration on the number of eggs eaten by parental males (Belles-Isles & FitzGerald, 1991). Similarly, Lindström and Sargent (1997) found no difference in the incidence of cannibalism by *Etheostoma flabellare* males fed *ad libitum* with earthworms or small arthropods and by control starved males. Within treatments, egg cannibalism was shown to lead to improved body condition.

Kvarnemo *et al*. (1998) provide the only laboratory proof that supplementary feeding can decrease the incidence of cannibalism. Common gobies *Pomatoschistus microps* fed with excess mussel meat or a combination of mussels and conspecific eggs exhibited lower cannibalism rates than starved males. No significant difference was found between the two feeding regimes, arguing against any special nutritional characteristic of eggs in this species.

(*c*) *Parent body mass*

Hyatt and Ringler (1989) provide the only available evidence to test the prediction that small males should eat fewer eggs than larger males. *Gasterosteus aculeatus* were sampled from a wild population from British Columbia using traps. Stomach content analysis revealed no correlation between body size and the number of eggs eaten. However, no distinction between filial and heterocannibalism was possible in their study, and the authors suggest that most cannibalism should be attributed to nest raiding from non-relatives.

(*d*) *Preferential cannibalism of young eggs*

Salfert and Moodie (1985) used radioisotopes to label eggs in the nests of brook sticklebacks *Culaea inconstans* (Kirtland) in the laboratory. By measuring the changes in radioactivity in the parental males, they were able to show that males preferentially ate younger eggs.

Sikkel (1994) found a change in preference during the two phases of the brood cycle [brood cycling is defined as the alternation of periods of mating activity ('mating phase') with days of full brood care ('parental phase'), *sensu* van Iersel (1953)]. During the parental phase, cannibal males mostly ate the youngest eggs. However, during the mating phase, exposed 'old' eggs were selectively consumed. This preference can be explained by considering the attractiveness of eggs to females (see Section V.1).

(*e*) *Seasonal trends*

As discussed above (Section III.2*b*), seasonal trends of filial cannibalism (e.g. Qasim, 1956, 1957; Belles-Isles & FitzGerald, 1991; Petersen & Hess, 1991; Marconato *et al.*, 1993) go in the opposite direction to that suggested by Rowher (1978) under the assumption that males value their late broods more than early ones.

(*f*) *Certainty of paternity*

Svensson *et al.* (1998) tested the effect of sneaking on filial cannibalism in the common goby *Pomatoschistus microps*. Treatment males were confined in a tank with another much smaller male, which often acted as a sneaker. The authors detected no difference in the number of eggs eaten by treatment and control males. There was also no effect on either fanning or defense against a simulated predator, the two other estimates of parental expenditure monitored during the experiment.

(3) Discussion

No relationship was found between brood size and the number of eggs cannibalized by parental males by most studies (e.g. Sargent, 1988; Petersen & Hess, 1991; Kraak, 1996; Lindström & Sargent, 1997). The right-hand side of the curve in Fig. 3A predicts such a trend. With smaller brood sizes, the theory predicts a decrease in the number of eggs eaten by the male, but this was not observed in any of the studies cited above. All the investigated species are polygamous and normally guard relatively large broods. Small broods are usually fully cannibalized (see Section II.2*a*), preventing the investigation of partial filial cannibalism when very small numbers of eggs are present in the nest. Monogamous species of substrate guarders, which will care for broods much smaller than those found in polygamous species, are the most likely candidates to show a decrease in the number of cannibalized eggs with decreasing brood size.

The only exception to the trend of no relationship between brood size and the number of eggs cannibalized by parents comes from the work of Svensson *et al.* (1998) on common gobies. The authors point out a possible interaction between variable parental effort and the number of eggs cannibalized. The current theoretical framework is inappropriate to investigate this issue. To my knowledge, all models of filial cannibalism (Rowher, 1978; Sargent, 1992; Hoelzer, 1995; Sargent *et al.*, 1995) assume a fixed level of parental investment: the male either cares for the brood or abandons it. The development of dynamic resource allocation models, which take into account variable effort, would probably provide further insights into the dynamics of filial cannibalism.

In the past, the major criticism to Rowher's (1978) theory has been the lack of empirical support for a link between energetics and filial cannibalism (e.g. Belles-Isles & FitzGerald, 1991; Smith, 1992). Hoelzer (1992) and Kvarnemo *et al.*'s (1998) studies provide strong evidence that fed males eat fewer eggs than starved ones, at least in gobies and damselfishes. The negative results obtained by other authors have been sometimes explained by the possible presence of nutrients in the eggs which may be rare in the parent diet (FitzGerald, 1991, 1992; Sargent, 1997). I do not know of any specific test of this hypothesis, and the concerns expressed regarding laboratory studies investigating total cannibalism apply here also. Hoelzer's (1992) field experiment suggests that the energetics of filial cannibalism might be complex, with multiple food-related resources. Egg cannibalism was never fully inhibited by supplementary feeding, and males fed with eggs did not show a significant decrease in their feeding on algae. Further empirical and theoretical work is needed to investigate the presence of multiple food-related resources and its possible effect on the dynamics of filial cannibalism (Sargent, 1997). Kraak (1996) provides an alternative explanation. She suggests that some of the observed filial cannibalism could be a form of cleaning behaviour, as the parent also needs to remove diseased and unfertilized eggs (see Section IV.2). Thus, a residual level of cannibalism would be expected after supplementary feeding, since egg mortality would be present irrespective of the parents condition. This hypothesis could be tested in a species where defense is the major source of mortality and oxygenation is relatively unimportant. In such species, the residual level of cannibalism after supplementary feeding should be similar to the baseline mortality found in unattended nests which are protected from predation.

IV. ALTERNATIVE EXPLANATIONS

(1) Filial cannibalism without parental care

Recently, filial cannibalism has also been documented in species with broadcast (or pelagic) spawning [e.g. razorfish *Xyrichtys splendens* (Nemtzov

& Clark, 1994), blue-headed wrasse *Thalassoma bifasciatum* (Bloch) (Warner, 1998)]. These reports clearly show that parental care is not necessary to explain filial cannibalism, which can be set in the more general framework of optimal reproductive investment. Parental care is just an extreme situation in which fish have very high energy expenditures and limited foraging opportunities. In highly polygynous species where males strongly compete for females by displaying on mating territories, males are also faced with high energy requirements (e.g. Warner, 1998). Furthermore, as females of these species appear to have a strong preference for sites rather than for intrinsic male traits, foraging might also be restricted as the male needs to keep control of the highly valuable breeding territory (Warner, 1998). Energy requirements can be so high that males are often sperm limited (Shapiro, Marconato & Yoshikawa, 1994; Warner *et al.*, 1995; Marconato & Shapiro, 1996; Shapiro & Giraldeau, 1996). The fundamental reasons for filial cannibalism in broadcast spawners are the same as those suggested for brood consumption by parental species, and most of the predictions formulated in Section III are expected also to apply to broadcast spawners (except for a preference for young eggs, as males are not in contact with the eggs except at the time of spawning).

(2) Non-energy-based explanations

Several alternative explanations not based on energetics have been suggested for partial filial cannibalism (e.g. Smith, 1992). Some of the eggs eaten by a parent can be attributed to the removal of unfertilized, malformed or diseased eggs (e.g. Thresher, 1984; Mrowka, 1987; Kraak, 1996). By manipulating the number of fertilized and unfertilized eggs brooded by female Egyptian mouthbrooders *Pseudocrenilabrus multicolor*, Mrowka (1987) clearly showed that females progressively remove all the unfertilized eggs present in their mouth over the first few days of parental care.

Some episodes of filial cannibalism might also be interpreted as ‘making the best of a bad job’. In threespine sticklebacks, schools of females are known to raid male nests and cannibalize eggs (a form of heterocannibalism, i.e. non-kin cannibalism; *sensu* Rowher, 1978). Females never initiate raids on nests where they have laid eggs, but they join in after the parental male has been overpowered and egg consumption by others has already started (FitzGerald & van Havre, 1987). Filial cannibalism is, in this case, an attempt to recover some of the somatic loss that the disruption of the nest will entail (FitzGerald & van Havre, 1987). Similarly, starved male sticklebacks join raids on their own nests but never initiate them (FitzGerald & van Havre, 1987).

In a few instances, filial cannibalism might indeed be a maladaptive behaviour. For example, mouthbrooders might eat a few of their eggs by mistake (FitzGerald & Whoriskey, 1992). While removing unfertilized eggs, females of *Pseudocrenilabrus multicolor* also consume a few fertilized eggs. These eggs might have been developing abnormally or the female might be actively feeding on them (Mrowka, 1987), but cannibalism might also be the result of eggs sticking together and limiting the ability of the parent to eliminate selectively only unfertilized eggs (FitzGerald & Whoriskey, 1992). Male pupfish *Cyprinodon pecosensis* fiercely defend their territories, excluding all other fish from the area (Kodric-Brown, 1983). Any egg located by a male within his territory is cannibalized, including ones he has fertilized, but clutches spawned by females within a guarded area often go undetected and receive protection from the territorial behaviour of the male (Kodric-Brown, 1983).

As with all maladaptive explanations, it is difficult to prove conclusively the absence of any adaptive component. It is important to note that parents have been shown to evolve behaviours that prevent accidental consumption of offspring, such as inhibition of egg consumption during parental care (e.g. Johns & Liley, 1970) and kin recognition (e.g. Loekle, Madison & Christian, 1982; FitzGerald & van Havre, 1987). The genetic basis for filial cannibalism has been demonstrated in guppies by Lima and Vrijenhoek (1996). By crossing the cannibalistic *Poeciliopsis monacha* and the non-cannibalistic *Poecilioposis lucida* Miller, they obtained several strains of hybrids that tended to be intermediate with respect to cannibalism. Thus, it seems unlikely that filial cannibalism could be so common if it was maladaptive, as natural selection would be expected to lead to the evolution of appropriate strategies to minimize mistakes.

Several reports of maladaptive cannibalism are likely to be due to laboratory artefacts or unusual conditions, as suggested in the early days of ethology. For example, both the mouthbrooder blackchin tilapia *Sarotherodon melanotheron* Rüppell and the substrate guarder redbelly tilapia *Tilapia zilli* (Gervais) are known to consume their brood as a response to capture (Eyeson, 1983). The paradise fish *Macropodus opercularis* (L.) (DeNeff & Villars, 1982) fails to develop parental behaviour and consumes the brood in very low light conditions, but it is arguable whether this response has any relevance in nature.

V. FILIAL CANNIBALISM AND SEXUAL SELECTION

(1) Female counter-strategies

Filial cannibalism imposes strong evolutionary pressures on the sex that does not cannibalize (usually the female), with a potential for strong intersexual conflict.

The most obvious strategy to minimize filial cannibalism is active policing by the non-cannibal sex. For example, female convict cichlids aggressively exclude males from the proximity of eggs until they hatch, and filial cannibalism in this species is only recorded at the wriggler (post-hatching) stage (Lavery & Keenleyside, 1990*a*, 1990*b*). In the biparental cichlid *Tilapia mariae*, males paired with females smaller than themselves are most likely to cannibalize the eggs (Schwank, 1986). Cannibalism in this case might be a simple response to brood size, but it might also be linked to the ability of the female to defend the brood (FitzGerald, 1992). Okuda and Yanagisawa (1996*b*) report anecdotal evidence that, in the paternal mouthbrooder *Apogon doederleini*, females attack their former mates following total cannibalism by the male. As a possible consequence, males of this species are more likely to cannibalize broods from non-resident females than from resident ones (Okuda & Yanagisawa, 1996*b*).

In species with paternal care, females usually abandon the eggs after laying in the males nest and so lose any direct control over the fate of their offspring. The only strategy available to females to minimize the effect of male cannibalism is mate choice. Females might prefer males in good condition, and thus less likely to cannibalize their eggs (e.g. Unger, 1983; Knapp & Kovach, 1991). However, alternative explanations, such as better brood defense or a direct signal of heritable fitness, can be argued to explain the preference for individuals in good condition (Knapp & Kovach, 1991; Knapp & Warner, 1991). Furthermore, the lack of a clear link between energetics and filial cannibalism does not allow us to evaluate such a strategy.

Females might also use test eggs to judge the quality of a potential father. In *Aidablennius sphynx*, males with an empty nest sometimes receive only 1–10 eggs (Kraak & van den Berghe, 1992). Males that eat the eggs are less likely to receive further eggs than males that care for the diminutive clutch. The initial clutch could thus function as a test to reveal the males' intention of cannibalizing the eggs.

Rowher (1978) suggested that females might minimize the risk of cannibalism by dilution. As discussed above, the proportional cost of cannibalism decreases with brood size. By laying in nests that already contain eggs, females can thus reduce the probability that one of their eggs will be eaten. This strategy also minimizes the risk of total filial cannibalism. There is much evidence from both field and laboratory experiments that females prefer males whose nests already contain eggs (Ridley & Rechten, 1981; Marconato & Rasotto, 1983; Marconato & Bisazza, 1986; Unger & Sargent, 1988; Gronell, 1989; Knapp & Sargent, 1989; Sikkel, 1989; Kraak & Videler, 1991; Kraak & Groothius, 1994). However, alternative explanations can be suggested for why such a preference should be adaptive: parental investment has been shown to increase with brood size (Coleman *et al*., 1985; Sargent, 1988); predation by non-kin could also be diluted with increasing clutch size (Ridley & Rechten, 1981; Unger & Sargent, 1988); females might minimize searching costs by imitating other females' choices (Losey *et al*., 1986; Dugatkin, 1992; Dugatkin & Godin, 1992; Gibson & Hoglund, 1992; Pruett-Jones, 1992); the presence of eggs in the nest could by itself confirm that the male is a good parent (Ridley, 1978; Sargent, 1988).

In a laboratory investigation on sand gobies, Forsgren *et al*. (1996) showed that females by choosing males with eggs gain a direct benefit mostly through a reduction in filial cannibalism. Kraak (1996) obtained similar results in the field working on *Aidablennius sphynx*. Kraak and Weissing (1996) analyzed the benefits and costs of female preference for nests with eggs in *Aidablennius sphynx* by means of a simulation model. They assume males to eat a constant number of eggs per day and demonstrate that, when female preference is widespread in the population, the preference is adaptive and can minimize the effect of filial cannibalism. However, the fitness of the preference is positively frequency dependent, and, according to their model, filial cannibalism is not sufficient to cause the spread of female preference when the latter trait is at low frequencies. The authors point out potential errors in the estimation of parameters used in their model, and discuss how these errors could account for why cannibalism did not lead to the evolution of female choice in their simulations. They also provide an alternative explanation, namely that the behaviour might arise for reasons independent of cannibalism, as discussed above. I have used a modified version of Kraak and Weissing's model to show that female preference (A. Manica, unpublished data), if present in a population of non-cannibal males, might even favour the evolution of cannibalism. The introduction of female choice into a population of randomly mating females leads to an increase in the variance of male reproductive success, with a few males obtaining the majority of matings and the remaining males mostly having empty nests (see Fig. 4 in Kraak & Weissing, 1996). Thus, the average clutch size of parental males (i.e. males guarding eggs) increases with female choice. As discussed above, the incidence of partial filial cannibalism is expected to increase with increasing brood size (Sargent, 1992). Under a broad range of parameter estimates, the introduction of female choice led to an increase in fitness of filial cannibalism, often shifting the relative fitness value from below to above 1 (i.e. making the behaviour adaptive when it was not adaptive in a randomly mating population).

Partial cannibals are expected to consume preferentially the youngest eggs in the nest (Rowher, 1978; Sargent, 1992). Thus, females should also prefer to spawn in nests which contain young eggs (e.g. Unger & Sargent, 1988; Petersen, 1990). Several field observations suggest that males with young eggs are more likely to receive further clutches (e.g. Petersen & Marchetti, 1989; Petersen, 1990; Goulet, 1997, 1998), but this result again might be due to other factors, such as a decrease in courtship behaviour by the male during the mating phase. Sikkel (1989) provides conclusive evidence that females prefer to spawn in nests with young eggs. By manipulating the nest contents of male garibaldi *Hypsypops rubicundus*, he showed that males with young eggs are much more likely to obtain further matings than males with older eggs. Furthermore, in nests with mixed broods of eggs at different developmental stages, females lay their eggs only among other eggs at an early developmental stage (see Knapp, Sikkel & Vredenburg, 1995 for an analysis of the potential benefits of within-nest spawning-site preferences).

Rowher (1978) also predicted that, if females prefer to spawn in nests with young eggs, males might preferentially cannibalize older eggs during the mating phase. Sikkel (1994), by manipulating the position and age of eggs in nests of *Hypsypops rubicundus*, conclusively showed that males selectively consume exposed old eggs during the mating phase. Furthermore, females spawning in an empty nest always lay their eggs close to the periphery of the nest, thus minimizing the chances that the eggs will remain exposed as they get older.

Another female strategy that could lead to a dilution effect is spawning synchronization in females. Robertson, Petersen and Brawn (1990) detected high-frequency cycles in spawning synchronization of several reef fishes, superimposed on the much stronger lunar cycles. By investigating the incidence of filial cannibalism in *Stegastes dorsopunicans*, Petersen and Hess (1991) demonstrated that high-frequency cycles in spawning have the effect of minimizing the impact of egg consumption by parental males. However, high-frequency synchronization is also favoured by other factors, such as reduced searching time for females and enhanced parental care due to larger clutch sizes (Petersen & Hess, 1991).

(2) **Effect on OSR**

As discussed above, the operational sex ratio (*sensu* Emlen & Oring, 1977), has the potential to affect the incidence of filial cannibalism. Recently, Smith and Wootton (1995*b*, 1998) pointed out that the opposite might also be true, namely that filial cannibalism can lead to a bias in the OSR. A bias in the OSR is of great interest as it can predict which sex will compete for access to mates and how intense sexual selection will be (Clutton-Brock & Parker, 1992).

According to Clutton-Brock and Parker's (1992) definition, the reproductive cycle of an individual (D) can be divided between the time of being sexually active ('time-in', S) and the time spent being sexually unreceptive ('time-out', G). Thus, $D = S + G$ for each sex. In a population with an unbiased sex ratio, the OSR is given by the average male time-in divided by the average female time-in ($\mathrm{OSR} = S_m/S_f$, where the subscripts m and f represent the values for males and females, respectively).

Smith and Wootton (1995*b*) argued that, in the case of male parental care, total filial cannibalism will lead to a decrease in male time-out (G_m) and thus to an increase in S_m (since $D_m = G_m + S_m$). Since $\mathrm{OSR} = S_m/S_f$, total filial cannibalism will lead to a more male-biased OSR. Analogously, total filial cannibalism in a species with maternal care allows the mother to recover some of the energy invested the aborted attempt and will lead to a decrease in G_f, and thus a more female-biased OSR. Smith and Wootton (1995*b*) also suggested that partial filial cannibalism, by enhancing male energy status and thus his attractiveness to females, would lead to a reduction in male time-in since cannibals will be faster in acquiring mates. Hence, partial cannibalism can be seen as leading to a more female-biased OSR. However, this conclusion only holds under the assumption that females will be entering the reproductive phase continuously (Smith & Wootton, 1998). Kvarnemo (1998) pointed out that, in a finite population, a shorter time-in for cannibals will imply a longer time-in for non-cannibals, thus leading to an unchanged population S_m. Kvarnemo (1998) argues that partial filial cannibalism, by allowing males to reduce the cost of caring for a brood, could lead to a decrease in the time-out of cannibals, and consequently to a more male-biased OSR.

VI. CONCLUSIONS

(1) Empirical evidence on the occurrence of total filial cannibalism provides strong support for this behaviour being a form of adaptive brood termination. The energetic explanation of total filial cannibalism is corroborated by field correlates, but has not received support from laboratory manipulations. Field experiments are necessary to test the adequacy of the laboratory approach. The effect of the OSR on filial cannibalism has yet to be investigated in detail, and it might reveal interesting aspects of brood termination.

(2) The basic predictions based on Rowher's (1978) theory have received enough support to confirm the adaptiveness of partial filial cannibalism in most instances. The theoretical framework, however, is still unsatisfactory, and filial cannibalism needs to be integrated within the broader approach of variable parental effort. The link between energetics and partial cannibalism has been fully confirmed in two manipulative studies, but the presence of multiple dimensions describing the energetics of parental care needs further attention. Several corollary hypotheses stemming from the energetic explanation of partial filial cannibalism also need further investigation, which might help in explaining some inconsistencies among different studies.

(3) The same argument used for parental males can be used to explain filial cannibalism in the absence of parental care, and most predictions made for parental males should also apply to broadcast spawners. A thorough investigation of cannibalism in broadcast spawners might provide an interesting testing ground for the theory developed so far. Alternative explanations of filial cannibalism which are not based on energetics appear unlikely to account for most instances of this behaviour.

(4) The sexual conflict arising from filial cannibalism is a fascinating example of an intersexual arms race. Most of the empirical evidence, however, is confused by the presence of multiple explanations for the results. There is a need for further theoretical work to provide clear alternative hypotheses to be tested by empiricists.

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