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Strategic parental investment: Cannibalism and courtship in fishes with exclusive paternal care

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Bachelor of Science Advanced with Honours



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Abstract

Exclusive paternal care occurs in a broad range of animals and is especially common in ray-finned fishes. In many such species, males also compete for access to mates. Understanding how males balance investment in mating and parental effort is the main focus of my thesis. In this regard, several characteristics of the breeding biology of fishes with paternal care allow for potentially complex resource allocation strategies. These characteristics include the prevalence of filial cannibalism (i.e. parental consumption of their own offspring) and female tendencies to mate with egg-tending males. Filial cannibalism can provide a range of benefits to males, including provision of energy, and, thus, may enable fathers to sacrifice existing young as an investment into future reproductive success. In this thesis, I explored whether the relative value of existing young and the likelihood of future reproduction influence plasticity in filial cannibalism. Here, I found that the literature documents a diversity of male filial cannibalism responses to the presence of females. In some cases, males appear to capitalise on the opportunity to replace existing young and engage in elevated levels of filial cannibalism. In other cases, however, filial cannibalism seems to be discouraged by female presence, possibly due to female reticence to spawn with cannibals, or because accumulation of large broods when females are abundant encourages brood care whereas temporary absence of mating opportunities may promote filial cannibalism as a means to provide nourishment and facilitate survival to more productive times. Using the exclusive paternal caring sand goby (*Pomatoschistus minutus*) as a model, I also experimentally tested whether competition from rival males and predation threat from a piscivore affected filial cannibalism due to the potential of these factors to reduce male expectations of future breeding opportunities. These tests involved comparing filial cannibalism levels of egg-tending male sand gobies that were exposed to predators or rival male conspecifics to control males that brooded their eggs in the absence of these stimuli. Whole clutch consumption was less common in the presence of predators, whereas rival males had no effect on filial cannibalism. The best predictor of whole clutch consumption was, however, the size of a male's brood, thus suggesting that the value of the existing brood is more influential than factors that may stochastically determine future breeding success. Further to this, by measuring the courtship of males in one of the above experimental tests, I explored whether male fish exploit female preferences to spawn with egg-tenders by maintaining eggs specifically to attract mates and by engaging in elevated courtship effort whilst egg-tending. Sand goby males did not avoid cannibalism even when mating competition was experimentally intensified. Similarly, in a study using three-spined stickleback (*Gasterosteus aculeatus*) I compared the courtship behaviour of males tending freshly spawned eggs with other males that had not spawned and other males that had their freshly spawned eggs removed. Here I found that males did not capitalise on the value of their freshly spawned eggs in attracting mates via altering their own courtship, although the courtship vigour of males that had their eggs removed

was depressed. Together, my results highlight the complexity and variability in mating and parental effort among paternal caring species.

Publications during enrolment

Deal N. D. S., Wong B. B. M. 2016. How mate availability influences filial cannibalism. *The Quarterly Review of Biology* **91**:47-67. doi: 10.1086/685303

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Thesis including published works declaration

I hereby declare that this thesis contains no material which has been accepted for the award of any other degree or diploma at any university or equivalent institution and that, to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

This thesis includes three original papers published in peer reviewed journals. The core theme of the thesis is filial cannibalism and courtship in fishes with exclusive paternal care. The ideas, development and writing up of all the papers in the thesis were the principal responsibility of myself, the student, working within the School of Biological Sciences under the supervision of Bob Wong and Topi Lehtonen.

The inclusion of co-authors reflects the fact that the work came from active collaboration between researchers and acknowledges input into team-based research.

In the case of chapters 2, 3, 4 and 5 my contribution to the work involved the following:

Thesis Chapter	Publication Title	Status	Nature and % of student contribution	Co-author name(s) Nature and % of Co-author's contribution*	Co-author(s), Monash student Y/N*
2	<i>How mate availability influences filial cannibalism</i>	<i>Published</i>	<i>85%; Contributed to conceptualisation, researching, drafting and preparation of the manuscript.</i>	<i>-Bob B. M. Wong: (15%) Contributed to manuscript conceptualisation and preparation.</i>	<i>-BBMW: No</i>
3	NA	<i>Unpublished manuscript</i>	<i>84%; Contributed to development of experimental design; carried out all experimentation (with assistance from co-authors in specified areas); conducted all data processing and statistical analyses; drafted and prepared manuscript.</i>	<i>-Tapi K. Lehtonen: (5%) Provided assistance with experimental design, fish collection and manuscript preparation. -Kai Lindström: (1%) Provided facilities and advice for experimental setups. -Bob B. M. Wong: (10%) Contributed to experimental design; assisted with fish collection, measuring, and experimental program; contributed to manuscript preparation.</i>	<i>-TKL: No -KL: No -BBMW: No</i>
4	<i>Paternal investment with an uncertain future: effects of predator exposure on filial cannibalism and nesting behaviour</i>	<i>Published</i>	<i>84%; Contributed to development of experimental design; carried out all experimentation (with assistance from co-authors in specified areas); conducted all data processing and statistical analyses; drafted and prepared manuscript.</i>	<i>-Tapi K. Lehtonen: (5%) Provided assistance with experimental design, fish collection and manuscript preparation. -Kai Lindström: (1%) Provided facilities and advice for experimental setups, contributed to manuscript preparation. -Bob B. M. Wong: (10%) Contributed to experimental design; assisted with fish collection, measuring, and experimental program; contributed to manuscript preparation.</i>	<i>-TKL: No -KL: No -BBMW: No</i>
5	<i>The influence of parental status on courtship effort in a paternal caring fish</i>	<i>Published</i>	<i>88%; Contributed to development of experimental design; carried out all experimentation (with assistance from co-authors in specified areas); conducted all data processing and statistical analyses; drafted and prepared manuscript.</i>	<i>-Isaac Gravalin: (2%) Assisted with fish collection, advised on experimental design and fish care, contributed to manuscript preparation. -Bob B. M. Wong: (10%) Contributed to experimental design; assisted with fish collection, measuring, and experimental program; contributed to manuscript preparation.</i>	<i>-IG: Yes -BBMW: No</i>

I have included additional page numbering throughout this thesis for consistency.

Student name: Nicholas Deal

I hereby certify that the above declaration correctly reflects the nature and extent of the student's and co-authors' contributions to this work. In instances where I am not the responsible author I have consulted with the responsible author to agree on the respective contributions of the authors.

Main Supervisor name: Bob Wong

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Contents

Front matter

Copyright notice	i
Abstract.....	ii
Publications during enrolment	iv
Thesis including published works declaration	v
Acknowledgements	vii
Contents.....	ix

Chapter 1

Introduction	1
--------------------	---

Chapter 2

How mate availability influences filial cannibalism	20
---	----

Chapter 3

Filial cannibalism by a fish with exclusive paternal care in a competitive mating environment.....	42
---	----

Chapter 4

Paternal investment with an uncertain future: effects of predator exposure on filial cannibalism and nesting behaviour	78
--	----

Chapter 5

The influence of parental status on courtship effort in a paternal caring fish	89
---	----

Chapter 6

Discussion.....	100
-----------------	-----

Chapter 1

Introduction

Introduction

In species with parental care, typically males compete for mating opportunities while females invest in looking after offspring (Kokko and Jennions 2008). In many fish, however, as well as a range of other taxa, males are the sole providers of parental care while also competing for access to females (Ridley 1978; Vincent 1991). In these cases, a major challenge is to understand the strategies that males use to regulate investment into each of these components of life history. Specifically, under what conditions should males allocate resources to mating effort and under what conditions should they allocate resources to looking after young? This is an important question, especially in species that engage in filial cannibalism (i.e. the consumption of one's own offspring). Filial cannibalism can permit males to terminate investment in care and potentially even recoup vital resources to advance future reproduction (Rohwer 1978; Manica 2002). In this way filial cannibalism may allow animals to employ complex resource allocation strategies. Moreover, evidence that females may sometimes prefer males that are brooding previously spawned young (Ridley and Rechten 1981; Sargent 1988; Jamieson 1995; Reynolds and Jones 1999), and the capacity for males of some species to efficiently rear the young of multiple females contemporaneously (Manica and Johnstone 2004), mean that there can be strong synergistic elements between parental care and courtship effort. Accordingly, using fish with exclusive paternal care, this thesis explores the strategies males employ to invest in care and courtship.

Exclusive Paternal Care

Parental care is most often provided by females (Kokko and Jennions 2003, 2008). However, in a broad array of taxa, males act as the sole care providers to their young. Indeed, this exclusive paternal care occurs in at least 15 independent arthropod lineages (Zeh and Smith 1985; Tallamy 2000, 2001; Requena et al. 2014), about 1% of extant bird species (Cockburn 2006), about half of amphibians that care for young (Beck 1998; Summers et al. 2007; Wells 2007; Balshine 2012), and is the predominant form of care seen in ray-finned fishes (Actinopterygii) with parental care (Blumer 1979, 1982; Gross and Sargent 1985; Reynolds et al. 2002; Mank et al. 2005). In some cases, male only care is accompanied by a complete reversal of conventional sex roles, with females competing for access to the care giving males (Eens and Pinxten 2000), as seen, for example, in various pipefish (Syngnathinae) (Vincent et al. 1992), black coucals (*Centropus grillii*) (Goymann et al. 2004) and the smooth guardian frog (*Limnonectes palavanensis*) (Goyes Vallejos

et al. 2017). Intriguingly, however, in a large number of species, males continue to be highly competitive over access to females despite also performing parental care (Vincent 1991; Stiver and Alonzo 2009). This breakdown of the sex separation of conventional sex roles creates an important opportunity to study how investment in mate acquisition and parental care can be balanced by individual animals.

Non-depreciable care and multiclutch brooding

In most cases of male only care, active provisioning of the offspring is not performed, instead the key feature of male care is often the defence and maintenance of a spawning or nest site in which offspring develop (Blumer 1982; Zeh and Smith 1985; Wells 2007). In such cases, where care is directed towards an entire brood rather than individual offspring within the brood, the benefit of parental expenditure is likely to be an increasing function of brood size (Lazarus and Inglis 1986; Smith 1991; Smith and Wootton 1995). In many cases, brood care may even be approximated as non-depreciable (i.e. the cost of providing a given level of care to young within the brood is independent of brood size; Clutton-Brock 1991).

An important consequence of this “economy of scale” is that the most cost efficient way to rear young is to do so within large broods. Males, however, have relatively little control over the number of young produced from a single breeding event (Smith and Härdling 2000; but see: Leahy 1966; Crudginton and Siva-Jothy 2000; Blanckenhorn et al. 2002; Wolfner 2002). For females, factors such as benefits from depositing eggs with multiple males and physical and energetic limitations, may result in the female optimum in clutch size being lower than that for males (Ankney and MacInnes 1978; Wootton 1991; Byrne and Roberts 2012). However, this sexual conflict may be resolved where males rear clutches from multiple females contemporaneously in a single brood. Indeed, such breeding systems are quite common amongst species with paternal care (e.g. harvestman (*Iporangaia pustulosa*): Requena and Machado 2015; glass frog (*Hyalinobatrachium cappellei*): Noronha and Rodrigues 2018; giant water bug (*Diplonchus rusticus*): Ohba et al. 2018), and the ability to brood multiple clutches together may be instrumental in the evolution of many cases of exclusive paternal care (Manica and Johnstone 2004; Gilbert and Manica 2015).

Here, the question of how males balance mating and parental investment, however, becomes particularly pertinent, as males that are engaged in parental care of an initial clutch must court

additional mates to acquire further clutches. Indeed, since the benefits of rearing multiple broods together should be greatest where there is a large overlap in development times, recently spawned males might seek further mating with increased urgency. Moreover, where males are capable of caring for the young of multiple females at once, competition for access to females will be exacerbated, as a single male can remove multiple females from the mating pool (until they are ready to remate) thereby biasing the operational sex ratio (*sensu* Emlen 1976; Emlen and Oring 1977) towards males.

Filial cannibalism

Filial cannibalism has been documented in a surprising diversity of taxa (e.g. arthropods: Bartlett 1987; Mori and Chiba 2009; fish: FitzGerald 1992; Manica 2002; Lindström and St. Mary 2008; amphibians: Okada et al. 2015; reptiles: Huang 2008; birds: Tortosa and Redondo 1992; Gilbert et al. 2005; mammals: Bronson and Marsteller 1985; Beery and Zucker 2012). Following the seminal writings of Rohwer (1978), the potential for this behaviour to be adaptive has been recognised. Here, several potential benefits of filial cannibalism have been postulated. The most obvious and widely explored is that filial cannibalism can provide the parent with energy or nutrients that will enable them to produce or better care for other offspring (Manica 2002). This claim is supported by studies showing that supplementing the diet of parents can reduce the incidence of filial cannibalism (Schneider and Wade 1989; Hoelzer 1992; Kraak 1996; Kvarnemo et al. 1998; Manica 2004; Okuda et al. 2004; but see: Belles-Isles and FitzGerald 1991; Kvarnemo 1997; Lindström and Sargent 1997; Candolin 2000a; Candolin 2000b; Klug and St Mary 2005; Segers et al. 2011), and engaging in filial cannibalism can help maintain the body condition or weight of parents (Bronson and Marsteller 1985; Lindström and Sargent 1997; Mehlis et al. 2009; Takeyama et al. 2013; but see: Klug and St Mary 2005). Nevertheless, despite these studies, relatively little is known about exactly how parents use the energy they gain from engaging in filial cannibalism. In a few species, it appears as though energy from offspring consumption directly enables care giving males to survive lengthy brood care periods (Marconato and Bisazza 1988; Marconato et al. 1993; Gomagano and Kohda 2008). However, the extent to which energy from eating young is used to facilitate other behaviours, such as courtship, is poorly understood. In this regard it is useful to distinguish between partial filial cannibalism, where only some offspring within a brood are consumed, and total filial cannibalism, where the entire brood is consumed. This is because partial filial cannibalism can conceivably be performed to assist the parent in investing in remaining

young, whereas total filial cannibalism essentially relies upon improvements to future reproduction for its adaptive basis (Manica 2002). Nevertheless, in many cases of partial filial cannibalism the relative importance of investment in current and future reproduction is unknown.

Beyond nutritional benefits, filial cannibalism may also allow parents to manipulate the size and composition of their broods. Eating some of the young in a brood can benefit the parent if the survival or quality of young reared is density dependent (Payne et al. 2002, 2004; Creighton 2005; Klug et al. 2006). For example, in beaugregory damselfish (*Stegastes leucostictus*), filial cannibalism of some eggs within the brood appears to be favoured as it improves oxygen availability and, thus, survival of remaining young (Payne et al. 2002). Similarly, amongst Syrian hamsters (*Mesocricetus auratus*), female offspring are eaten when resources are limited and conditions dictate that male offspring will have higher fitness (Beery and Zucker 2012). Filial cannibalism may also be employed to help parents avoid wasting resources caring for low value offspring (Klug and Bonsall 2007; Klug and Lindström 2008). To better understand which of these potential motives underpin various instances of filial cannibalism, more work exploring the environmental conditions that promote this behaviour is required.

Mate choice and courtship-care synergy

In many species with exclusive paternal care, females preferentially mate with egg-tending males (e.g. Ridley and Rechten 1981; Marconato and Bisazza 1986; Sikkell 1988, 1989; Unger and Sargent 1988; Knapp and Sargent 1989; Kraak and Videler 1991; Goldschmidt et al. 1993; Kraak and Groothuis 1994; Thomas and Manica 2005; Gilbert et al. 2010; Manica 2010; Nazareth and Machado 2010; Requena and Machado 2015; Ohba et al. 2016; Ohba et al. 2018; also reviewed in: Sargent 1988; Jamieson 1995; Reynolds and Jones 1999). A range of benefits may underpin this behaviour, including reduced costs of mate assessment, and sexy sons benefits associated with choosing a mate that has already had a history of mating success (Ridley 1978; Pruett-Jones 1992). However, direct benefits to offspring survival are probably most important in motivating this female preference (Jamieson 1995). Specifically, when females add their eggs to an existing brood, the increased number of young may elicit greater levels of care from the father and also protect the young from predation via a dilution effect (Sargent 1988). Perhaps most importantly in this regard, eggs in larger broods may be less likely to succumb to filial cannibalism from the father, as males consuming eggs to fuel brood care may not need to consume proportionately as many eggs (Rohwer 1978; Ridley and Rechten 1981). Moreover, males rarely abort brood care via complete

cannibalism of large broods (Manica 2002), since the benefits of caring for a large brood will be too great to forego.

From a male perspective, in species where females prefer males with eggs already in the nest, the presence of eggs could also be used by males to attract additional mating opportunities (Rohwer 1978). There is some evidence that male ornamentation has evolved to mimic the presence of eggs within the nest and thus entice female partners to spawn in fantail darters (*Etheostoma flabellare*) (Knapp and Sargent 1989). However, behavioural strategies employed by males to exploit female attraction benefits of parental care have not been extensively investigated. It has been suggested that, in some cases, males steal eggs from others in order to use these eggs to attract mates (Rohwer 1978), however more recent research has cast doubt over this potential explanation with the observation of such egg-stealing even in the absence of female mate choice benefits (Jamieson and Colgan 1992; Östlund-Nilsson 2002). Nevertheless, recent observations that, in some species, males increase their parental effort in the presence of females (Lindström et al. 2006), raise the important question of whether such behaviour is motivated by the value of existing young in mate attraction.

More broadly, given that, in a diverse range of species, females favour males that demonstrate proficiency of parental care (e.g. savannah sparrow (*Passerculus sandwichensis*): Freeman-Gallant 1996, 1997; fifteen-spined stickleback (*Spinachia spinachia*): Östlund and Ahnesjö 1998; human (*Homo sapiens*): Anderson 2011; see also: Hoelzer 1989; Stiver and Alonzo 2009), the potential for males to take advantage of these mate choice patterns to attract females needs to be explored. Little is known about the extent to which female mate choice patterns govern male parental care behaviour. Accordingly, understanding how this synergy between male parental care and courtship effort influences behavioural plasticity in male courtship and care effort is thus a promising avenue for investigation. Do males avoid consuming their own eggs in situations where the capacity of the eggs to attract females is important? Do recently spawned males capitalize on the attractive nature of their eggs and alter their mating effort accordingly?

Study species

Two model species were employed for my studies in this thesis. The first of these, the sand goby (*Pomatoschistus minutus*), is a small fish species found within inshore Atlantic waters around Europe as well as the Black, Mediterranean and Baltic Seas (Stefanni and Thorley 2003).

Reproduction occurs seasonally in shallow waters (Nelbring 1993). Male sand gobies typically excavate a hole underneath a rock or mollusc shell which serves as a nesting site (Lindström 1988). In some populations, competition for nesting sites can be intense, and it is common for other males to evict resident male sand gobies and usurp their nest (Lindström 1988, 2001; Forsgren, Kvarnemo and Lindström 1996; Lehtonen and Lindström 2004). From the nest site, male sand gobies court passing females with a multifaceted display, one particularly noticeable feature of which involves swimming back and forth to the nest “leading” the female (Lehtonen 2012; Blom et al. 2016). Female sand gobies spawn with males within the nesting cavity adhering their eggs to the roof of the cavity (Lindström 1988). After spawning, males are solely responsible for brood care, which lasts until the emergence of fry (around 1-3 weeks after spawning depending on temperature: Kvarnemo 1994). Paternal care in sand gobies involves the males tending to their developing eggs and guarding them from potential predators (Lindström 1998; Lissåker and Kvarnemo 2006; Olsson et al. 2016). Egg-tending males regularly continue to court additional females from the nest (Pampoulie et al. 2004), and will often rear clutches from multiple females simultaneously (Jones et al. 2001). Indeed, previous research suggests that female sand gobies often prefer to spawn in the nests of egg-tending males (Forsgren, Karlsson and Kvarnemo 1996; but see: Lindström and Kangas 1996). Moreover, female sand gobies prefer males that perform vigorous parental care activity (Lindström et al. 2006), and achieve high hatching success of their young (Forsgren 1997). Filial cannibalism is also well documented in this species, with males frequently consuming a small portion of their eggs prior to hatching (partial filial cannibalism) or, in some cases, the entire clutch (total filial cannibalism) (Forsgren, Karlsson and Kvarnemo 1996). Accordingly, sand gobies are an excellent study species with which to explore how the synergy between mating and parental effort influences male reproductive tactics.

My second model species, the three-spined stickleback (*Gasterosteus aculeatus*), is another small fish species that is widely distributed in coastal, fresh and brackish waters of the northern hemisphere, and is a classic model in behavioural ecology (Bell and Foster 1994; Östlund-Nilsson 2006; Heng et al. 2016). Like sand gobies, males provide all parental care, including nest defence and ventilation (van Iersel 1953; Whoriskey and FitzGerald 1994; Östlund-Nilsson 2006), and are also known to engage in filial cannibalism (Belles-Isles and FitzGerald 1991). Care is delivered inside and around a nest that males construct within their territory from sediment and plant or algal material (Östlund-Nilsson 2006). Courtship in the three-spined stickleback is also performed in and around the nest, and involves males engaging in a characteristic zig-zag display towards

potential suitors (Wootton 1976, 1984). Male sticklebacks will court additional females for several days following their attainment of an initial clutch (van Iersel 1953), and are capable of caring for the young of several females at once (Kraak et al. 1999a,b). Finally, like sand gobies, female sticklebacks are also known to preferentially spawn in nests that contain eggs (Ridley and Rechten 1981; Belles-Isles et al. 1990; Goldschmidt et al. 1993; but see: Jamieson and Colgan 1989; Jamieson et al. 1992; Jamieson 1994).

Thesis structure

Using sand gobies and three-spined sticklebacks as models, this thesis explores patterns of parental and mating effort. The aims of my thesis were to:

1. test plasticity of filial cannibalism behaviour and identify how males adjust this behaviour in response to environmental cues that may influence future breeding opportunities (i.e. mate availability, predator presence); and
2. investigate whether males use eggs to attract additional mates and, in so doing, strategically invest in courtship to exploit the benefits of rearing overlapping broods.

Chapter 2 comprises a literature review that explores how mate availability influences filial cannibalism. Using sand gobies, I then examine, in Chapters 3 and 4 respectively, how filial cannibalism is influenced by mating competition and predation risk. Finally, in Chapter 5, using three-spined sticklebacks, I present an experiment testing whether egg-tending males elevate their courtship effort to capitalise on the potential ornamental value of their eggs, and the efficiencies of rearing multiple clutches together.

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Chapter 2

How mate availability influences filial cannibalism

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HOW MATE AVAILABILITY INFLUENCES FILIAL CANNIBALISM

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ABSTRACT

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

INTRODUCTION

KILLING one's own offspring appears to be the antithesis of a good reproductive strategy, yet such behavior is likely to be a significant—but poorly recognized—

source of mortality among developing juveniles in many species (Mock 2004; Moreno 2012). One especially intriguing form of infanticide is filial cannibalism, which involves parents not only killing, but also eat-

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ing their own offspring. This phenomenon has been reported in a wide range of taxa, including arthropods (Bartlett 1987; Mori and Chiba 2009), fish (FitzGerald 1992; Manica 2002b; Lindström and St. Mary 2008), amphibians (Okada et al. 2015), reptiles (Huang 2008), birds (Tortosa and Redondo 1992; Gilbert et al. 2005), and mammals (Bronson and Marsteller 1985; Beery and Zucker 2012).

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

Scientists recognize two forms of filial cannibalism: total filial cannibalism, where all of the young a parent currently has un-

der its care are consumed, and partial filial cannibalism, where only a fraction of the brood is consumed (Rohwer 1978; Manica 2002b). Both of these forms of cannibalism can offer nutritional benefits to parents (Candolin 2000a; Kume et al. 2000; Manica 2004; Okuda et al. 2004; Gomagano and Kohda 2008; Mehliis et al. 2009; Takeyama et al. 2013). Furthermore, both can function as brood management. For example, total filial cannibalism can enable parents to free up valuable space for larger more profitable broods, as seen in Egyptian mouthbrooders (*Pseudocrenilabrus multicolor*; Mrowka 1987) and fantail darters (*Etheostoma flabellare*; Lindström and Sargent 1997). Similarly, partial filial cannibalism can enable parents to remove slower developing offspring or ensure that the number of offspring in a brood does not exceed that which can be supported by parental provisioning, as shown, for instance, in burying beetles (*Nicrophorus tomentosus*; Trumbo 1990) and sand gobies (*Pomatoschistus minutus*; Klug and Lindström 2008). In the case of Syrian hamsters (*Mesocricetus auratus*), consumption of offspring may even enable parents to manipulate the sex ratio of their broods (Beery and Zucker 2012).

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

The costs associated with parental effort required to replace eaten offspring can help to predict the circumstances under

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

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

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

the term “mate availability” (Kondoh and Okuda 2002). Thus, it has previously been predicted that animals experiencing high mate availability should, on average, commit more filial cannibalism, as they can more easily replace young (Okuda and Yanagisawa 1996b; Manica 2002b). This possibility, which was raised as a key area for research in the last major review of the topic (Manica 2002b), was, at the time, based on a single study (Okuda and Yanagisawa 1996b). Since then, however, there have been several more empirical contributions investigating the role of mate availability on filial cannibalism (Table 1).

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

Once we have outlined the possible mechanisms through which mate availability

TABLE 1
Summary of the results of studies examining the relationship between the availability of mates to parental male fish and the filial cannibalism levels of these males

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

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

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

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

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

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

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

tive success of individuals is limited by access to food rather than mates, then filial cannibalism could provide a means of acquiring the limiting resource. This might be especially important if increased levels of mate availability lead to the acquisition and consumption of young becoming a more viable means of attaining food than traditional foraging.

EMPIRICAL EVIDENCE

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

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

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

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

MECHANISMS FAVORING A NEGATIVE ASSOCIATION BETWEEN MATE AVAILABILITY AND FILIAL CANNIBALISM

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

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

The tendency for parents to completely consume small broods might result in increased total filial cannibalism by individuals experiencing low mate availability. This is because, in species where males can care for the young of multiple females at once, low mate availability may result in males acquiring smaller broods due to access to fewer females. Consequently, under such a scenario, total filial cannibalism may be

come more prevalent, as it tends to occur in response to small brood size. It should be noted, however, that this phenomenon should only occur if males can expect mate availability to increase in the future, since males should only commit total filial cannibalism of small broods if they can expect to attain larger broods in the future.

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

To recap, we have outlined two logical mechanisms through which the increase in expected future reproductive success that corresponds to high mate availability might influence filial cannibalism. From the orthodox position, animals should be more willing to commit filial cannibalism when future mating is likely, since consumed young are easily replaced. Paradoxically, an elevated likelihood of additional mating might also favor reduced total filial cannibalism, since the possibility of adding more young to a brood could increase the incentive to provide care. Differences between these two mechanisms do seem to accord with the available empirical evidence. For example, the expected brood size mechanism is only relevant for cases of total filial cannibalism, because it is total and not partial filial cannibalism that tends to be committed in response to small brood size (Manica 2002b; Myint et al. 2011a). In accordance with this, we note that it is only total filial cannibalism that has been observed to decrease

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

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

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

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

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

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

Perhaps the most widespread phenomenon that could result in sexual selection operating against filial cannibals is the preference of females to deposit their eggs in

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

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

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

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

1991; Milinski and Bakker 1992). This, in turn, should provide further disincentive for males to engage in filial cannibalism during times of high mate availability.

EFFECTS OF MATE AVAILABILITY ON TOTAL AND PARTIAL FILIAL CANNIBALISM

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

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

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

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

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

how brooding style interacts with the effect of mate availability on filial cannibalism.

EXPERIMENTAL CONSIDERATIONS

Timing of Presentation of Prospective Additional Mates

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

importance of prespawning cues, future studies are needed that examine the effects of prespawning mate availability in species that have previously been shown not to alter their filial cannibalism in response to postspawning mate exposure.

Role of Physical Contact with Prospective Additional Mates

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

Food Availability

An additional component of experimental design worthy of consideration in future experiments is the provisioning of food to parents. As noted in the introduction, one

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

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

gage in mouthbrooding or hold themselves up inside their nest during parental care; see Okuda and Yanagisawa 1996b; Myint et al. 2011a; Takeyama et al. 2013) could be more likely to respond to increased access to mates by engaging in greater levels of filial cannibalism.

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

RELATIONSHIP BETWEEN OFFSPRING CONSUMPTION AND ATTRACTIVENESS OF THE CANNIBAL

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

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

WHY ARE ATTRACTIVE INDIVIDUALS LESS PRONE TO FILIAL CANNIBALISM

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

The reverse causality is also possible: attractiveness can potentially influence an individual's access to mates and, in so doing, affect their inclination to engage in cannibalism. For instance, already attractive males may avoid eating their young, as

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

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

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

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

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

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

The behavior of potential suitors could also be influential in driving parents to commit filial cannibalism. In some species, prospective mates are known to kill the offspring of caring parents so as to coerce the parents into breeding with them (Hrdy 1974; Palombit 2015). A range of coun-

terstrategies have evolved to help parents protect their young from this fate, or lessen the cost when it occurs (Palombit 2015). One potential counterstrategy (the Bruce effect), well documented among a range of rodent species (among other mammals), involves female termination of pregnancy in response to encountering unfamiliar males (Bruce 1959; Labov 1981; Becker and Hurst 2008; Roberts et al. 2012). An analogous strategy available to parents caring for young after parturition or oviposition would involve parents eating their own young before infanticidal prospective mates are able to kill the young. This would allow the parent to recover some nutritional resources from their offspring before remating (Labov 1981). There is some evidence to suggest that this counterstrategy is employed by parental male sticklebacks (FitzGerald and van Havre 1987). However, as far as we are aware, it remains to be investigated whether such a strategy also exists in mammalian taxa, such as rodents, which display the Bruce effect (e.g., Bruce 1959; Heske and Nelson 1984; Hackländer and Arnold 1999; Pillay and Kinahan 2009; Marashi and Rülcke 2012) and engage in high levels of filial cannibalism (Day and Galef 1977; Bronson and Marsteller 1985; but see Weber et al. 2013).

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

ism as a counterstrategy to infanticide, and that used to trade up, would be that only in the former would the capacity of the caring parent to defend their brood from the new prospective mate influence the likelihood of cannibalism.

THE MACROEVOLUTIONARY EFFECT OF MATE AVAILABILITY ON FILIAL CANNIBALISM

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

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

experience lulls in mate availability. Accordingly, we believe that future work will benefit from explicitly differentiating between species- and individual-level effects of mate availability.

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

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

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

Kondoh and Okuda (2002) developed the only model that sets out to determine how mate availability influences filial cannibalism at the species level. They modeled a population of exclusive paternal carers with filial cannibalistic males that care for a set number of clutches per brood. A game theoretic approach was used to determine an evolutionary stable strategy for the number of clutches cannibalized per brood. Consistent with empirical studies of *Apogon* cardinalfish, they found that, at the species level, high mate availability facilitates increased filial cannibalism. The value of this model to the development of the field cannot be underestimated. Nonetheless, as is nearly always the case with modeling, certain simplifying assumptions were made that could influence the results. Extension of this model could help determine if mechanisms that might influence the individual-level effects of mate availability (especially those listed in the section, Mechanisms Favoring a Negative Association Between Mate Availability and Filial Cannibalism) also lead to species-level effects. At present, this remains a largely unresolved question. In particular, it would be instructive to develop models that include temporal and spatial fluctuations in mate availability, sexual selection against cannibals, and brood size effects on parental care and offspring survival.

Furthermore, Kondoh and Okuda's (2002) model assumes that filial cannibalism is a genetic, fixed strategy without phenotypic plasticity (Okuda et al. 2004). Developing filial cannibalism models in which animals can respond to their environment with a conditional strategy would be more realistic and, most importantly, provide insights into both species-level and individual-level effects of mate availability on cannibalism (Okuda et al. 1997, 2004; Takeyama et al. 2002). Although such models have been created (see, for example, Sargent 1992; Sargent et al. 1995), they have not yet been used to substantially investigate mate availability effects. Furthermore, models could be useful in gaining insight into whether partial and total filial cannibalism levels are each affected differently by changing mate availability at the species level; an area of particular interest as Kondoh and Okuda (2002) only addressed partial filial cannibalism in their model. Clearly, more investigations into the species-level effects of mate availability on filial cannibalism are needed to test the predictions of Kondoh and Okuda's (2002) model and verify the findings in a wider range of taxa. Experimental evolution with manipulations to mate availability should provide further insight into species-level effects. The challenge is to find a species that displays adequate levels of filial cannibalism and an appropriately short life cycle.

CONCLUSIONS

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

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

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

for which the cost of caring outweighs the reproductive gain. A second explanation for why some animals have an increased propensity for filial cannibalism when mate availability is low is that filial cannibalism may be used as a strategy by parents to facilitate their survival until times of higher mate availability. Finally, it could be that mate choice against individuals that have recently engaged in filial cannibalism encourages parents to avoid eating their own young when many potential mates are around as doing so could lead to large costs in lost mating opportunities. Future research testing the veracity of these mechanisms is needed.

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

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

Lehtonen and Lindström 2007). Research is needed to determine whether this is a consequence of females preferring males that are unlikely to commit filial cannibalism or whether attractive males avoid filial cannibalism as a consequence of increased access to mates. Similarly, future research should investigate whether parents take into account the quality of prospective mates when deciding to eat their young. Specifically, consideration should be given to the possibility that such behavior may represent parents attempting to trade up to higher quality mates or, alternatively, to avoid infanticide or offspring predation by potential mates.

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

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Chapter 3

Filial cannibalism by a fish with exclusive paternal care in a competitive mating environment

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Abstract

Parental consumption of their own offspring is often thought to be an adaptive behaviour that enables parents to sacrifice existing young for benefits to future reproduction. However, such filial cannibalism might also impinge on future reproductive success of the parent if potential mates avoid spawning with cannibals or prefer mates that are tending offspring. We examined whether mating competition influenced filial cannibalism in a fish with exclusive paternal care, the sand goby (*Pomatoschistus minutus*), by comparing behaviour of egg-tending males that were left alone during brooding or exposed to either a rival male conspecific or a congeneric fish that does not pose a sexual threat. The incidence of whole clutch consumption by parental males was not affected by exposure treatment and neither was the number of eggs eaten when broods were only partly consumed. Instead, poor male body condition and small initial clutch size best predicted whole clutch cannibalism indicating that intrinsic characteristics of the brood and parental male more strongly influence filial cannibalism than mating competition that may only stochastically relate to future breeding opportunities. An examination of male nest attendance and courtship behaviour during the brooding period did not reveal any effects of exposure treatment, except that males exposed to a congeneric fish spent less time inside their nest and engaged in less vigorous courtship when they had consumed their whole brood, possibly indicating increased vigilance and reduced desire to respawn around a potential nest predator. Courtship vigour was not linked to the number of eggs consumed by males but was positively associated with the number of eggs remaining at the end of brooding. Taken together our results suggest that filial cannibalism may be more strongly influenced by qualities of the existing brood and parental male and is not avoided nor employed to help overcome potential mating competition.

Introduction

The consumption of offspring by parents (i.e. filial cannibalism) is prevalent in a wide range of taxa, including arthropods (Bartlett 1987; Mori and Chiba 2009), amphibians (Okada et al. 2015), reptiles (Huang 2008), birds (Tortosa and Redondo 1992; Gilbert et al. 2005), mammals (Bronson and Marsteller 1985; Beery and Zucker 2012) and especially fish (FitzGerald 1992; Manica 2002b; Deal and Wong 2016). Even when the parent consumes the entire brood (known as total filial cannibalism), this behaviour may represent an adaptive mechanism through which the parent trades current offspring for improved future reproductive success (Rohwer 1978; Manica 2002b). Such reproductive success might be facilitated either by nutritional gain from offspring consumption or simply the result of the parent freeing themselves from the demands of caring for existing young (Petersen and Marchetti 1989; Smith and Wootton 1995). Partial filial cannibalism (where only a fraction of the brood is consumed) may improve future reproductive success in the above fashion as well, but it can also benefit remaining uneaten young. This may be via a reduction of within-brood competition (Payne et al. 2002, 2004; Creighton 2005), through other density-dependent survival effects (Klug et al. 2006; Davenport 2019), or via sustaining the parent during the brooding cycle (Marconato and Bisazza 1988; Marconato et al. 1993; Gomagano and Kohda 2008). Indeed, a range of studies have shown that supplementing the diet of parents can reduce the incidence of filial cannibalism (Schneider and Wade 1989; Hoelzer 1992; Kraak 1996; Kvarnemo et al. 1998; Manica 2004; Okuda et al. 2004; but see: Klug and St Mary 2005; Segers et al. 2011) or that engaging in filial cannibalism can help parents maintain a higher weight or body condition (Bronson and Marsteller 1985; Lindström and Sargent 1997; Mehlis et al. 2009; Takeyama et al. 2013; but see: Klug and St Mary 2005). What is less well understood, from a life history perspective, is how the energy gained from offspring consumption might impact parental behaviour (but see: Hoelzer 1992). Are parents using energy from filial cannibalism to reduce the need to forage, or to fuel parental care or courtship activities?

Where filial cannibalism is employed to improve future reproductive success, the incidence of this behaviour should be governed by the relative contributions of

current and future reproductive success to remaining lifetime reproductive success (Williams 1966; Sargent and Gross 1986; Sargent 1992). For example, the presence of offspring predators that diminish the expected success of a current reproductive bout can promote the occurrence of filial cannibalism (Huang 2008; Chin-Baarstad et al. 2009), whereas offspring that are at a later stage in their development, and thus more likely to contribute to lifetime reproductive success, are less likely to be consumed (Schwanck 1986; Petersen and Marchetti 1989; Lavery and Keenleyside 1990; Petersen 1990; Manica 2002a). Evidence showing the responsiveness of filial cannibalism to the expected value of future reproduction is, however, less conclusive. For example, access to prospective mates appears to promote filial cannibalism in some species (Okuda and Yanagisawa 1996; Okuda et al. 2004; Myint et al. 2011; Takeyama et al. 2013), while in others, it may have no effect (Bjelvenmark and Forsgren 2003) or even lead to a reduced incidence of total filial cannibalism (Pampoulie et al. 2004; Klug et al. 2005). Several potential mechanisms have been proposed to explain the latter observation. These include the possibility that sexual selection against filial cannibals might discourage parents from consuming young when prospective mates are around (Bjelvenmark and Forsgren 2003, Deal and Wong 2016). In addition, the likelihood of potential mates adding more young to a brood receiving paternal care may deter total filial cannibalism since provision of care to large broods is typically an efficient use of parental investment (Pampoulie et al. 2004, Deal and Wong 2016).

To date, all of the experimental studies that have investigated the effect of mate availability on filial cannibalism have done so by manipulating the number of females that parental males are exposed to (Bjelvenmark and Forsgren 2003; Okuda et al. 2004; Pampoulie et al. 2004; Klug et al. 2005; Myint et al. 2011; but see: Okuda and Yanagisawa 1996). However, it is widely believed that the operational sex ratio (OSR) is the crucial factor in determining the intensity of mating competition, and OSR is influenced by the presence of males as well as females (Emlen 1976; Emlen and Oring 1977; Kvarnemo and Ahnesjö 1996; Kokko et al. 2012). Despite this, few studies have investigated whether the presence of rival males influences filial cannibalism (but see: Bjelvenmark and Forsgren 2003).

Moreover, the effect of male mating competition may help us to understand the mechanism through which exposure to females can result in decreased total filial cannibalism, observed in some species (Pampoulie et al. 2004; Klug et al. 2005). If filial cannibalism reduces the desirability of males to potential mates (Lindström and Kangas 1996; Manica 2010), then increased male mating competition might lower the incidence of filial cannibalism (Deal and Wong 2016), as a competitive environment increases the importance of attractiveness (Noë 2017). Similarly, the same effect might occur if males switch to a more caring strategy when competition reduces the likelihood of further mating. On the other hand, a competitive mating environment could make it difficult for males to attract multiple females to spawn with them. This, in turn, may encourage greater levels of total filial cannibalism (Deal and Wong 2016), which is often employed when males do not attain a large enough number of eggs to warrant parental care (Schwanck 1986; Mrowka 1987; Petersen 1990; Forsgren, Karlsson and Kvarnemo 1996; Manica 2002a).

Here, we aim to examine the effects of mating competition on filial cannibalism and explore how the extent of filial cannibalism relates to subsequent behaviour in the sand goby, *Pomatoschistus minutus*. Offspring care in this species is performed exclusively by the male and consists of guarding and fanning eggs within a nest that males excavate in the sand beneath a rock, mollusc shell or similar artificial substitute (Lindström 1988). Males are known to frequently consume eggs they are guarding, engaging in either partial or total filial cannibalism (Forsgren, Karlsson and Kvarnemo 1996). Male sand gobies regularly rear the eggs of multiple females within their nest at the same time (Jones et al. 2001), and often continue to court and spawn with females for several days after receiving their initial clutch (Pampoulie et al. 2004). Previous research has shown that egg-tending males are less likely to engage in total filial cannibalism when exposed to females during brood care (Pampoulie et al. 2004). However, the reason for this response remains unclear. In this regard, absence of total filial cannibalism could be a strategy in response to female mate choice against filial cannibalism (Deal and Wong 2016). Indeed, sand goby females prefer males that are good fathers (Forsgren 1997; Lehtonen and Lindström 2007) and males that

display elevated levels of parental care in their presence (Lindström et al. 2006). Furthermore, females are much more likely to spawn in nests that contain eggs over those that have recently lost a brood (Forsgren, Karlsson and Kvarnemo 1996; Lindström and Kangas 1996). On the other hand, the presence of females may cause egg-tending males to expect that they will be able to add additional eggs to their broods. Correspondingly, this increased expectation of brood size may discourage total filial cannibalism since the rewards of caring for a large brood outweigh the costs (Deal and Wong 2016), as evidenced by previous studies which show that sand gobies are less likely to completely consume larger broods (Forsgren, Karlsson and Kvarnemo 1996; Lissåker and Kvarnemo 2006; Lissåker and Svensson 2008; Andrén and Kvarnemo 2014; Deal et al. 2017).

In this study we manipulated the perceived mating competition of egg-guarding male sand gobies by exposing them to either a rival conspecific male, a sympatric congener that does not pose a sexual threat (common goby, *Pomatoschistus microps*), or a control treatment without any competitor present. Here we anticipated that the way in which filial cannibalism was employed in response to competition would indicate the adaptive significance of this plasticity. Specifically, we predicted that, if males avoid filial cannibalism due to female mate choice against cannibals, then the presence of a rival male should discourage whole clutch cannibalism, since the rival increases the opportunity for females to exert mate choice. By contrast, if total filial cannibalism is used to eliminate broods that will not contain enough young to warrant continued care, we expected the opposite response to mating competition. That is, total filial cannibalism will be encouraged by the presence of a rival male conspecific as mating competition makes it more difficult for brooding males to entice additional females to add more eggs to their brood. Further to this, in order to provide insights into how any energetic gains from egg consumption are directed, we explored the relationships between filial cannibalism and male time budgets, courtship effort and weight change.

Methods

Collection and housing

This experiment was carried out in southern Finland on the coast of the Baltic Sea at the Tvärminne Zoological Station (59°50.7' N, 23°15.0' E) during the sand goby breeding seasons (May-June) of 2013 and 2014. Sand gobies and common gobies were collected from the nature reserve surrounding the station using both hand trawls (Evans and Tallmark 1979; Lehtonen and Kvarnemo 2015a) and dip-nets. After collection, fish were transported back to the station where they were housed in a semi-outdoor laboratory facility with natural light. The fish were separated out into single species stock tanks, and sand gobies were further divided by sex. All fish were then fed daily on a diet comprising of frozen chironomid larvae and live *Neomysis* shrimp. Stock tanks, as well as experimental aquaria (see below), within the facility were provided with a continuous flow through of sea water pumped from the Baltic Sea.

Spawning

To begin each replicate, a focal male sand goby was selected (using the criteria described below) and his total length and mass were measured. Males that appeared to be in poor health (for example, showing signs of fungal infection or with severely frayed pectoral fins) were not used and neither were especially small males (less than 38 mm), because competition for nesting sites disproportionately excludes small males from nesting in this species (Lindström 1988; Magnhagen and Kvarnemo 1989; Lindström and Pampoulie 2005). Each focal male was then placed into an individual experimental aquarium (length × width × water level: ~70cm × 30cm × 25cm) containing a sand substrate, with each aquarium divided into two compartments with a transparent acrylic divider (Figure 1). In this aquarium, the male was fed a diet of three frozen chironomid larvae per day for the duration of the experiment. The compartment into which the focal male was added contained a clay halved flowerpot (diameter of the mouth: 8 cm) that served as a nesting resource onto which the focal male could pile sand to construct a nest. The roof of the interior of the pot was lined with a

thin acetate sheet, to which spawning females can adhere their eggs. The other compartment was left bare. After a male was introduced into the experimental aquarium, it was given up to 2 days to construct a nest. Any males that did not build a nest within this period were excluded from further experimentation and returned to the sea. For males that constructed a nest, a gravid female (as indicated by her swollen abdomen; Forsgren 1995) was then introduced into the aquarium and left overnight to spawn. Females and any non-spawning males were not used for further analysis. For males that spawned, we then removed and photographed the acetate sheet lining the nest, in order to later count the attached eggs using the *ImageJ* (version 1.50b) manual cell counter plugin (Rasband 1997-2015). Care was taken to ensure the sheet and eggs remained submerged in a shallow tray of water during this procedure, after which they were quickly returned to the nest.

Brooding

After returning eggs to the nest, we allocated the attendant male randomly to one of three treatments. In the 'rival male' treatment, we added a randomly selected sand goby male into the experimental compartment adjoining the focal male's compartment. This ensured that the 'rival male' was visible to the focal male, but could not directly interfere with his parental care by taking over the nesting site or consuming the focal male's eggs. Moreover, the set-up of all experimental aquaria was such that sea water from the flow through system was first pumped into the compartment containing the rival male, and then flowed through holes in the barrier separating the compartments before exiting the aquarium via an overflow hole drilled in the focal male's compartment. This enabled olfactory cues from the rival male to reach the focal male. In the 'common goby' treatment, we added a common goby to the compartment adjoining the focal male (Figure 1). This treatment allowed us to control for the presence of another fish that could still pose a threat as a potential egg predator but is not otherwise a mating competitor to the focal male. In the 'control' group, the compartment next to the brooding male remained empty.

After treatment allocation, each male was left to brood his eggs until close to hatching (i.e. 7 days) while the stimulus fish (for relevant treatments) remained nearby in the adjoining aquarium compartment. At the conclusion of this brooding period we again removed and photographed the nest lining acetate sheet, so that we could later compare the number of eggs remaining with the size of the initial clutch that was spawned. This allowed us to deduce the number of eggs consumed by each brooding male (Lehtonen and Lindström 2007; Klug and Lindström 2008). After this final photograph was taken, we re-measured the wet mass of the male so that we could determine the extent of weight loss and then returned the fish to the sea. Males that died during brooding, $n = 11$, were excluded from analysis leaving a final sample size of $n = 16$ for rival male treatment, $n = 15$ for common goby treatment and $n = 16$ for the control.

Male behaviours

During the brooding period, we also assayed the behaviour of each male on three occasions so that we could uncover potential relationships between behaviour and filial cannibalism that might indicate the functional basis of filial cannibalism. These assays took place on days 3, 4 and 5 post-spawning, when male sand gobies are known to actively court additional females (Pampoulie et al. 2004). For each of these behavioural assays, we filmed the brooding male for two 30 minute periods that were separated by, at most, 30 minutes. During the first period of filming, the experimental tank was left undisturbed in order for us to gain insight into activity of males during the brooding period in the absence of females. For the second period of filming, we placed an opaque barrier between the two compartments of the experimental aquarium so that the brooding male could not see the adjoining compartment and any fish contained within. A clear plastic container (~12cm × 10cm × 30cm) housing a gravid female was then introduced to the focal male's compartment in front of his nest entrance in order for us to elicit and film male courtship behaviour (Figure 1). At the completion of this assay the female and divider were removed.

All filming for these behavioural assays was achieved with two cameras, one focused on the whole compartment housing the focal male and the other focused specifically on the male's nest entrance. We did not analyse the first 10 minutes of footage when males were potentially still in the process of recovering from any disturbance caused by setting up the cameras and becoming aware of the presence of a female. Instead, we watched the second 10 minutes of each filming period and, using a custom event recorder program written in *MATLAB 2013b*, measured various aspects of male behaviour. Specifically, we looked at male time budgets both in the absence and the presence of a female to enable us to understand male activity levels and fidelity to the nest site in both a non-courting and courting context. Here we divided male time into three mutually exclusive categories: time spent within the nest, time spent inactive while outside the nest, and time spent actively moving about outside the nest. In addition, as a further measure of courtship effort we counted the number of times males entered and exited their nest in the presence of a female as this easily quantified behaviour is performed frequently during courtship where males appear to attempt to lead females to their nest (Lehtonen 2012).

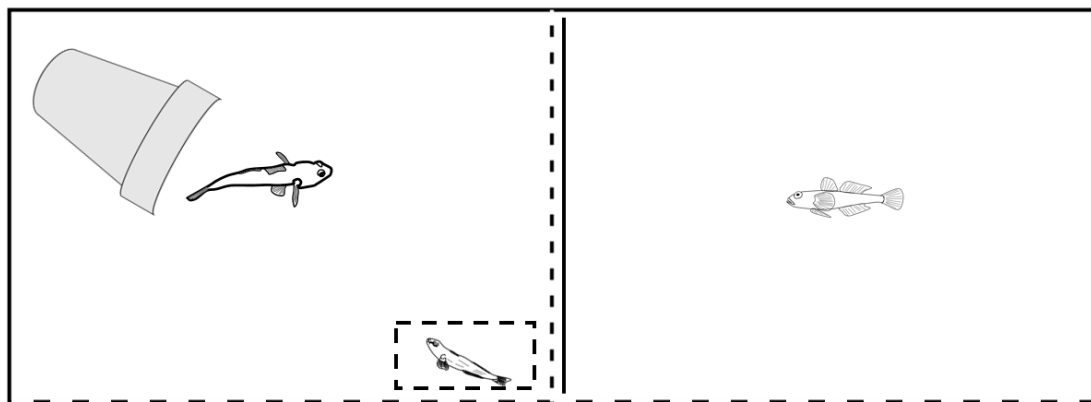


Figure 1. Overhead view of experimental aquarium layout. Note that solid and dashed lines represent opaque and transparent barriers respectively. Here, the second half of a behavioural assay is shown where a female sand goby is confined to a small receptacle in front of the focal male sand goby's nest. This receptacle, the female and the opaque divider in the middle of the aquarium were only present during this half of the behavioural assay and were otherwise not present during male brooding. The common goby shown in the large compartment on the right, adjacent to the focal male compartment indicates that this is a 'common goby' treatment. This common goby would be absent in the 'control' treatment, and replaced by a male sand goby in the 'rival male' treatment.

Statistical analysis

Statistical analysis was conducted using *R* (version 3.5.3; R Core Team 2019). With the exception of time budget models, we draw inference on the effect of each model parameter with use of likelihood ratio tests, comparing the full model with that excluding the parameter of interest. Thus, unless otherwise specified, we focus on the marginal effects of different predictor variables. All reported *p* values are two tailed (with significance level of $\alpha = 0.05$). For all analyses non-categorical predictor variable inputs were standardized via mean centring and scaling by two standard deviations following Gelman (2008). The dummy variable for filial cannibalism mode (partial or total) was also mean centred when used as a categorical predictor, whereas for exposure treatment we coded contrasts to express the intercept as the unweighted average of treatment means. However, to look at treatment effects we also recoded contrasts to allow us to examine pairwise differences between treatments means.

All males had fewer eggs in their nest at the conclusion of their trial. Accordingly, we categorised all males as either total filial cannibals, or partial filial cannibals. Here, to account for the potential for males to miss a few eggs when engaging in total filial cannibalism and the slight underestimation of cannibalism levels that may result from tallying remaining eggs prior to hatching we followed Lissåker (2007) and classified males that consumed a large portion of their brood and had a small number of eggs remaining as total filial cannibals. Specifically males with 0-143 eggs remaining (which was equivalent to 0-20% of the initial clutch) were considered total filial cannibals. By contrast, other males had 381-2175 eggs remaining (33-99% of the initial clutch). We based our categorization threshold of 143 eggs on the approximately bimodal distribution of number of eggs remaining (Figure 2). Lowering this threshold to a max of 24 eggs remaining only caused one male to change classification, and did not qualitatively affect the results of any of our statistical analyses, except that the significant loss of weight we observed amongst all brooding males (see results section) became marginally non-significant ($p = 0.060$).

Filial cannibalism analysis

To examine filial cannibalism, we employed two separate generalized linear models. First, a logistic regression model, with filial cannibalism mode (partial or total) as a response, to determine what factors influences the occurrence of total filial cannibalism. Then, considering only partial filial cannibals, we used a negative binomial regression model with a natural log link function to determine how various factors related to the number of eggs consumed by these males. For both models, we used exposure treatment, (natural log transformed) number of eggs initially spawned in the clutch and pre-spawning male body condition as predictor variables. Male body condition was approximated using the scaled mass index following Peig and Green (2009) with the *smatr* R package used for standardized major axis regression (Warton et al. 2012).

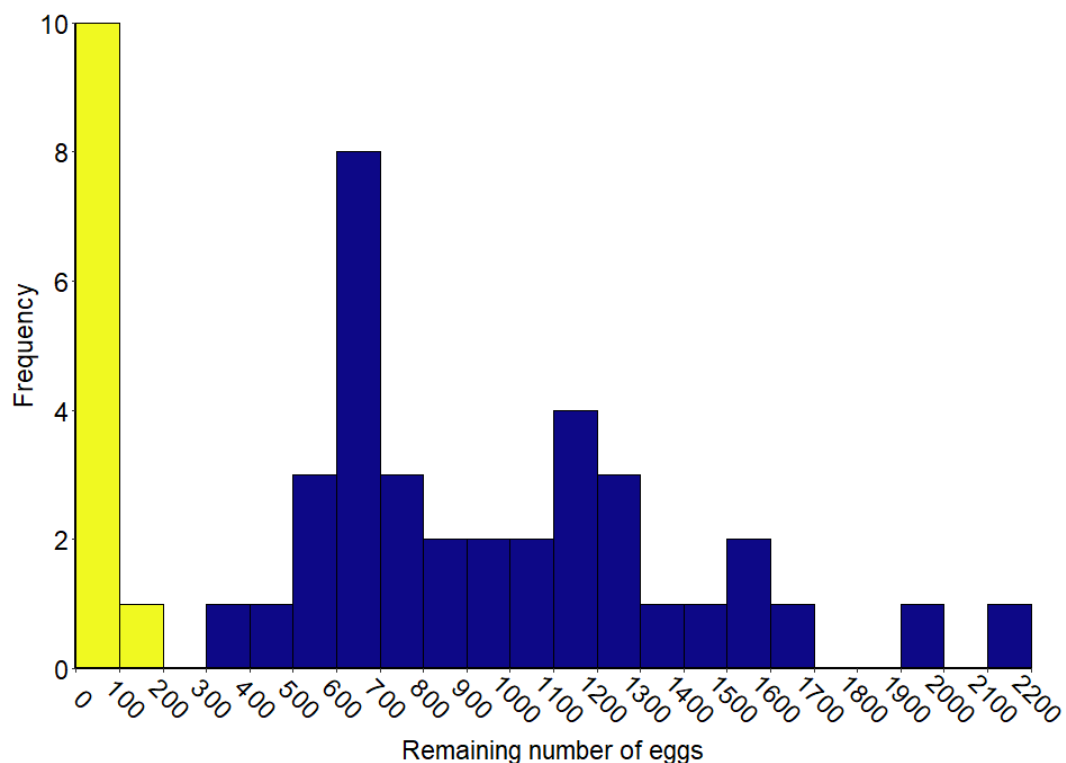


Figure 2. Histogram showing the distribution of the number of eggs remaining in the nests of male sand gobies at the conclusion of their brooding trials. Yellow bars are used for males that were classified as total filial cannibals and indigo bars for those classified as partial filial cannibals.

Weight change analysis

To analyse male weight change over the course of the brooding period, we used a general linear model. Here, the full model considered the following predictors: the exposure treatment, the number of eggs eaten by a male, the average proportion of time males spent outside of their nest during each observation session (including observation in the presence and absence of females), as well as the total number of nest transitions performed by males when in the presence of a female. In addition, to account for possible differences in energy budgets between partial and total filial cannibals, we included filial cannibalism mode and each of its two-way interactions with the other predictors in the model.

Time budget analysis

Male time budgets were explored using Dirichlet regression implemented with the *DirichletReg* R package with the 'alternative' parameterisation following Maier (2014). Separate models were created for time budgets in the absence and presence of females. In each case, the time budget for every male comprised time inside the nest, time moving whilst outside the nest and time outside the nest whilst stationary. These were all measured as proportions of the total of 30 minutes of recorded behaviour for each fish across the three days of observations (i.e. 3 x 10 minute observations). Where likelihood ratio tests revealed a significant effect of a parameter of interest on the overall time budget, we used Wald tests to explore the effects of this parameter. Specifically, we examined the parameter's effect on both the amount of time inside the nest and the amount of time moving whilst outside the nest, relative to the reference category of time outside the nest whilst stationary. The predictor variables for our time budget models' means included exposure treatment, natural log transformed number of eggs eaten, and filial cannibalism mode, as well as its two-way interactions with the preceding terms. We also used the natural log transformed size of clutch (i.e. number of eggs) remaining in nest at the end of the brooding period as a predictor. Here, we centred this predictor about the mean for partial filial cannibals and set the value of this transformed predictor as zero for all total filial

cannibals so that only partial filial cannibals (i.e. males that reared a brood) would influence the estimate of this effect. Within these models precision was predicted by the main effects of filial cannibalism mode and exposure treatment. In addition, we constructed models of behaviours in the presence of a female that included transformed measures of male time use in the absence of a female (i.e. time active outside the nest and time inside the nest) to help us determine whether observed effects during courtship were specifically associated with female presence. The specific transformation applied to each of these time budget components was a logit transformation applied following the compression transformation described in Maier (2014) to accommodate data in the [0, 1] interval.

Nest transitions analysis

Finally, we analysed male movement in and out of the nest (i.e. nest transitions) in the presence of the female using a negative binomial regression model with a natural log link function. The predictors used for this analysis were the same as those used for our initial models of time budgets (i.e. exposure treatment, natural log transformed size of clutch remaining, natural log transformed number of eggs eaten, filial cannibalism mode, and two-way interactions between filial cannibalism mode and both exposure treatment and natural log transformed number of eggs eaten).

Results

Filial cannibalism

Fish exposure treatment did not significantly alter the likelihood of males engaging in total filial cannibalism ($\chi^2_2 = 0.640$, $p = 0.726$, Table 1). However, we found that males with small clutches ($\chi^2_1 = 11.816$, $p = 0.001$) and those in poor body condition prior to spawning ($\chi^2_1 = 4.403$, $p = 0.036$) were significantly more likely to perform total filial cannibalism (Figure 3, Table 1).

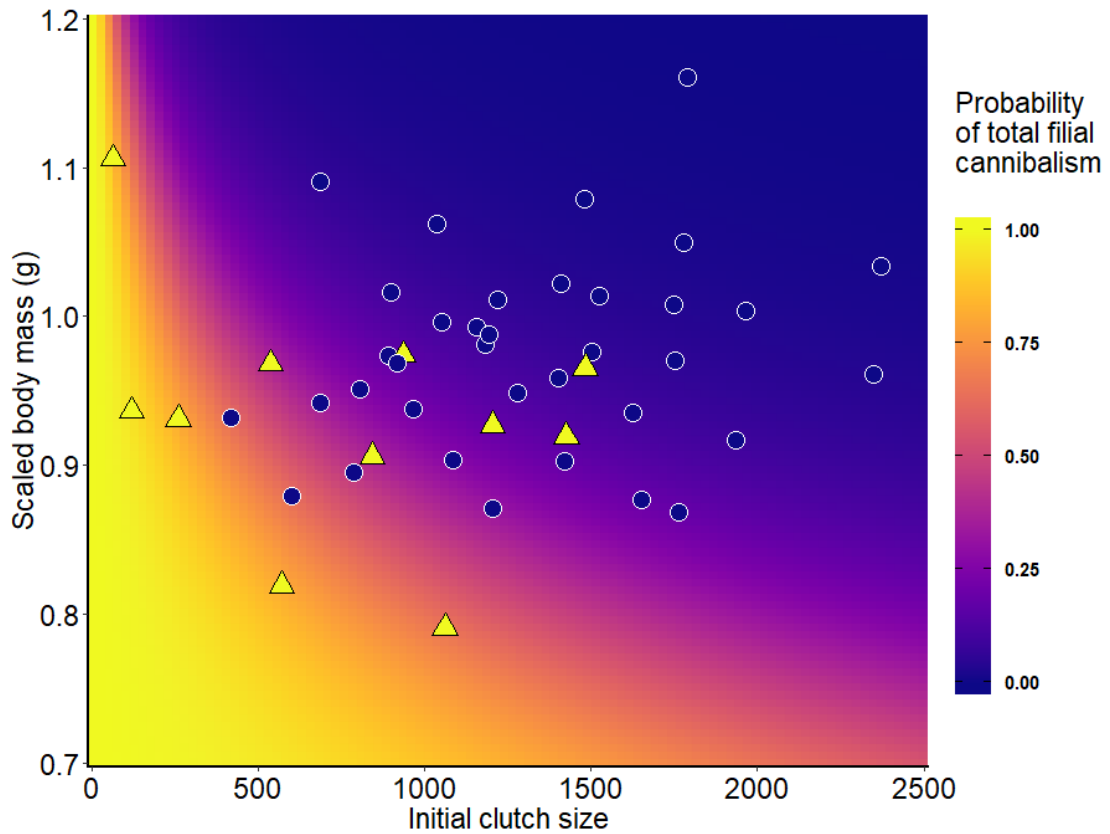


Figure 3. Heatmap of marginal predicted probability of total filial cannibalism occurring based upon the initial number of eggs in the clutch being tended and male body condition as measured by body mass scaled according to length. Actual observations of total filial cannibalism (yellow triangles) and partial filial cannibalism (indigo circles) overlay the heatmap.

Table 1. Total filial cannibalism logistic regression model estimates of standardized regression coefficients and linear combinations thereof. Note that for clarity we present estimates of the pairwise comparisons between the three treatment effects whilst the intercept shown represents the treatment average.

Predictor	β_s	95% Confidence Interval
Intercept	-1.672	(-2.831, -0.797)
Common goby exposure – control	-0.149	(-2.441, 2.220)
Sand goby exposure – control	0.616	(-1.556, 3.001)
Sand goby exposure – common goby exposure	0.765	(-1.201, 2.874)
Male body condition	-1.963	(-4.278, -0.122)
Initial clutch size	-2.721	(-5.332, -1.054)

Considering only partial filial cannibals, neither exposure treatment ($\chi^2_2 = 0.914$, $p = 0.633$, Figure 4) nor body condition ($\chi^2_1 = 0.899$, $p = 0.343$) had a significant effect on the number of eggs eaten (Table 2). However, partial filial cannibals that initially received larger clutches ate more eggs ($\chi^2_1 = 11.053$, $p = 0.001$, Figure 4, Table 2).

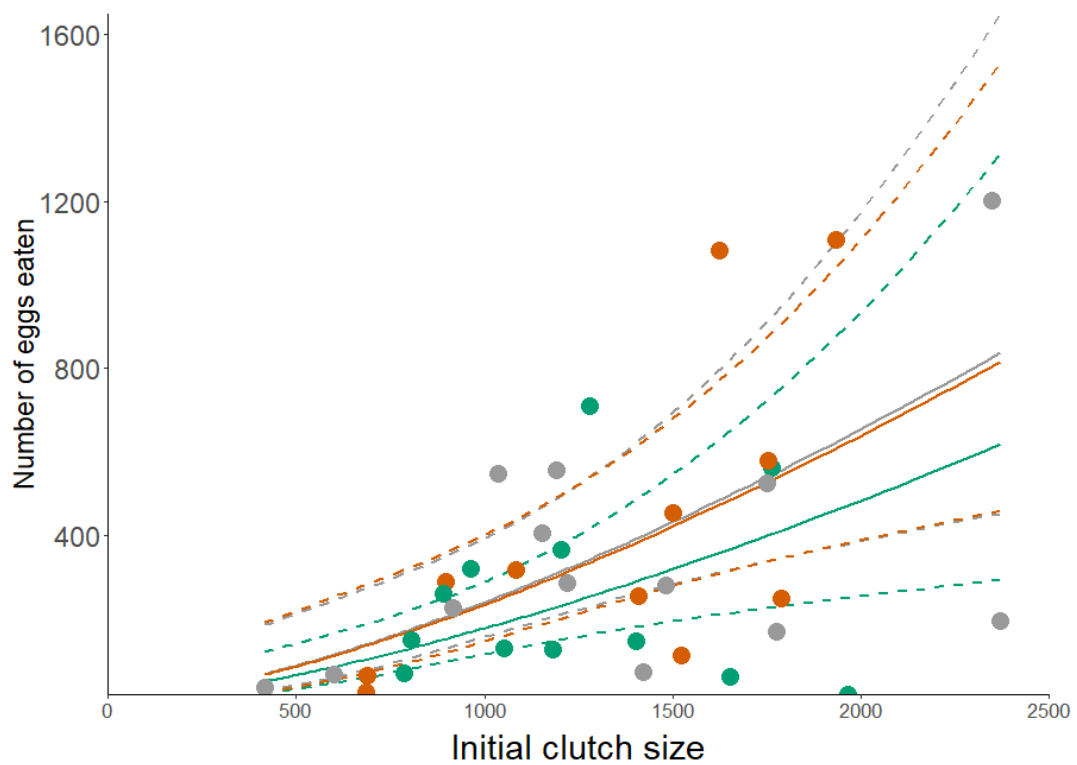


Figure 4. Number of eggs eaten by male sand gobies that engaged in partial filial cannibalism in relation to the initial number of eggs in the clutch. Individual observations, modelled predictions and 95% confidence intervals are depicted with circular data points, solid lines and dashed lines respectively. Control, common goby exposure and rival male sand goby exposure treatments are indicated by grey, teal and orange colours respectively.

Table 2. Partial filial cannibalism generalized linear model estimates of standardized regression coefficients and linear combinations thereof. Note that for clarity we present estimates of the pairwise comparisons between the three treatment effects whilst the intercept shown represents the treatment average.

Predictor	β_s	95% Confidence Interval
Intercept	5.673	(5.439, 5.926)
Common goby exposure – control	-0.303	(-0.973, 0.364)
Sand goby exposure – control	-0.025	(-0.633, 0.595)
Sand goby exposure – common goby exposure	0.278	(-0.383, 0.951)
Male body condition	-0.300	(-0.897, 0.323)
Initial clutch size	1.141	(0.523, 1.731)

Weight change

We found that males were significantly lighter at the end of the brooding period than prior to spawning ($F_{1,35} = 4.523$, $p = 0.041$, Table 3). However, none of the other factors we investigated, including exposure treatment ($F_{2,35} = 1.540$, $p = 0.229$), time inside the nest ($F_{1,35} = 3.307$, $p = 0.078$), number of eggs eaten ($F_{1,35} = 0.913$, $p = 0.346$), nor the interaction between these terms and filial cannibalism mode (exposure treatment interaction: $F_{2,35} = 0.782$, $p = 0.465$; time inside the nest interaction: $F_{1,35} = 2.824$, $p = 0.102$; number of eggs eaten interaction: $F_{1,35} = 0.421$, $p = 0.521$) significantly influenced male weight loss (Table 3). The one exception was male courtship vigour, where we found that engaging in more nest transitions was associated with significantly greater weight loss ($F_{1,35} = 5.859$, $p = 0.021$, Table 3).

Table 3. Weight change linear model estimates of standardized regression coefficients and linear combinations thereof. Note that for clarity we present estimates of the pairwise comparisons between the three treatment effects whilst other parameters represent marginal effects at the treatment average.

Predictor	β_s	95% Confidence Interval
Intercept	-29.845	(-58.336, -1.354)
Common goby exposure – control	-31.172	(-89.864, 27.521)
Sand goby exposure – control	19.784	(-34.632, 74.201)
Sand goby exposure – common goby exposure	50.956	(-8.074, 109.986)
Time inside nest	-77.749	(-164.548, 9.050)
Courtship nest transitions	-82.688	(-152.039, -13.336)
Amount of eggs eaten	-26.729	(-83.529, 30.072)
Filial cannibalism mode	19.424	(-59.978, 98.826)
Filial cannibalism mode: common goby exposure – control	-78.852	(-231.591, 73.887)
Filial cannibalism mode: sand goby exposure – control	2.569	(-128.505, 133.643)
Filial cannibalism mode: sand goby exposure – common goby exposure	81.421	(-59.109, 221.951)
Filial cannibalism mode: time inside nest	114.602	(-23.846, 253.050)
Filial cannibalism mode: courtship nest transitions	94.455	(-28.460, 217.369)
Filial cannibalism mode: amount of eggs eaten	34.149	(-72.654, 140.951)

Time budget in the absence of a female

Our model of male time budgets in the absence of a female revealed no significant interactions between filial cannibalism mode and the number of eggs eaten by males ($\chi^2_2 = 3.472$, $p = 0.176$). Similarly, we found that neither the number of eggs that males ate ($\chi^2_2 = 1.619$, $p = 0.445$), nor the number that remained at the end of care ($\chi^2_2 = 2.214$, $p = 0.331$), had a significant effect on their time budgets. While there was no significant interaction between filial cannibalism mode and male exposure treatment ($\chi^2_4 = 0.767$, $p = 0.943$), each of these factors had a significant main effect on male time budget (filial cannibalism mode: $\chi^2_2 = 37.781$, $p < 0.001$; exposure treatment: $\chi^2_4 = 31.238$, $p < 0.001$). Specifically, we found that total filial cannibals spent significantly less time inside their nest than partial filial cannibals (Table 4). We also found that common goby exposed males spent less time in the nest than either rival male or control treatments (Table 4). On the other hand, the activity levels of males outside the nest did not significantly change with filial cannibalism mode or exposure treatment (Table 4).

Table 4. Estimates of standardized regression coefficients and linear combinations thereof for Dirichlet model of male time budgets in the absence of a female. Note that for clarity we present estimates of the pairwise comparisons between the three treatment effects whilst other parameters represent marginal effects at the treatment average.

Time inside the nest		
Predictor	β_s	95% Confidence Interval
Intercept	3.000	(2.709, 3.290)
Common goby exposure – control	-1.641	(-2.412, -0.870)
Sand goby exposure – control	-0.334	(-0.933, 0.264)
Sand goby exposure – common goby exposure	1.307	(0.544, 2.070)
Size of clutch reared	0.013	(-0.514, 0.540)
Amount of eggs eaten	0.263	(-0.284, 0.810)
Filial cannibalism mode	-2.788	(-3.605, -1.972)
Filial cannibalism mode: common goby exposure – control	-0.328	(-2.426, 1.771)
Filial cannibalism mode: sand goby exposure – control	-0.551	(-2.051, 0.949)
Filial cannibalism mode: sand goby exposure – common goby exposure	-0.224	(-2.127, 1.680)
Filial cannibalism mode: amount of eggs eaten	1.451	(-0.014, 2.917)

Time active outside the nest		
Predictor	β_s	95% Confidence Interval
Intercept	-0.037	(-0.380, 0.306)
Common goby exposure – control	0.274	(-0.606, 1.154)
Sand goby exposure – control	0.246	(-0.507, 0.999)
Sand goby exposure – common goby exposure	-0.028	(-0.862, 0.806)
Size of clutch reared	0.433	(-0.316, 1.182)
Amount of eggs eaten	-0.002	(-0.746, 0.742)
Filial cannibalism mode	-0.531	(-1.489, 0.428)
Filial cannibalism mode: common goby exposure – control	-0.315	(-2.762, 2.132)
Filial cannibalism mode: sand goby exposure – control	-0.817	(-2.890, 1.256)
Filial cannibalism mode: sand goby exposure – common goby exposure	-0.502	(-2.627, 1.622)
Filial cannibalism mode: amount of eggs eaten	1.000	(-1.005, 3.005)

Time budget in the presence of a female

In the presence of a female, our model of the time budget of males revealed no significant effect of exposure treatment ($\chi^2_4 = 3.122$, $p = 0.538$) nor its interaction with filial cannibalism mode ($\chi^2_4 = 6.423$, $p = 0.170$). However, filial cannibalism mode had a significant main effect on male time budget ($\chi^2_2 = 22.187$, $p < 0.001$), with total filial cannibals spending significantly less time inside the nest than partial filial cannibals (Table 5). The number of eggs reared by a male also explained variation in his time budget ($\chi^2_2 = 11.366$, $p = 0.003$), with larger broods remaining in the nest at the conclusion of brooding being associated with

significantly more activity when outside the nest (Table 5). The number of eggs eaten by males did not have a significant main effect on their time budget ($\chi^2_2 = 2.700$, $p = 0.259$), and there was no interaction with filial cannibalism mode ($\chi^2_2 = 5.080$, $p = 0.079$). A separate model, taking into account the behaviour of males in the absence of females revealed qualitatively similar results (Table 5). Thus, it appears that the lower degree of nest occupancy by total filial cannibals in the presence of females is not solely due to their tendency to be outside the nest even when there are no females around.

Nest transitions in the presence of a female

The number of eggs eaten by males did not have a significant effect on the number of transitions in and out of the nest performed in the presence of a female ($\chi^2_1 = 1.214$, $p = 0.271$, Table 6) and this factor did not significantly interact with filial cannibalism mode ($\chi^2_1 = 0.764$, $p = 0.382$, Table 6). However, filial cannibalism mode did have a significant interaction with exposure treatment ($\chi^2_2 = 11.894$, $p = 0.003$, Table 6). Exposure treatment significantly affected nest transitions among total, but not partial, filial cannibals (total: $\chi^2_2 = 10.863$, $p = 0.004$; partial: $\chi^2_2 = 2.541$, $p = 0.281$; Table 6). For the former, males that were exposed to a common goby were found to transition in and out of their nests significantly less than either control ($\beta_s = -4.119$, 95% CI = (-6.754, -1.678), Figure 5A) or rival sand goby exposed males ($\beta_s = -4.460$, 95% CI = (-6.884, -2.112), Figure 5A). Rival exposed and control total filial cannibals, by contrast, did not significantly differ from each other ($\beta_s = 0.341$, 95% CI = (-1.779, 2.149), Figure 5A). Lastly, we found that males that cared for a larger number of eggs (i.e. had a greater number of eggs remaining in their nest at the end of the brooding period) engaged in significantly more transitions in and out of the nest ($\chi^2_1 = 7.887$, $p = 0.005$, Figure 5B, Table 6).

Table 5. Estimates of standardized regression coefficients and linear combinations thereof for two Dirichlet models of male time budgets in the presence of a female. Model 1 is the base model and model 2 incorporates predictors based on male behaviour in the absence of a female. Note that for clarity we present estimates of the pairwise comparisons between the three treatment effects whilst other parameters represent marginal effects at the treatment average.

Time inside the nest		Model 1		Model 2	
Predictor	β_s	95% Confidence Interval	β_s	95% Confidence Interval	
Intercept	2.052	(1.713, 2.390)	2.161	(1.835, 2.487)	
Common goby exposure – control	-0.245	(-1.062, 0.571)	0.148	(-0.696, 0.992)	
Sand goby exposure – control	0.252	(-0.539, 1.043)	0.452	(-0.292, 1.196)	
Sand goby exposure – common goby exposure	0.497	(-0.334, 1.328)	0.304	(-0.497, 1.104)	
Non-courtship time inside nest	NA	NA	1.738	(0.345, 3.130)	
Non-courtship time active outside the nest	NA	NA	0.532	(-0.822, 1.886)	
Size of clutch reared	-0.146	(-0.795, 0.503)	0.121	(-0.596, 0.837)	
Amount of eggs eaten	0.223	(-0.378, 0.823)	-0.141	(-0.754, 0.472)	
Filial cannibalism mode	-2.086	(-2.984, -1.187)	-1.232	(-2.112, -0.351)	
Filial cannibalism mode: common goby exposure – control	0.825	(-1.133, 2.784)	0.632	(-1.113, 2.376)	
Filial cannibalism mode: sand goby exposure – control	0.596	(-1.155, 2.348)	0.712	(-0.892, 2.317)	
Filial cannibalism mode: sand goby exposure – common goby exposure	-0.229	(-1.958, 1.501)	0.081	(-1.450, 1.612)	
Filial cannibalism mode: amount of eggs eaten	1.708	(0.075, 3.341)	1.008	(-0.373, 2.389)	
Time active outside the nest		Model 1		Model 2	
Predictor	β_s	95% Confidence Interval	β_s	95% Confidence Interval	
Intercept	0.334	(-0.025, 0.693)	0.397	(0.045, 0.749)	
Common goby exposure – control	-0.127	(-0.993, 0.739)	-0.026	(-0.898, 0.845)	
Sand goby exposure – control	-0.212	(-1.041, 0.618)	-0.198	(-1.009, 0.614)	
Sand goby exposure – common goby exposure	-0.084	(-0.943, 0.774)	-0.171	(-1.002, 0.659)	
Non-courtship time inside nest	NA	NA	1.496	(-0.202, 3.193)	
Non-courtship time active outside the nest	NA	NA	1.053	(-0.531, 2.637)	
Size of clutch reared	0.914	(0.097, 1.732)	1.036	(0.159, 1.912)	
Amount of eggs eaten	-0.252	(-0.977, 0.473)	-0.465	(-1.217, 0.287)	
Filial cannibalism mode	-0.552	(-1.437, 0.332)	-0.206	(-1.237, 0.826)	
Filial cannibalism mode: common goby exposure – control	-1.562	(-3.702, 0.577)	-1.659	(-3.677, 0.358)	
Filial cannibalism mode: sand goby exposure – control	-0.082	(-1.849, 1.685)	0.379	(-1.383, 2.140)	
Filial cannibalism mode: sand goby exposure – common goby exposure	1.480	(-0.579, 3.539)	2.038	(0.123, 3.954)	
Filial cannibalism mode: amount of eggs eaten	1.840	(0.192, 3.488)	1.099	(-0.422, 2.620)	

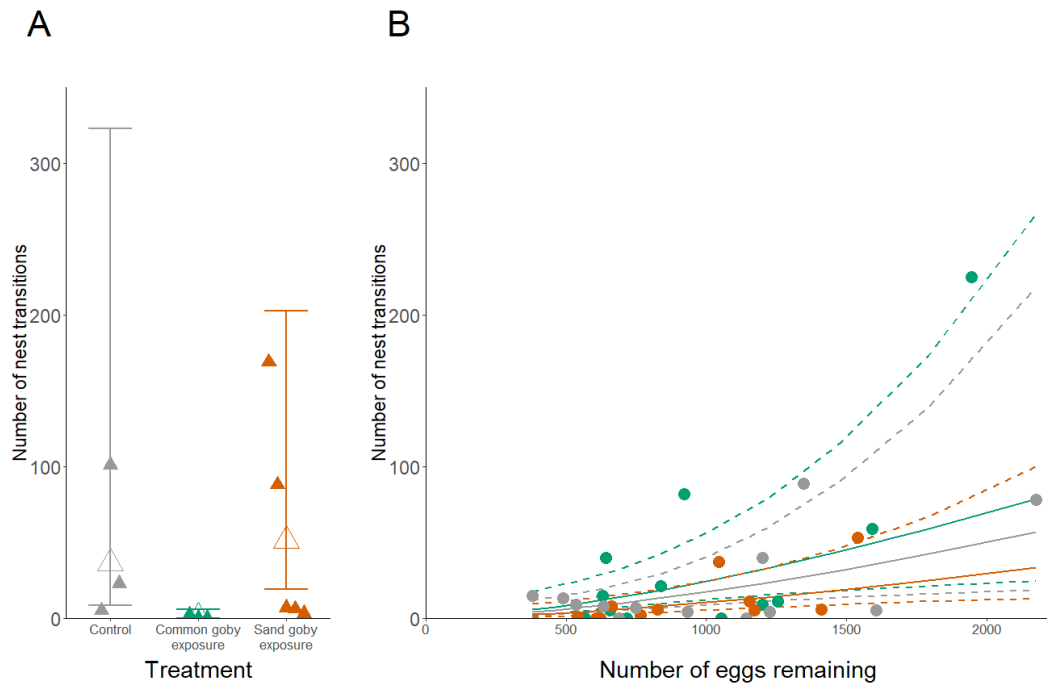


Figure 5. Number of transitions in and out of the nest performed by male sand gobies during courtship assays. For total filial cannibals (A), observations, modelled means and 95% confidence intervals are depicted with solid triangles, open triangles and error bars respectively. For partial filial cannibals (B), observations, predicted values and 95% confidence intervals are shown with circles, solid lines and dashed lines respectively in relation to the number of eggs that males cared for (i.e. the number remaining in the male's nest at the conclusion of the experiment). Control, common goby exposure and rival male sand goby exposure treatments are indicated by grey, teal and orange colours respectively.

Table 6. Generalized linear model estimates of standardized regression coefficients and linear combinations thereof for model of the number of transitions in and out of the nest by males during exposure to a female. Note that for clarity we present estimates of the pairwise comparisons between the three treatment effects whilst other parameters represent marginal effects at the treatment average.

Predictor	β_s	95% Confidence Interval
Intercept	2.570	(2.175, 3.019)
Common goby exposure – control	-0.711	(-1.677, 0.241)
Sand goby exposure – control	-0.322	(-1.288, 0.632)
Sand goby exposure – common goby exposure	0.390	(-0.609, 1.413)
Size of clutch reared	1.277	(0.440, 2.115)
Amount of eggs eaten	-0.494	(-1.463, 0.362)
Filial cannibalism mode	-0.307	(-1.425, 1.084)
Filial cannibalism mode: common goby exposure – control	-4.449	(-7.248, -1.826)
Filial cannibalism mode: sand goby exposure – control	0.865	(-1.493, 2.978)
Filial cannibalism mode: sand goby exposure – common goby exposure	5.314	(2.732, 7.957)
Filial cannibalism mode: amount of eggs eaten	1.074	(-1.485, 3.295)

Discussion

We found that the presence of a rival male did not influence the occurrence of total filial cannibalism. If sexual selection operates against males that have empty nests due to full clutch cannibalism (Forsgren, Karlsson and Kvarnemo 1996; Lindström and Kangas 1996), we might have expected males to avoid complete clutch consumption in the more competitive environment when a rival was present (Deal and Wong 2016). However, our results did not match this prediction. Likewise, although we found that males are more prone to total filial cannibalism when their initial brood size is small, a competitive mating environment did not seem to elicit the same response. This suggests that rival competition does not alter the reproductive value of the current brood to the father relative to future broods, as might otherwise be expected if competition reduced the likelihood of further clutches being added to the current brood (without a similar effect on long term mating success).

In addition to having no influence on the occurrence of total filial cannibalism, rival male exposure had no effect on male courtship of a subsequent female. This further indicates that the lack of rival effects may simply be due to the presence of a conspecific male not being perceived as a reliable cue of future mating success for male sand gobies. Perhaps, in natural conditions, lost mating opportunities caused by the presence of rivals are made up for by greater attraction of females to the local area, as has been argued to be the case amongst some lekking species (Westcott 1994; Isvaran and Ponkshe 2013; Macedo et al. 2018). Alternatively, males that are successful enough to establish a nest and spawn may perceive themselves to have a mating advantage over randomly selected males from the population (Kokko and Jennions 2008), and consequently lack the compulsion to modify their behaviour in response to such competitors. Moreover, since not all male sand gobies defend nest sites and some males act as sneakers, it is possible that other males do not represent sufficient mating competition to warrant adjustment of filial cannibalism levels, especially in light of earlier research that shows that males do not adjust filial cannibalism levels in response to sneak attempts or lost paternity to sneakers (Svensson and Kvarnemo 2007). Nevertheless, our findings that control and rival male exposed

sand gobies did not differ in behaviour around a female highlight the need to question the assumption that mating effort increases as a response to elevated mating competition. Although exposure to increased numbers of rivals, or more attractive rivals, has been shown to elevate male investment in mating display in some species (e.g. three-spined sticklebacks, *Gasterosteus aculeatus*: Kim and Velandro 2014; white-bearded, manakins *Manacus manacus*: Cestari et al. 2016) intense competition can also lead to investment in alternative reproductive strategies (Weir et al. 2011). For sand gobies though, competition did not increase parental care with no change in filial cannibalism or time budget during brooding observed. Future studies may seek to expand on these findings by testing if they hold true under even more intense levels of mating competition or in relation to rivals of different (especially higher) quality.

In agreement with a large body of literature in both sand gobies (Forsgren, Karlsson and Kvarnemo 1996; Klug et al. 2006; Lissåker and Svensson 2008; Andrén and Kvarnemo 2014; Deal et al. 2017), and other species (Kramer 1973; Lavery and Keenleyside 1990; Petersen and Hess 1991; Lindström and Sargent 1997; Neff 2003), we found that total filial cannibalism was promoted by small initial clutch size. This phenomenon is believed to occur as a result of the costs of providing care to a brood outweighing the benefits when the number of eggs is small (Sargent 1992; Manica 2002b). Poor male body condition also predicted the occurrence of total filial cannibalism, suggesting that whole clutch consumption might be employed to provide sustenance, or when males lack sufficient energy reserves to provide care. While this does accord with similar observations in some other species (Marconato et al. 1993; Kvarnemo et al. 1998; Candolin 2000; Manica 2004; Takahashi and Kohda 2004) it is intriguing that several studies focusing on sand gobies have not previously detected this effect (Forsgren 1997; Lissåker et al. 2003; Klug et al. 2006; Chin-Baarstad et al. 2009; Deal et al. 2017). Differences among sand goby studies, in this regard, could be due to differences in study populations or differences in the baseline nutritional state of a population in any given year. While these interesting possibilities remain to be tested, there is a precedent for both inter-year and inter-population variance in sand goby breeding biology with respect to other characteristics (Forsgren,

Kvarnemo and Lindström 1996; Lehtonen and Wong 2009; Lehtonen et al. 2010). Overall, our findings suggest that total filial cannibalism is more strongly influenced by characteristics of the male and his brood rather than his social environment, indicating that males may regard these former intrinsic factors as more predictable cues of the costs and benefits of brood care.

As with total filial cannibalism, we found that partial filial cannibalism was not influenced by the mating competition treatment. Similarly, no clear difference in filial cannibalism rates has been observed between two wild populations of the European bullhead (*Cottus gobio*) with pronouncedly different nesting male densities (Marconato et al. 1993). Our results also correspond with the absence of a female exposure effect on partial filial cannibalism reported in the sand goby (Pampoulie et al. 2004) and related two-spotted goby (*Gobiusculus flavescens*) (Bjelvenmark and Forsgren 2003). In contrast, presence of females (mate availability) does appear to affect filial cannibalism in more distantly related *Rhinogobius* (Myint et al. 2011; Takeyama et al. 2013). The lack of an effect of social context in many species suggests that the main motives for partial filial cannibalism in these species are due to factors other than external cues about the current versus future reproduction trade-off. Indeed, other external factors that could feasibly govern the relative importance of current and future broods, such as the time of the breeding season and the presence of either egg-targeting or adult-targeting predators, have all been shown to be unrelated to the extent of partial filial cannibalism in sand gobies (Lissåker 2007; Chin-Baarstad et al. 2009; Deal et al. 2017; Lehtonen et al. 2018). Moreover, we found no evidence for a relationship between the number of eggs eaten in partial filial cannibalism and behaviour of the parental male when exposed to a female. This finding suggests that partial filial cannibalism is not used to provide energy for courtship displays. Similarly, egg consumption was not related to either male attendance within the nest or male weight change, nor did partial filial cannibalism relate to pre-spawning male body condition. Thus, it seems unlikely that partial clutch consumption was performed for the primary motive of providing energy for either nest tending or energetic gain more generally, as may be the case in other species (Marconato and Bisazza 1988; Marconato et al. 1993; Manica 2002b). For

sand gobies, partial filial cannibalism may instead be employed mainly to optimise conditions inside the nest for egg survival. For example, sand gobies may engage in partial filial cannibalism to assist in the control of pathogenic water moulds (*Saprolegnia*) (Lehtonen and Kvarnemo 2015a,b; Vallon et al. 2016; Vallon and Heubel 2017). Indeed, elevated benefits of pathogen control by partial filial cannibalism may explain our observation that, under partial filial cannibalism, males with larger initial clutches consumed slightly more eggs. When there are more eggs within the brood, thinning out more eggs may be compensated for by improved survivorship of uneaten young (Klug et al. 2006). Nevertheless, we cannot rule out another explanation, that increased numbers of eggs consumed by apparent partial filial cannibalism simply reflect increased consumption of inviable eggs in large broods. Taken together, the above findings highlight the importance of recognising the apparent diversity of factors that could motivate partial filial cannibalism among different species.

Males did not seem to consume eggs to provide energy for courtship of females, as we found no relationship between courtship effort and quantity of eggs consumed. Contrastingly, we found that males which reared a larger number of eggs (i.e. had more eggs in the nest at the conclusion of their trial) engaged in more vigorous courtship and were more active while outside the nest in the presence of a female. This probably does not represent males specifically trying to advertise the size of their broods to females as evidence suggests that females actually prefer nests that contain a small number of eggs over those with a larger brood (Andrén and Kvarnemo 2014). Instead, it seems more likely a latent common factor underpins both vigorous courtship and superior parental success. Consistent with this interpretation, both Forsgren (1997) and Lehtonen and Lindström (2007) reported greater success at rearing young by males that are preferred by females, and Lehtonen (2012) found a nonsignificant tendency for the same in males that engaged in intense prespawning courtship. Exactly what factor causes both extensive courtship and parenting success requires further investigation though. In some other fish species (Knapp and Kovach 1991; Takahashi and Kohda 2004), high energetic reserves appear to enable some males to both court intensely and rear young successfully thereby linking parental

success and courtship vigour. However, we note that partial filial cannibalism did not relate to body condition in our experiment (cf. Takahashi and Kohda 2004), which suggests that body condition may not be responsible for the positive association between courtship and parental success in the sand goby. It also seems unlikely that differential allocation of eggs by females is responsible, since female sand gobies do not seem to alter characteristics of their brood based on the quality of their mate (Lehtonen and Lindström 2007). Further research is therefore warranted to investigate why good fathers court intensely.

We found that the presence of a common goby did not influence either the occurrence, or mode, of filial cannibalism. This result is consistent with those reported in studies in which gobies were presented with an egg-eating crab (Lindström 1998; Lissåker and Kvarnemo 2006; Lehtonen et al. 2018), but contrasts with the results of Chin-Baarstad et al (2009) who found that males perform total filial cannibalism in response to egg-eating sand shrimp. This difference in response however might arise if nest-tending males have a greater ability to defend their brood from common gobies and crabs as compared to shrimp (but see: Lehtonen et al. 2018). Nevertheless, common gobies did alter other aspects of male behaviour in our study. Specifically, brooding male sand gobies spent more time outside the nest when common gobies were present and total filial cannibals that were exposed to common gobies engaged in less vigorous courtship. These observations are consistent with sand gobies perceiving common gobies as nest predators and could represent increased nest-defence vigilance outside the nest and reluctance to start a fresh brood in the presence of nest predators. It remains unclear, however, why exposure to rival male sand gobies did not elicit similar effects, as they are also potential nest predators. More broadly, these results highlight the need for future research to consider how the nature of different predators might influence parental care.

Overall, the results of this study indicate that parental male sand gobies do not alter their tendency to consume their own eggs in response to the presence of rival males. Instead we found that total filial cannibalism was more strongly influenced by characteristics of the male and his brood, especially body condition and clutch size. However, comparisons with previous research where female

exposure did influence total filial cannibalism highlight the need for research into mating conditions to independently consider the effects of both males and females rather than assuming that they will simply be the inverse of each other. With regards to partial filial cannibalism, our findings suggest that partial brood consumption is not performed to provide energy for future reproduction or parental care in sand gobies. This underscores the importance of tracking post cannibalism behaviour to reveal the purpose of offspring consumption.

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Chapter 4

Paternal investment with an uncertain future: effects of predator exposure on filial cannibalism and nesting behaviour

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Paternal investment with an uncertain future: effects of predator exposure on filial cannibalism and nesting behaviour



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Owing to trade-offs between investment in current and future reproduction, factors that diminish a parent's survival prospects, such as predation threat, are expected to increase investment in existing young. Nevertheless, effects of predation risk on parental investment have only rarely been examined, and not at all within the context of filial cannibalism (parental consumption of their own offspring). We examined filial cannibalism and nest characteristics in a small fish with paternal egg care, the sand goby, *Pomatoschistus minutus*, both when exposed to a common piscivore, the perch, *Perca fluviatilis*, and in the absence of predators. We found that when males consumed only some of their eggs (partial filial cannibalism), the number of eaten eggs did not depend on predation threat, possibly indicating that partial clutch consumption is largely motivated by benefits to existing young. Total filial cannibalism (whole clutch consumption) was marginally less common under predator exposure, while its strongest predictor was small clutch size. This suggests that the return on parental investment has a greater influence on total filial cannibalism than the likelihood of future breeding. Regarding nest architecture, males that consumed their entire brood after exposure to a predator built larger nest entrances, possibly to facilitate predator evasion. Males that cared for at least part of their brood, however, maintained small nest entrances regardless of predation threat. Furthermore, more elaborate nests were not associated with greater egg consumption, suggesting that filial cannibalism is not employed to sustain nest building. © 2017 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Parental care confers important fitness benefits to parents by improving the survival of their offspring (Alonso-Alvarez & Velando, 2012; Clutton-Brock, 1991). However, looking after young can be costly (Alonso-Alvarez & Velando, 2012; Clutton-Brock, 1991). It can be time consuming (e.g. Thomson et al., 2014), energetically demanding (e.g. Gravel & Cooke, 2013), and expose parents to predation (e.g. Li & Jackson, 2003) or disease (e.g. Nordling, Andersson, Zohari, & Lars, 1998). As a result, parents may have to trade off investment in existing young against investment in future reproduction (Clutton-Brock, 1991; Trivers, 1972). In this regard, a range of factors can alter the optimal balance of investment in these two fitness components (Klug, Alonzo, & Bonsall, 2012). For instance, a parent may benefit from providing greater care to its current brood when prospects of future reproduction are bleak, as shown, for example, in eiders, *Somateria mollissima*, in

which immune-challenged mothers spend more time incubating their eggs and are less likely to abandon their ducklings (Hanssen, 2006). On the other hand, when there are abundant opportunities to breed in the future, parents may be more inclined to reduce or even terminate investment in existing young to mitigate the costs of current reproduction (Gross, 2005; Klug et al., 2012; Magnhagen, 1992; Sargent & Gross, 1985; Williams, 1966a, 1966b). To this end, one way in which parents can reduce or terminate investment in the current brood is to consume their own young.

Apart from preventing the costs of parental care from impinging on future reproduction, consuming one's own offspring, known as filial cannibalism, can also provide energy and nutrition to parents (Manica, 2002). In the case of partial filial cannibalism, where only some of the young under a parent's care are eaten, resources acquired from offspring consumption may be used to support the parent in caring for uneaten young, as seen in river bullheads, *Cottus gobio*, and cardinalfish, *Apogon lineatus* (Kume, Yamaguchi, & Taniuchi, 2000; Marconato, Bisazza, & Fabris, 1993). In these cases, filial cannibalism may simply be an investment in current reproduction. However, if resources acquired from consuming young are

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used to promote further breeding, filial cannibalism is, at least partially, an investment in future reproduction. In acts of total filial cannibalism especially, that is, when parents consume all young under their care, the motivation is likely to be solely investment in future reproduction (Manica, 2002). Accordingly, parents are expected to commit more filial cannibalism when the potential for future reproduction is high (Rohwer, 1978). However, not all empirical evidence supports this prediction. For example, elevated levels of filial cannibalism are not usually reported to occur early in the breeding season (e.g. Lissåker, 2007; Marconato et al., 1993; Okuda & Yanagisawa, 1996; but see Mehliis, Bakker, Engqvist, & Frommen, 2010; Okuda, Takeyama, & Yanagisawa, 1997; Takeyama, Okuda, & Yanagisawa, 2002), and only occasionally occur in response to heightened access to mates (Bjelvenmark & Forsgren, 2003; Okuda, Ito, & Iwao, 2004; Pampoulie, Lindström, & St Mary, 2004; reviewed in Deal & Wong, 2016), even though both these conditions may increase the prospects of future reproduction. Meanwhile, the effects of other factors that could predict the likelihood of future breeding remain rarely tested. For example, despite theoretical models that suggest that the likelihood of parents being preyed upon (hereafter referred to as 'parental predation risk') is one of the most significant factors determining the occurrence of brood abandonment (Steinhart, Dunlop, Ridgway, & Marschall, 2008), the effects of parental predation risk are, to our knowledge, untested within the context of filial cannibalism, and largely also that of parental care in general (for exceptions, see Arundell, Wedell, & Dunn, 2014; Fox & McCoy, 2000; Javois & Tamaru, 2004).

The sand goby, *Pomatoschistus minutus*, is a small marine and brackish water fish that performs both total and partial filial cannibalism (Forsgren, Karlsson, & Kvarnemo, 1996). In this species, uniparental egg care by the male takes place within a nesting chamber that he excavates underneath a rock or empty mussel shell, onto which he piles sand (Lindström, 1988). The nest then serves as a protective location for the eggs, with some evidence suggesting that nests with narrow entrances and those covered with large sand piles provide concealment and protection from egg predators (Lissåker & Kvarnemo, 2006; see also Jones & Reynolds, 1999; Lehtonen, Lindström, & Wong, 2009; Svensson & Kvarnemo, 2003). The nest may also play a role in mate attraction. In particular, sand piled above the nest amplifies male vocalizations (Lugli, 2013) and females appear to prefer to spawn in nests covered by larger sand piles, at least under a subset of conditions (Lehtonen & Lindström, 2009; Lehtonen & Wong, 2009; Lehtonen, Wong, & Lindström, 2010; Svensson & Kvarnemo, 2005). Within the nest, males can care for the eggs of multiple females, either contemporaneously or in sequence (Jones, Walker, Lindström, Kvarnemo, & Avise, 2001). However, individuals generally do not survive to participate in multiple breeding seasons (Fonds, 1973; Healey, 1971).

Partial filial cannibalism can benefit male sand gobies, for example by improving the survivorship of eggs within crowded nests (Klug, Lindström, & St Mary, 2006; Lehtonen & Kvarnemo, 2015a, 2015b; Lindström, 1998). Males may also use energy from egg consumption to improve their body condition (Klug et al., 2006; Lindström, 1998; Lissåker, Kvarnemo, & Svensson, 2003). However, whether energy acquired through egg consumption is used to improve predominantly future or current reproduction is at present unclear. Moreover, total filial cannibalism in sand gobies appears to be a facultative strategy employed when the costs of providing care to young are high and the potential benefits low (Chin-Baarstad, Klug, & Lindström, 2009; Klug et al., 2006). However, certain factors that should promote increased future reproductive potential for male sand gobies, such as heightened access to gravid females, have not been found to be linked with higher rates

of total filial cannibalism (Pampoulie et al., 2004). These findings suggest that responsiveness of male filial cannibalism to determinants of future reproduction are not yet well understood and further investigations are therefore warranted.

Throughout their life span, sand gobies are vulnerable to a range of predators, especially birds (Lindström & Ranta, 1992) and fish (Hansson, Arrhenius, & Nellbring, 1997; Koli, Rask, & Aro, 1985; Lappalainen, Rask, Koponen, & Vesala, 2001). Indeed, it is likely that the level of this predation pressure will influence the prospects of future reproduction of parental male gobies. This is not only because falling victim to predators prevents further reproduction, but also because attempting to remain inconspicuous to predators may restrict the courtship and spawning activities of sand gobies (Forsgren & Magnhagen, 1993; Wong, Järvenpää, & Lindström, 2009; see also: Magnhagen, 1990; Magnhagen & Forsgren, 1991). Therefore, under a higher risk of predation, the potential to reinvest resources gained via filial cannibalism may be particularly limited. We can thus predict that sand gobies that perceive a relatively high risk of predation will be less likely to engage in total filial cannibalism and, in cases of partial filial cannibalism, eat fewer of their eggs, especially if filial cannibalism is performed primarily to improve future rather than current reproductive success.

In this study, we set out to examine the effect of perceived predation risk on filial cannibalism in the sand goby by comparing the behaviour of egg-tending males exposed to a perch, *Perca fluviatilis*, a common predator of sand gobies (Koli et al., 1985; Lappalainen et al., 2001), with that of males guarding eggs in a comparatively safe environment. We also examined the effect of predation threat on nest construction. This could elucidate the motives behind any adjustment of the level of filial cannibalism and test whether filial cannibalism is employed to acquire energy for nest maintenance and construction as suggested by earlier findings showing that good body condition and supplemental feeding in sand gobies promote higher quality or more extensive nest building (Lehtonen & Wong, 2009; Lindström, 1998; Olsson, Kvarnemo, & Svensson, 2009).

METHODS

Experimentation took place during the sand goby breeding season (May–July 2014) at the Tvärminne Zoological Station (59°50.7'N, 23°15.0'E) on the Baltic Sea's coast. Gobies were collected within the nearby nature reserve using a hand trawl (Evans & Tallmark, 1979; Lehtonen & Kvarnemo, 2015a) and dip-nets, while a gillnet was used to capture perch. After capture, all fish were brought to the station and placed in single-species stock aquaria within a semi-outdoor laboratory facility where experimentation occurred. Within this facility, all aquaria received sea water flow-through and were exposed to natural light and temperature conditions. Sand gobies housed in stock aquaria were segregated by sex and fed daily on frozen chironomid larvae and live *Neomysis* shrimp. Perch remained unfed for the duration of the experiment.

To initiate a replicate, a male and female sand goby were selected and their wet mass and standard length were measured. Females were chosen based on the presence of a distended abdomen, indicating gravidity (Kvarnemo, 1997). Males were selected haphazardly but those under 30 mm standard length were avoided, as larger males dominate nesting sites in this species (Lindström, 1988; Lindström & Pampoulie, 2005; Magnhagen & Kvarnemo, 1989), with smaller males often prevented from spawning or resorting to sneak spawning tactics (Takegaki, Svensson, & Kvarnemo, 2012). After selection, each male–female pair of gobies was added to an experimental aquarium (Fig. 1). Each of these aquaria contained a pair of plastic barriers, one opaque and

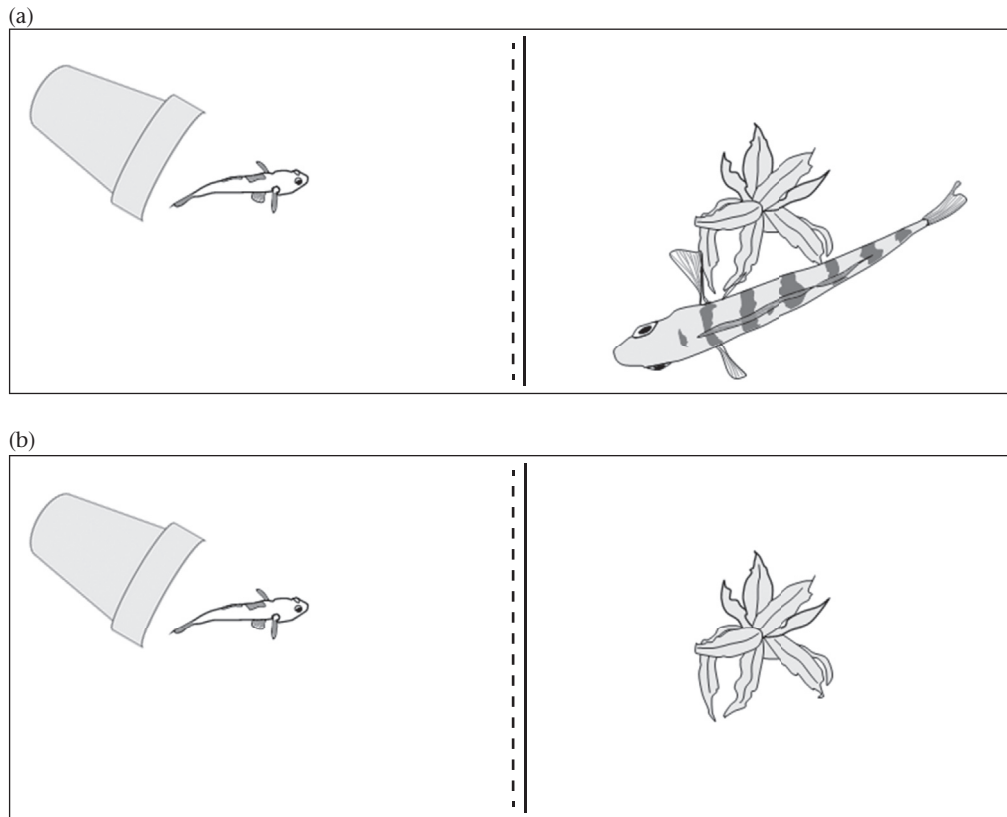


Figure 1. Top-view schematic layout of experimental aquaria for the (a) 'predator' treatment and (b) 'control' treatment. Dashed lines are used to depict clear aquarium dividers, while solid lines represent opaque dividers. Schematic is not to scale.

one clear, which divided them into a 'nesting compartment' and an 'exposure compartment' (Fig. 1). The male–female pair was introduced to the nesting compartment, which had been provided with a sand substrate and an artificial nesting site. The nesting site comprised a flowerpot half (diameter of the mouth: 8 cm) with its interior lined with a thin acetate sheet, upon which females attached their eggs during spawning. Initially, the male was released directly into the nesting compartment, whereas the female was held in a clear plastic receptacle in front of the nesting site to encourage the male to begin nest construction. This involved the male piling sand directly on top of the flowerpot and excavating a nesting chamber underneath it, leaving a single entry passageway (which varied in size from a completely open flowerpot mouth indicating a low level of nest construction) to a sand-enclosed passageway just large enough for the male to pass through (which is found only in thoroughly constructed nests). The following day, the female's receptacle was removed releasing her into the nesting compartment to spawn. The pair was left for 1 more day to spawn, and then the female was removed and released back into the sea. In some cases ($N = 44$), no spawning occurred within this timeframe and so the replicate was aborted and the male was also released. For pairs that did spawn ($N = 79$), we removed and photographed the sheet lining the nest, to which their eggs were attached, in order to later count the eggs spawned (Pampoulie et al., 2004). Care was taken to ensure the sheet and eggs remained submerged in a shallow tray of water during this procedure, after which they were quickly returned to the nest.

After the eggs were returned to the nest-holding male, he was randomly assigned to either the 'predator' ($N = 40$) or 'control' ($N = 39$) treatment. In the predator treatment, we then added a perch (standard length: 176 ± 31 mm [mean \pm SD], $N = 40$) and a plastic plant to the aquarium's exposure compartment, with the

plastic plant providing refuge for the perch. In the control treatment, only a plastic plant was added to the exposure compartment. This ensured that all fish were subject to novel stimuli. In both treatments, we then removed the opaque barrier dividing the nesting and exposure compartments, leaving only the transparent barrier in the tanks. To prevent other cues disturbing the fish after this, we wrapped the exterior vertical walls of the aquaria in black plastic and left the males to brood their eggs. We did not offer any food to males during this brooding period, as opportunities to forage are restricted during brood care (Lindström & Hellström, 1993; Salgado, Cabral, & Costa, 2004).

There is some evidence that dissolved oxygen levels may influence filial cannibalism rates (Klug et al., 2006; but see Lissåker et al., 2003). To account for this in our analysis, we measured the dissolved oxygen in each nesting compartment using a dissolved oxygen meter (model: YSI ProODO; YSI Inc., Yellow Springs, OH, U.S.A.) 7 days after the male had been left to brood. At this point, sand goby eggs are close to hatching (Kvarnemo, 1994). After measuring the dissolved oxygen, we then measured the height and width of the nest entrance and the amount of sand piled on the nest (assessed as the height of sand piled on the nest, as measured from the base of the tank; see Lehtonen, Wong, & Kvarnemo, 2016). We then immediately removed the lining sheet from the male's nest and photographed it using the same procedure as for the initial photograph. This enabled us to estimate how many eggs were consumed by males by counting the eggs on the photographs of their nest-lining sheets from the beginning and end of the brooding period using the manual cell counter plugin of ImageJ (Rasband, 1997–2015). This measure of filial cannibalism follows previously published studies (e.g. Klug & Lindström, 2008; Lehtonen & Lindström, 2007), with male consumption of eggs being the only plausible explanation for egg disappearance, whereas egg viability

at the point of consumption could not be ascertained in this study. Finally, male sand gobies were removed from their tanks and reweighed before we returned them, and any perch used in the trial, back to the sea. Some males ($N = 14$) died during the brooding period, and one control male was accidentally removed from his tank too early. Measurements from these replicates were not used for our analyses (except in determining the relationship between male length and weight for body condition calculations). The final sample size was thus 33 predator treatment males and 31 control males. No sand gobies were used across multiple replicates, and perch were only reused when the first male to which they were exposed died during brooding.

Statistical Analyses

Filial cannibalism

All analyses were conducted using R (R Core Team., 2016). Since total filial cannibalism and partial filial cannibalism are thought to be distinct phenomena (Manica, 2002), we modelled each of these separately. A probit regression model was used to analyse the occurrence of total filial cannibalism and an ordinary least squares (OLS) regression model was used to analyse the number of eggs eaten in cases of partial filial cannibalism. For our analyses we classified males that consumed all of their eggs, as well as one male that consumed all but eight of the eggs in his brood (>99%), as total filial cannibals. Observations from these males were truncated from the data set for the partial filial cannibalism model. Furthermore, we performed a natural logarithm transformation on the number of eggs consumed for this model to achieve approximately normally distributed residuals. Both models of filial cannibalism were fully additive with predation threat treatment, prespawning male body condition and dissolved oxygen level used as predictors. Furthermore, the initial number of eggs spawned was used as a predictor for the total filial cannibalism model only, since we believe that the weight of the existing empirical evidence supports the assumption that, for sand gobies, the occurrence of total filial cannibalism is influenced by initial clutch size (Andr n & Kvarnemo, 2014; Forsgren et al., 1996; Klug et al., 2006; Liss ker & Svensson, 2008; Pampoulie et al., 2004; but see Chin-Baarstad et al., 2009), whereas the number of eggs consumed in cases of partial filial cannibalism is not (Andr n & Kvarnemo, 2014; Kvarnemo, 1997; Liss ker & Kvarnemo, 2006; see also: Lindstr m, 1998; Pampoulie et al., 2004). Inclusion of male body condition in our analyses allowed us to account for the possibility that individuals might adjust their egg consumption based on their body condition if filial cannibalism is performed to acquire energy (Manica, 2002). As a proxy of male body condition, we used the scaled mass index, which we calculated following the procedure described by Peig and Green (2009) using the *smatr* R package for the necessary standardized major axis regression (Warton, Duursma, Falster, & Taskinen, 2012). Measurements from all 79 males that spawned in this experiment were used to calculate the value of the scaling coefficient and exponent of the power law assumed to describe the relationship between male standard length and prespawning body mass in these gobies. The use of dissolved oxygen level as a predictor can account for the possibility that oxygen saturation might have been affected by perch in the predator treatment. However, this was a cautious approach, given that the dissolved oxygen levels dealt with in this experiment (predator treatment: $99 \pm 14\%$ [mean \pm SD], $N = 33$; control treatment: $103 \pm 8\%$, $N = 31$) far exceed the hypoxic conditions where it is thought filial cannibalism and nest building may be influenced (Klug et al., 2006; Liss ker & Kvarnemo, 2006; Liss ker et al., 2003). For all the presented regression models, we draw inference based on Wald *t* tests of coefficients.

One potential issue with our OLS model of partial filial cannibalism is that the sample we examined was no longer random as a result of total filial cannibals being excluded from this analysis. To address this, we also fitted a Heckman sample selection model (Tobit-2 model) to the data, but since this revealed qualitatively similar results to the OLS model with minimal bias in parameter estimates, we elected to focus on the simpler OLS analysis here, with the sample selection model presented in the Appendix.

Male weight change

To determine whether the consumption of eggs influenced the change in male weight over the duration of the brood care period, we used two general linear models each with male weight change as the response variable. First, we tested whether mode of filial cannibalism (partial or total) in isolation influenced weight change. Second, we included the mode of filial cannibalism, the number of eggs consumed and the interaction between these two terms as predictors, to test whether the effects of filial cannibalism mode could be attributed to the different number of eggs eaten by males that engaged in these two modes of filial cannibalism.

Nest construction and maintenance

We constructed three separate general linear models, each examining one nest architecture parameter (nest opening width, nest opening height and nest sand pile height) as a response variable. The included predictor variables, which were the same for each model, were predation treatment, male standard length, prespawning male body condition, oxygen saturation level, the number of eggs consumed by the male, and whether or not the male engaged in total filial cannibalism. We also included terms for the two-way interactions between the mode of filial cannibalism and each of the other predictors. This was done because we wanted to account for the possibility that total and partial filial cannibals alter the construction of their nests in response to environmental variables differently.

Ethical Note

Experiments were approved by the Biological Sciences Animal Ethics Committee of Monash University (BSCI/2014/01) and complied with the laws of Finland, where the procedures met the standards of 'ELLA' (the Finnish Animal Experiment Board) for noninvasive animal experiments. Some sand gobies died during brooding as part of this study ($N = 14$), which probably reflects natural mortality where most adults do not survive for multiple breeding seasons (Fonds, 1973; Healey, 1971). All surviving fish from this experiment were returned to the sea after the experiment.

RESULTS

Filial Cannibalism

After spawning, males had 1226 ± 545 (mean \pm SD) eggs ($N = 64$), with 414 ± 388 of these typically being consumed by the end of the trial. All males consumed at least some eggs (minimum consumed = 12 eggs) and 18 of the 64 males in the final sample engaged in total filial cannibalism. Males with small initial clutches were significantly more likely to engage in total filial cannibalism (Table 1, Fig. 2). Exposure to a perch also tended to decrease the likelihood of a male engaging in complete clutch cannibalism, occurring in seven of 33 (21%) perch-exposed males compared to 11 of 31 (35%) unexposed males, although this effect was marginally nonsignificant (Table 1, Fig. 2). Neither prespawning male body

Table 1
Parameter estimates from models of filial cannibalism

Predictor	Total filial cannibalism (Probit model)			Partial filial cannibalism (OLS regression model)		
	β_S (SE)	β (SE)	t (P)	β_S (SE)	β (SE)	t (P)
Intercept	−0.909 (0.240)	−0.909 (0.240)	−3.785 (<0.001)	5.357 (0.124)	5.371 (0.123)	43.507 (<0.001)
Initial clutch size	−2.448 (0.595)	−0.002 (0.001)	−4.117 (<0.001)	—	—	—
Prespawning male body condition (g)	−0.226 (0.477)	−1.642 (3.458)	−0.475 (0.635)	−0.350 (0.247)	−2.540 (1.793)	−1.417 (0.164)
Perch exposure	−0.808 (0.442)	−0.808 (0.442)	−1.828 (0.068)	−0.038 (0.251)	−0.038 (0.251)	−0.153 (0.879)
Dissolved oxygen levels (%)	−0.035 (0.481)	−0.002 (0.021)	−0.072 (0.942)	−0.012 (0.223)	−0.001 (0.010)	−0.052 (0.959)

Perch exposure was dummy coded with 'predator' treatment as 0.5 and 'control' as −0.5, and all other predictor variables were mean centred. Regression coefficients based on raw predictor values (β) as well as rescaled regression coefficients (β_S) from scaling nonbinary inputs by two standard deviations are reported following Gelman (2008).

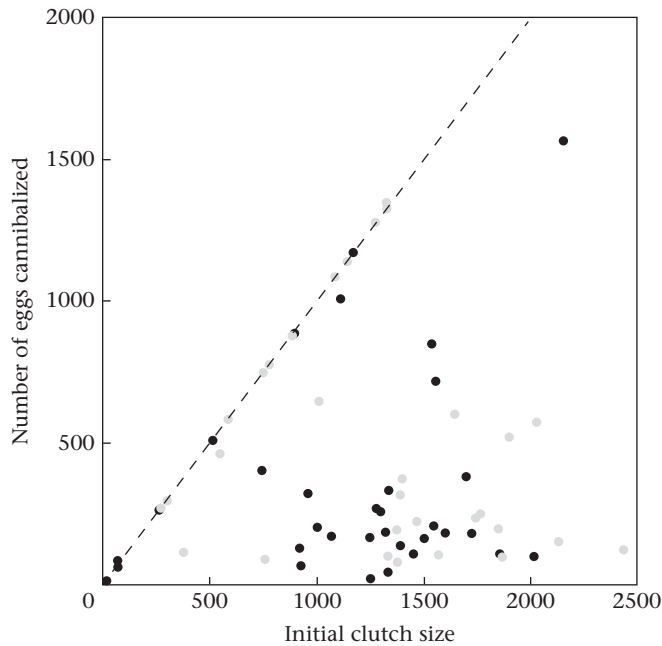


Figure 2. Plot of the number of eggs cannibalized by males during brooding against the initial clutch size for males exposed to a perch in the 'predator' treatment (black dots) and males in the 'control' treatment that did not encounter a predator (grey dots). Points lying on the diagonal ($N = 18$), where the initial clutch size is equal to the number of cannibalized eggs, represent cases of total filial cannibalism. Two data points that fall on the diagonal have been displaced upwards by 20 units to prevent overplotting.

condition nor the level of dissolved oxygen had significant effects on total filial cannibalism (Table 1).

For partial filial cannibalism, none of the potential predictors we examined (predation treatment, prespawning male body condition and dissolved oxygen levels) had significant effects on the number of eggs eaten (Table 1).

Male Weight Change

Males, on average, lost weight between the start of spawning and the completion of brooding (Wald test: $t_{62} = -3.734$, $P < 0.001$; see also Table 2). Total filial cannibals lost significantly less weight than partial filial cannibals ($t_{62} = 3.116$, $P = 0.003$). However, once we took the effect of the number of eggs eaten by each male and its interaction with filial cannibalism mode into account by including them in the model, the marginal effect of filial cannibalism mode was no longer significant (Table 2). The interaction between the number of eggs eaten and mode of filial cannibalism was also not significant but males lost significantly less weight with an increased number of eggs consumed (Table 2).

Nest Construction and Maintenance

There was a positive correlation between nest entrance height and width at the end of the brooding period ($r_s = 0.791$, $t_{62} = 10.195$, $P < 0.001$). Both dimensions were negatively correlated with the amount of sand piled above the nest, and while the relationship regarding nest entrance height was marginally nonsignificant, that involving nest entrance width was significant (nest entrance height: $r_s = -0.225$, $t_{62} = -1.818$, $P = 0.074$; width: $r_s = -0.294$, $t_{62} = -2.421$, $P = 0.018$).

For both nest entrance height and width, there was a significant interaction between the effects of predation treatment and whether or not males engaged in total filial cannibalism (Table 3). Specifically, the height and width of nest entrances was unrelated to the predation treatment among partial filial cannibals (nest entrance height: $\beta_S = -1.024 \pm 1.117$, $t_{52} = -0.917$, $P = 0.364$; width: $\beta_S = 2.718 \pm 3.29$, $t_{52} = 0.826$, $P = 0.412$), whereas among total filial cannibals, exposure to a perch was associated with significantly taller and wider nest entrances (nest entrance height: $\beta_S = 4.500 \pm 2.133$, $t_{52} = 2.109$, $P = 0.040$; Fig. 3a; width: $\beta_S = 19.217 \pm 6.279$, $t_{52} = 3.061$, $P = 0.003$; Fig. 3b). For both nest entrance height and width, the mode of filial cannibalism did not interact significantly with prespawning male body condition, male length, number of eggs consumed or dissolved oxygen level (Table 3). Similarly, nest entrance height and width were not significantly affected by prespawning male body condition, male length, number of eggs consumed or dissolved oxygen level, although there was a marginally nonsignificant tendency for longer males to build taller nest entrances (Table 3).

The height of sand piled on the nest was not affected by perch exposure or dissolved oxygen, with total and partial filial cannibals behaving similarly in this regard (Table 3). Longer males piled significantly more sand on their nests regardless of the mode of filial cannibalism (Table 3). The relationship between the number of eggs eaten and the height of the sand piled on a male's nest depended on the mode of filial cannibalism (Table 3, Fig. 4). Specifically, for partial filial cannibals, there was no significant relationship between the number of eggs consumed and the height of

Table 2

Parameter estimates from model of change in male wet mass (mg) over the brooding period

Predictor	β_S (SE)	β (SE)	t (P)
Intercept	−25.584 (5.622)	−25.584 (5.622)	−4.551 (<0.001)
Number of eggs eaten	62.042 (12.554)	0.080 (0.016)	4.942 (<0.001)
Total filial cannibalism	5.901 (13.073)	5.901 (13.073)	0.451 (0.653)
Number of eggs eaten * Total filial cannibalism	21.861 (23.168)	0.028 (0.030)	0.944 (0.349)

Predictor variables were mean centred. Regression coefficients based on raw predictor values (β) as well as rescaled regression coefficients (β_S) from scaling nonbinary inputs by two standard deviations are reported.

Table 3
Parameter estimates for models of nest architecture at the completion of brooding

Predictor*	Nest entrance height (mm)			Nest entrance width (mm)			Nest sand pile height (mm)		
	β_S (SE)	β (SE)	t (P)	β_S (SE)	β (SE)	t (P)	β_S (SE)	β (SE)	t (P)
Intercept	10.837 (0.523)	10.837 (0.523)	20.709 (<0.001)	39.253 (1.540)	39.253 (1.540)	25.487 (<0.001)	67.070 (1.008)	67.070 (1.008)	66.513 (<0.001)
Total filial cannibalism	4.236 (1.228)	4.236 (1.228)	3.449 (0.001)	10.679 (3.615)	10.679 (3.615)	2.954 (0.005)	0.097 (2.367)	0.097 (2.367)	0.041 (0.967)
Perch exposure	0.530 (1.002)	0.530 (1.002)	0.528 (0.600)	7.358 (2.950)	7.358 (2.950)	2.494 (0.016)	-0.335 (1.932)	-0.335 (1.932)	-0.174 (0.863)
Number of eggs eaten	0.090 (1.185)	0.000 (0.002)	0.076 (0.940)	5.408 (3.488)	0.007 (0.004)	1.550 (0.127)	-2.594 (2.284)	-0.003 (0.003)	-1.136 (0.261)
Prespawning male body condition	-0.818 (0.963)	-5.934 (6.985)	-0.850 (0.399)	-0.711 (2.834)	-5.160 (20.558)	-0.251 (0.803)	-1.163 (1.855)	-8.440 (13.460)	-0.627 (0.533)
Male length (mm)	1.862 (0.976)	0.182 (0.096)	1.907 (0.062)	4.661 (2.874)	0.456 (0.281)	1.622 (0.111)	5.102 (1.881)	0.500 (0.184)	2.712 (0.009)
Dissolved oxygen levels (%)	0.610 (1.072)	0.027 (0.047)	0.569 (0.572)	-2.353 (3.155)	-0.102 (0.137)	-0.746 (0.459)	0.760 (2.066)	0.033 (0.090)	0.368 (0.714)
Perch exposure*Total filial cannibalism	5.524 (2.408)	5.524 (2.408)	2.294 (0.026)	16.499 (7.088)	16.499 (7.088)	2.328 (0.024)	-3.497 (4.641)	-3.497 (4.641)	-0.754 (0.455)
Number of eggs eaten*Total filial cannibalism	1.186 (2.313)	0.002 (0.003)	0.513 (0.610)	4.623 (6.808)	0.006 (0.009)	0.679 (0.500)	-10.904 (4.457)	-0.014 (0.006)	-2.446 (0.018)
Prespawning male body condition*Total filial cannibalism	-2.437 (2.254)	-0.177 (0.164)	-1.081 (0.285)	-5.034 (6.633)	-36.519 (48.126)	-0.759 (0.451)	7.689 (4.343)	55.782 (31.510)	1.770 (0.083)
Male length (mm)*Total filial cannibalism	0.068 (2.371)	0.007 (0.232)	0.029 (0.977)	-0.523 (6.978)	-0.051 (0.683)	-0.075 (0.941)	3.486 (4.569)	0.341 (0.447)	0.763 (0.449)
Dissolved oxygen levels (%)*Total filial cannibalism	4.063 (2.935)	0.177 (0.128)	1.384 (0.172)	5.993 (8.639)	0.261 (0.376)	0.0694 (0.491)	3.461 (5.656)	0.151 (0.246)	0.612 (0.543)

Perch exposure was dummy coded with 'predator' treatment as 0.5 and 'control' as -0.5, and all other predictor variables were mean centred. Regression coefficients based on raw predictor values (β) as well as rescaled regression coefficients (β_S) from scaling nonbinary inputs by two standard deviations are reported.

the sand pile ($\beta_S = 0.473 \pm 2.886$, $t_{52} = 0.164$, $P = 0.871$; Fig. 4). By contrast, for total filial cannibals, consumption of more eggs was associated with piling less sand above the nest ($\beta_S = -10.431 \pm 3.397$, $t_{52} = -3.071$, $P = 0.003$; Fig. 4). There was also a marginally nonsignificant tendency for the effect of pre-spawning male body condition on nest sand pile height to differ between partial and total filial cannibals but the main effect of body condition was not significant (Table 3).

DISCUSSION

We predicted that exposure to a predator would result in increased investment in the existing young, since the perceived likelihood of surviving to engage in future reproduction should be diminished by a seemingly risky environment. However, we found that partial filial cannibalism was not influenced by the presence of a predatory perch. For total filial cannibalism, males tended to consume their entire brood less often in the presence of a perch, although this result was marginally nonsignificant. Therefore, there is currently insufficient evidence to show that parental predation risk influences filial cannibalism. Future research addressing total filial cannibalism should thus consider predation risk. First, our results suggest that threat of predation may have a more prominent effect on this form of filial cannibalism. Second, total filial cannibalism is only thought to be adaptive if parents can survive to reproduce again (Manica, 2002), which is contingent on avoiding predation. By contrast, partial filial cannibalism may be less (or not at all) influenced by predation risk because it can benefit parents in ways that do not depend on further reproduction, such as through improved survival of existing young (Klug et al., 2006; Lehtonen & Kvarnemo, 2015a, 2015b; see also Klug & Lindström, 2008).

As far as we are aware, the influence of parental predation risk has not previously been specifically investigated within the context of filial cannibalism. However, in contrast to our findings, some studies on other forms of parental investment have shown increased investment in existing young in response to predation threat. For example, in the side-blotched lizard, *Uta stansburiana*, and shaded broad-bar moth, *Scotopteryx chenopodiata*, females that have been injured, and are thus less able to evade predators, appear to elevate their level of parental expenditure on current offspring (Fox & McCoy, 2000; Javoiš & Tammaru, 2004). Thus, injury may have a more direct bearing on parents' perception of predation risk and, as a result, their current reproductive decisions. Similarly, the timing of predator cues may be important especially for total filial cannibalism, which typically occurs soon after spawning (Forsgren et al., 1996; reviewed in Manica, 2002). However, while pre-spawning exposure to predators may elicit a stronger effect on filial cannibalism, such patterns could be confounded by the potential of predator exposure to also affect courtship and spawning (Forsgren & Magnhagen, 1993; Wong et al., 2009). It also remains possible that filial cannibalism is not selected to be sensitive to predation threat in sand gobies. However, sand gobies should at least have the capacity for plasticity of filial cannibalism, because the behaviour is modulated by other environmental factors (Chin-Baastad et al., 2009; Pampoulie et al., 2004). Similarly, other behaviours in sand gobies can respond to predation threat (foraging: Magnhagen, 1988; courtship and spawning: Forsgren & Magnhagen, 1993; Wong et al., 2009), suggesting that variation in predation risk is present and perceived by sand gobies. Finally, it remains feasible that filial cannibalism behaviour is retained during periods of elevated predation risk despite reduced parental expectation of future reproduction due to yet unknown benefits of offspring consumption during such circumstances. For example, if predation threat restricts the ability of individuals to forage (Magnhagen, 1988), parents may be selected to exploit their own young as a

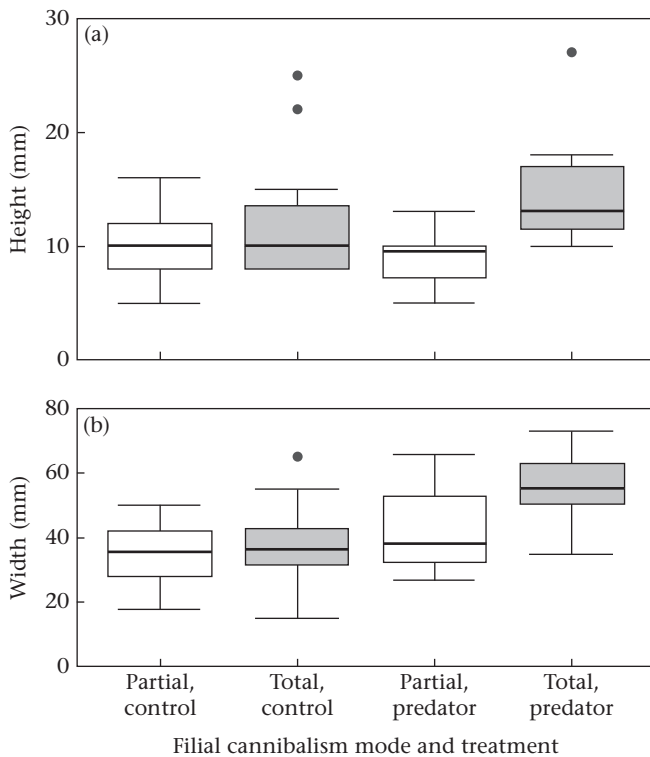


Figure 3. Tukey box plots showing the distribution of nest entrance (a) heights and (b) widths for male sand gobies that committed total or partial filial cannibalism and were either exposed to a perch in the predator treatment or nothing in a control treatment. The internal line of each box represents the median value and the edges the first and third quartiles. The whiskers denote the lowest and highest data points that are within one step of the first and third quartiles, respectively, where one step is 1.5 times the interquartile range. Values greater than one step above the third quartile are denoted with black dots.

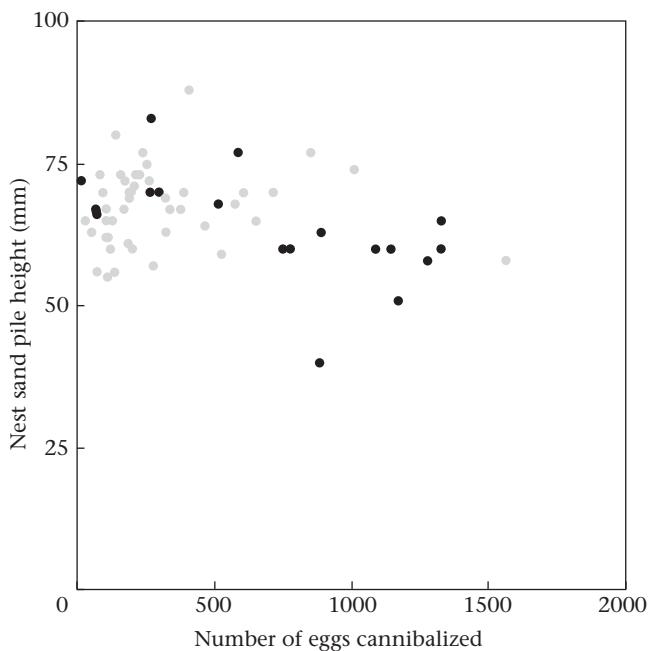


Figure 4. Plot of nest sand pile heights against the number of eggs consumed by the nest-holding male during the brooding period. Data points from total filial cannibals are black and those from partial filial cannibals are grey.

safe energy source (cf. McNamara, 1990). Therefore, further research exploring how predation risk relates to specific activities, such as nest tending and foraging, is necessary.

Previous studies indicate that consuming eggs can reduce weight loss by males, suggesting energetic benefit from this activity (Klug et al., 2006; Lindström, 1998; Lissåker et al., 2003). In the current study, our results suggest that any such energetic advantage enjoyed by total filial cannibals is not a direct result of avoiding caring for young. In particular, although total filial cannibals lost less weight than partial filial cannibals (which cared for the young over the full duration of the brood care phase), this difference appears to be explained by the greater number of eggs consumed by total filial cannibals, even without considering the reduced parental expenditure of total cannibals. Furthermore, we found that nest structure was unrelated to the number of eggs consumed by male gobies except for total filial cannibals, in which males that consumed more eggs piled less sand on their nests. Thus, there is no evidence to suggest that energy from egg consumption was used for nest construction. Finally, our finding that neither form of filial cannibalism was related to male body condition is in contrast with the idea that males in poor condition use filial cannibalism to replenish energy reserves. While such a result is in accordance with earlier work on sand gobies (Chin-Baarstad et al., 2009; Forsgren, 1997; Klug et al., 2006; Lissåker et al., 2003), the situation in other taxa might be different (Neff, 2003; Okuda et al., 2004 see also: Candolin, 2000; Kvarnemo, Svensson, & Forsgren, 1998; Manica, 2004; Marconato et al., 1993; Takahashi & Kohda, 2004). For example, in the mouthbrooding cardinalfish, *Apogon doederleini*, males tend to engage in greater amounts of filial cannibalism towards the end of the breeding season when their body condition has deteriorated as a result of restricted foraging opportunities during earlier breeding attempts (Okuda & Yanagisawa, 1996; Takeyama et al., 2002).

The factor that most strongly influenced the occurrence of total filial cannibalism was clutch size. In line with findings from previous work on both sand gobies (see Methods section), as well as other species (see Manica, 2002 for a review) such as the fantail darter, *Etheostoma flabellare* (Lindström & Sargent, 1997) and blue-gilled sunfish, *Lepomis macrochirus* (Neff, 2003), males were more likely to engage in total filial cannibalism when their initial clutch size was small. This suggests that the benefits of total filial cannibalism outweigh the costs of offspring consumption when brood size is small. Moreover, our finding that consumption of a large number of eggs among total filial cannibals was associated with piling less sand onto the nest suggests that those males that totally consume larger clutches may be less motivated to maintain the nest site or are inherently less capable of doing so.

We found that among total filial cannibals, males that were exposed to predatory perch constructed larger nest entrances than other males. This could be adaptive if small nest entrances inhibit predator evasion, or if nest construction incites predation, as suggested by Magnhagen and Forsgren (1991). Alternatively, nest maintenance may be reduced as a strategy to renege at a safer time or location (but see Magnhagen, 1990; Magnhagen & Forsgren, 1991). Curiously though, the amount of sand piled on the nest was not similarly affected. This may reflect the importance of the sand pile in concealing the nest from predators (Lindström & Ranta, 1992), or the potential greater value of a large sand pile in attracting mates (Lehtonen & Lindström, 2009; Lugli, 2013; Svensson & Kvarnemo, 2005; cf. Lehtonen & Wong, 2009) compared to a small nest entrance (Svensson & Kvarnemo, 2005, 2007). Intriguingly, unlike total filial cannibals, for males that cared for at least some of their eggs, predator exposure was unrelated to nest architecture. Perhaps, the possibility of increased vulnerability to egg predators associated with larger nest entrances (Lissåker &

Kvarnemo, 2006) explains why predator-exposed parental males still built small nest entrances. In other words, males that are committed to rearing at least some of their brood appear not to compromise care even when doing so could jeopardize their own survival.

In conclusion, our results indicate that partial filial cannibalism was not affected by the perceived threat of predation to the parent, possibly because this type of cannibalism is performed to benefit the current brood. Our results with regard to total filial cannibalism were less clear-cut, with a nonsignificant tendency for males to avoid total filial cannibalism when predation threat was high, suggesting that further research into this area could be informative. With regard to nest construction, we showed that consumption of a larger clutch was not linked to more elaborate nest construction, which may indicate that males do not consume eggs for the purpose of nest maintenance. Moreover, we found that aspects of nest architecture were influenced by the presence of a predatory perch only in total filial cannibals, suggesting that care-giving males do not compromise nest maintenance when confronted by a predator. Predator presence was linked to large nest entrances among total filial cannibals, possibly due to reluctance to re-nest in the vicinity of a predator or because large-entrance nests may be safer to build or occupy. Overall, the findings of this study highlight the importance of considering the effect of adult predation risk on parental effort decisions.

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APPENDIX. SAMPLE SELECTION MODELLING

As an alternative approach to examine what influences the number of eggs eaten during partial filial cannibalism, we fitted a Heckman sample selection model (Tobit-2 model) to our data using full information maximum likelihood estimation with the sampleSelection R package (Toomet & Henningsen, 2008). This model had two parts. First, a probit regression model was used to estimate the effect of predictors upon the likelihood of the occurrence of partial (rather than total) filial cannibalism. Just like the probit model of the occurrence of total filial cannibalism presented in the main text, we used prespawning male body condition, oxygen saturation level, predation treatment and initial number of eggs spawned as predictors. This first part of the Heckman selection model was thus identical to the probit model in the main text, except that the sign of all regression coefficients was reversed since the occurrence of partial filial cannibalism is effectively the opposite of the occurrence of total filial cannibalism (as all males ate some eggs). Accordingly, we do not present the results of this selection part of the model.

The second part of the Heckman selection model determined the effects of predictors on the response variable, in this case, the natural logarithm of the number of eggs consumed during partial filial cannibalism. This is analogous to the ordinary least squares (OLS) model of the same response variable presented in the main text except this model corrects for biases in the estimates of independent variable effects on egg consumption during partial filial cannibalism that may have arisen as a result of males nonrandomly engaging in total filial cannibalism (see Wooldridge, 2002). We also used the same predictors here as the OLS model (male body condition, oxygen saturation levels and predation treatment). Beyond the empirical justification for not including initial number of eggs spawned as a predictor of the extent of partial filial cannibalism discussed in the main text there is also a practical benefit to this choice: that model identification is improved when a variable is used to predict the occurrence of an event but not the extent of the response when the event occurs (Vance & Ritter, 2014).

The results of the Heckman selection model were qualitatively similar to those of the OLS model (Table A1, cf. Table 1). Specifically, we found no significant effect of male body condition, oxygen saturation level or predation treatment on the number of eggs

eaten in cases of partial filial cannibalism (Table A1). Furthermore, there was no significant correlation between the errors of the selection equation (describing the occurrence of total filial cannibalism) and outcome equation (describing the number of eggs eaten during partial filial cannibalism) in the Heckman selection model ($r_s = 0.028$, $t_{52} = 0.056$, $P = 0.955$). The interpretation of this is that after taking into account a male's body condition, clutch size, oxygen saturation level and predator exposure level his propensity to engage in total filial cannibalism does not influence the number of eggs he will consume when he engages in partial filial cannibalism. In other words, there is no evidence that selection bias arising from nonrandom occurrence of total filial cannibalism was a serious problem in this experiment (see Vance & Ritter, 2014).

Table A1
Parameter estimates from Heckman sample selection model of partial filial cannibalism outcome equation

Predictor	β_s (SE)	β (SE)	t (P)
Intercept	5.363 (0.165)	5.363 (0.165)	32.513 (<0.001)
Prespawning male body condition (g)	−0.347 (0.241)	−2.521 (1.748)	−1.442 (0.149)
Perch exposure	−0.043 (0.256)	−0.043 (0.256)	−0.170 (0.865)
Dissolved oxygen levels (%)	−0.012 (0.219)	−0.001 (0.010)	−0.053 (0.958)

Perch exposure was dummy coded with 'predator' treatment as 0.5 and 'control' as −0.5, and all other predictor variables were mean centred. Regression coefficients based on raw predictor values (β) as well as rescaled regression coefficients (β_s) from scaling nonbinary inputs by two standard deviations are reported.

Chapter 5

The influence of parental status on
courtship effort in a paternal caring fish

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The Influence of Parental Status on Courtship Effort in a Paternal Caring Fish

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Abstract

It is widely assumed that caring for young limits the motivation of parents to seek additional mating opportunities. However, in situations where parental care does not involve direct provisioning of the offspring, but rather activities directed at the brood as a whole (e.g. guarding), it may be more efficient for parents to care for large numbers of young at once. This may be especially true for species with exclusive paternal care, with fathers that have recently acquired a brood of young potentially benefiting from vigorously courting prospective mates, so as to maximise their chances of attaining a large number of young to rear together. We experimentally tested this hypothesis in the three-spined stickleback (*Gasterosteus aculeatus*), a fish with male only care. Contrary to our predictions, we found no evidence of any differences in courtship between recently spawned egg-tending fathers and males that had not spawned. However, males that were permitted to spawn, but then had their eggs taken from them, courted less vigorously. Together, the results of our study suggest that the potential benefits of vigorous courtship in terms of acquiring additional young may be offset by additional costs faced by parental males.

Introduction

In species with paternal care, both courting mates and caring for offspring can be time-consuming and energetically demanding. Such temporal and energetic limitations, in turn, can result in conflict between mating and parental effort (Magrath & Komdeur 2003). For example, in a bird, the Temminck's stint (*Calidris temminckii*), males that opt to incubate their eggs miss out on further mating opportunities (Thomson et al. 2014) whilst, in many other species, parents that are given the chance to pursue additional mates provide less care to their young (Magrath & Elgar 1997; Bjelvenmark & Forsgren 2003; Bonnevier et al. 2003; Symons et al. 2011) or even abandon them altogether (Keenleyside 1983; Townshend & Wootton 1985). However, recently, it has been highlighted that courtship and parental activities are not always incompatible with one another (Tallamy 2000, 2001; Stiver & Alonzo 2009). For instance, in species where parents perform courtship and rear offspring in the

same location, parents may be able to engage in courtship and care simultaneously (Stiver & Alonzo 2009). Moreover, even where parental and mating effort draw on the same limited resources, individuals may still opt to invest in both of these aspects of life history at the same time and sacrifice investment in other components of life history, such as somatic investment, in order to do so (Magrath & Komdeur 2003).

To date, the majority of research investigating the association between parental care and courtship effort has focused principally on how courtship of potential mates influences the quality of care individuals provide (Magrath & Elgar 1997; Bjelvenmark & Forsgren 2003; Bonnevier et al. 2003; Pampoulie et al. 2004; Symons et al. 2011). Less well understood, however, is how parental care might influence prevailing courtship levels (but see: Kraak & Groothuis 1994; Green et al. 1995; Pitcher & Stutchbury 2000). Here, the nature of parental care within a species is likely to be important. Where offspring within a brood compete for resources provided by their parent, there may be little benefit to

an individual parent in attracting new mates prior to the independence of existing offspring because intra-brood competition may cause parental care costs to scale with the number of offspring being cared for (cf. Ahnesjö 1996). By contrast, where parental care is non-depreciable (i.e. where the cost of rearing a brood is independent from the number of young in the brood; *sensu* Altmann et al. 1977), or where only modest increases in the cost of care arise from adding young to the brood, it may actually benefit individuals to rear multiple batches of young contemporaneously as this reduces the per capita cost of offspring care (see Smith 1992; Smith & Wootton 1995a). For males, in particular, which generally cannot directly control the number of young produced by a single mating, courting and mating with additional females after the acquisition of an initial clutch of young may represent the most effective strategy to increase the number of young in their brood, and thus capitalise on such economies of scale in parental care. Indeed, intense courtship could be employed by parental males in these circumstances, so that they can acquire additional clutches as soon as possible after the initial spawning, so as to maximise the overlap in the brooding period of existing and potential new clutches. Further to this, given evidence that females may even prefer males that are engaged in parental care (e.g. Thomas & Manica 2005; Lindström et al. 2006; Manica 2010; Nazareth & Machado 2010; also reviewed in: Jamieson 1995; Reynolds & Jones 1999), there may be additional incentive for parental males to court in order to capitalise on their enhanced attractiveness. Alternatively, however, it is also possible that parental males may reduce their courtship effort as the elevated attractiveness afforded by their parental status means that intense courtship is no longer necessary to outcompete rivals in mating competition.

Here, we set out to empirically test the influence of parental status on the courtship of male three-spined sticklebacks (*Gasterosteus aculeatus*). During the breeding season, male sticklebacks compete for territories and construct nests from sediment and plant material (Östlund-Nilsson 2006). Males then attract passing females to their nest using elaborate zigzag courtship displays (Wootton 1976; Rowland 1994). If a male is successful in his efforts, the female will deposit her eggs within his nest. The male then becomes the sole care provider of the eggs, defending them from potential predators as well as fanning them with his pectoral and caudal fins to provide ventilation (van Iersel 1953; Whoriskey & Fitzgerald 1994; Östlund-Nilsson 2006). Male sticklebacks are capable of caring for the young of multiple females at once (Kraak et al. 1999a,b), and it seems likely that the cost of guarding

multiple clutches of young is not substantially greater than that of defending a single clutch (Perrone & Zaret 1979; Lazarus & Inglis 1986; Smith & Wootton 1995a). Moreover, although competition for dissolved oxygen may be increased when males rear multiple clutches simultaneously (van Iersel 1953; Reeb et al. 1984; Coleman & Fischer 1991; Bakker et al. 2006; see also: Perrin 1995), it appears that males can compensate for this with modest changes in fanning behaviour and loss of energetic resources relative to the total cost of brood care (van Iersel 1953; van den Assem 1967; Sargent & Gebler 1980; Coleman & Fischer 1991). Taken together, this suggests that it is likely to be more efficient for males to rear multiple clutches simultaneously rather than sequentially in this species. Therefore, we predict that male sticklebacks that have recently acquired an initial clutch of eggs will court more vigorously than non-parental males, as intense courtship may help these recently spawned egg-tending males quickly acquire additional clutches that they can then rear alongside their existing eggs, thereby increasing the reproductive pay-offs for providing care with minimal additional parental investment (cf. Jamieson & Colgan 1989; Jamieson et al. 1992). To date, few studies have directly compared measures of mating effort between parental and non-parental males, and among the few that have the previous breeding experience of non-parental males did not always match that of parental individuals (Jamieson & Colgan 1989; Goldschmidt et al. 1993). Consequently, the effect of parental status may potentially be influenced by differences in prior breeding experience. Thus, to enable us to disentangle these two phenomena, we compared the courtship behaviour of parental male sticklebacks with both non-parental males that had been given the opportunity to court but not spawn with a female as well as non-parental males that had been permitted to spawn but subsequently had their eggs removed.

Methods

This study was approved by the Monash University Biological Sciences Animal Ethics Committee (permit BSCI/2014/15) and complies with all the relevant laws of Finland and Australia for research involving live vertebrates.

Collection and Pre-experimental Housing

We collected three-spined sticklebacks from the littoral zone of the Baltic Sea near the Tvärminne Zoological Station (59°50.7'N, 23°15.0'E) using minnow

traps between May and July 2014. Fish were transported back to the station in 50L coolers, segregated by sex based on hints of nuptial coloration (males have blue eyes and red throats) and housed in 200L stock aquaria (~50 fish per tank) until their use in experiments. These stock aquaria, as well as experimental aquaria, were situated in an outdoor aquarium facility exposed to ambient outdoor light (~18.5-h light per day) and temperature conditions (measured mean = 13°C, range = 10–19°C) and provided with continuous flow-through of sea water. Fish in the stock aquaria were fed daily on chironomid larvae and *Neomysis* shrimp *ad libitum*.

Nest Building

We began each replicate by removing a single male from the stock tank, measuring his standard length and weight, and then placing him alone in an experimental aquarium (40 × 40 × 40 cm). Each aquarium was supplied with a (14 cm diameter) round dish filled with sand and 7 ± 0.1 g of filamentous green algae (*Cladophora*) to enable the male to construct a nest (Candolin 2000b). We checked experimental aquaria daily for a completed nest, which we identified by the appearance of a distinct tunnel with an exit (van Iersel 1953). Any males that had not constructed a nest after 3 days were excluded from the experiment and returned to the sea. During the nest-building phase, and for the rest of experimentation, individual males were fed three chironomid larvae

per day, which is sufficient for males to complete multiple consecutive parental cycles (Candolin 2000a).

Baseline Courtship Assay

To allow us to obtain a baseline measure of the courtship intensity of individual male sticklebacks, we assayed the courtship effort of each male the day after it had completed nest construction. To assay male courtship, we exposed each male to a ready-to-spawn (as indicated by her distended abdomen: Wootton 1984) female (standard length: 58 ± 4 mm [\bar{x} ± SD]; mass: 2.8 ± 0.6 g) selected from a stock tank (Fig. 1: Stage 1). The female was held inside a (10 × 7.5 × 40 cm) clear acrylic container positioned inside the corner of the experimental aquarium during this assay. This container was perforated with tiny holes and filled with sea water to a depth slightly greater than the water level of the experimental aquarium. As a result of this water flow was primarily from the container holding the female to the experimental aquarium with the male, encouraging the male to receive female olfactory cues whilst reducing the amount of olfactory cues reaching the female. After the female was introduced into her holding container, we allowed the female five min to acclimate. During this time, visual contact between the sexes was prevented by placing an opaque acrylic barrier around the female container. Immediately following this acclimation period, we removed the opaque barrier, thereby permitting visual contact between the

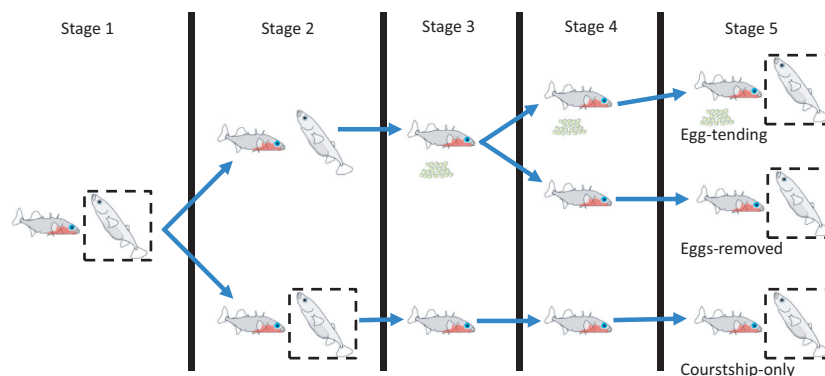


Fig. 1: Schematic of the experimental procedure. In stage 1, male sticklebacks that had constructed a nest were given the opportunity to court a ready-to-spawn female that was held within a clear, perforated receptacle. A baseline measure of male courtship effort was recorded during this initial assay. In stage 2, males were either permitted to continue courting the female whilst she remained in the receptacle or the female was released from the receptacle thereby making spawning possible. Following this, males in stage 3 had either acquired eggs as a result of spawning or had no eggs as a result of not being given the opportunity to spawn. In stage 4, half of the males that were spawned had their eggs experimentally removed, creating three treatments: 'egg-tending', 'eggs-removed' and 'courtship-only' males. Finally, in stage 5, males in each of the treatments were permitted to court a new female, enabling their courtship to be assayed (not shown is the fact that this assay was conducted twice with a separate female each time). [Colour figure can be viewed at wileyonlinelibrary.com]

male and female. We then observed the behaviour of the male for 10 min quantifying his courtship behaviour by counting the number of zigzag dances performed by the male. A zigzag dance involves rapid side-to-side movements of the male whilst approaching the female (for a detailed description see: Wootton 1976, 1984 and references within). Counts of zigzag dances were chosen as the measure of courtship effort, as they were the most clearly discernible and frequently performed courtship behaviour (see also: Sevenster-Bol 1963; van Iersel 1953) and are also repeatable (Dzieweczynski & Forrette 2015). Moreover, there is evidence to suggest that males that engage in greater numbers of zigzag dances are more successful at attracting females to mate (von Hippel 2000; but see: Rowland 1995) and engaging in more rapid zigzag dances may augment the effectiveness of other attractive male traits too (Künzler & Bakker 2001).

Manipulating Male Parental Status

At the end of the baseline courtship assay, we randomly assigned each male to a treatment group (Fig. 1: Stages 2–4). For two of these treatments ('egg-tending' and 'eggs-removed'; see description below), males were permitted to spawn with the female that was used as the stimulus during their baseline courtship assay. After releasing the female to spawn, each experimental aquarium was checked over the course of the next 24 h, with the female removed after spawning had occurred. Following removal of the female, we then waited for the clutch of eggs to harden within the nest (Swarup 1958; Kraak & Bakker 1998). For males in the 'eggs-removed' treatment, we carefully removed the entire clutch from the nest with a pair of tweezers on the same night that spawning had occurred. Males in the 'egg-tending' group were allowed to retain their eggs, but to ensure that the disturbance of the nest was similar across treatments, we also disturbed their nest with tweezers without ultimately removing eggs.

For the third treatment of this experiment, referred to as 'courtship-only', we did not allow the males to spawn. Instead, the stimulus female from the baseline courtship assay remained confined to the container so that the male could continue courting her. We removed the female after a period of time that was comparable to the time that males in the other treatments were in contact with a female. The mean time females were left with males across treatments was 9 ± 6 h [$\bar{x} \pm \text{SD}$], with no significant difference between treatment groups (single-factor ANOVA:

$F_{2,71} = 1.09$, $p = 0.341$). As with males in the other two treatments, 'courtship-only' males also had their nests disturbed with tweezers.

For the experiment, a larger proportion of males ($n = 65$ in total) were assigned to the treatments that required spawning (i.e. 'egg-tending' and 'eggs-removed') to account for some males failing to spawn within the 24-hour period given. Males that did not spawn ($n = 17$) were excluded from our main data analysis, with no further testing carried out on them. To rule out the possibility that exclusion of these males caused among treatment differences in courtship motivation, we tested (using a negative binomial generalised linear model) whether the baseline courtship level of males was related to treatment group, including those males that failed to spawn as a fourth treatment. Here, we found no evidence that the treatment group was related to the number of zigzag dances performed by males in the baseline assay (likelihood ratio test: $\chi^2_{3,86} = 2.864$, $p = 0.413$), suggesting that sampling bias was not an issue.

The final sample sizes for the 'egg-tending', 'eggs-removed' and 'courtship-only' treatment groups were 24, 24 and 26, respectively. The standard length of the males was 53 ± 5 mm [$\bar{x} \pm \text{SD}$], and their mass was 2.0 ± 0.6 g, with ANOVA revealing no significant difference in size among treatments (standard length: $F_{2,71} = 1.511$, $p = 0.2278$; mass: $F_{2,71} = 0.984$, $p = 0.379$).

Male Courtship Post-manipulation

Following manipulation of male parental status, we quantified the courtship effort of males by exposing them to additional ready-to-spawn females presented inside a clear container (Fig. 1: stage 5). These assays took place on the day following the baseline courtship assay 18 ± 5 h [$\bar{x} \pm \text{SD}$] (range: 6–31 h) after manipulation of male parental status, with no difference in commencement time between treatments (single-factor ANOVA: $F_{2,71} = 0.521$, $p = 0.596$). This timeframe was chosen as it fits within a critical window whereby it is long enough after the spawning of males (where this occurred) that males have recovered their courtship drive (van Iersel 1953; Wootton 1976) whilst still being close enough to the time of the initial spawning that the putative benefits of concurrent clutch rearing should be large for 'egg-tending' males.

The procedure for acclimating and exposing the females was identical to that used for the baseline courtship assay, with male zigzag displays quantified over a 10-min exposure period. To obtain a precise estimate of each male's propensity to court that is

minimally biased by differences in stimulus females, we tested each male twice, using a different female each time presented one after another (female standard length: 58 ± 5 mm [$\bar{x} \pm \text{SD}$]; mass: 2.7 ± 0.7 g), with a 5-min break in between. As with females that were used for the baseline assays, each female was used only once, with no difference in female standard length (single-factor ANOVA: $F_{2,145} = 1.09$, $p = 0.340$) or mass (single-factor ANOVA: $F_{2,145} = 1.38$, $p = 0.256$) between treatments.

Statistical Analysis

To investigate whether males in each of the three treatment groups differed in their motivation to court following the manipulation of their parental status, we used R (R Core Team 2016) to analyse the number of zigzag dances performed by males during these post-manipulation courtship assays with generalised linear mixed models (GLMM(s)). We used fixed effects for treatment assignment ('egg-tending', 'eggs-removed' or 'courtship-only'), and, as the courtship of individual males was tested twice following manipulation of parental status, we included male ID as a random effect in our models (Crawley 2005). Additionally, to control for variation in the courtship vigour of males that was unrelated to treatment, a measure of male performance in the baseline courtship assay was also used as a covariate. Specifically, here we took the natural logarithm of the sum 1 + the number of zigzag dances observed in the baseline courtship assay for each male and then standardised the result for our covariate measure. The log transform was chosen here to maintain direct proportionality between the number of zigzag dances observed in the baseline assay and the number of zigzag dances predicted by the model. However, as some males did not engage in zigzag dances in the baseline courtship assay, it was necessary to add one to each baseline assay zigzag dance count as a pragmatic solution to potential undefined values, which does not require estimation of additional parameters.

We initially modelled the data using a Poisson GLMM (with log link function). However, as this proved to be overdispersed, a negative binomial GLMM was employed (which also used a log link function). In the light of the controversy over how best to conduct hypothesis testing for GLMMs using Wald tests or likelihood ratio tests under a frequentist framework, we fitted the model using a Bayesian approach (Bolker et al. 2009). Here, the posterior distributions of the model parameters were estimated

using Markov Chain Monte Carlo simulation via the R interface to JAGS (version 3.4.0) (Plummer 2003) in the R2jags package (version 0.04-03) (Su & Yajima 2014). Every 100th value from three Markov chains of 1 000 000 iterations in length was used, with the first 100 000 iterations of each chain discarded as burn-in. The chains were visually assessed for convergence, and potential scale reduction factor values were all less than 1.002 (Brooks & Gelman 1998). Following Zuur et al. (2012), vague priors were used for all parameters, with priors for the mean and fixed effects all being normal distributions centred on 0 with variance 100 000, and the prior for the standard deviation of the male ID effect was a uniform distribution from 1 to 10 000. The negative binomial dispersion parameter prior was a uniform distribution from 0.5 to 5. Inferences were drawn from 95% credibility intervals from the Bayesian analysis, where credibility intervals that do not overlap zero are considered as significant. We also note that fitting the same model using frequentist methods (via the R package glmmADMB (version 0.8.1); Fournier et al. 2012; Skaug et al. 2015) and testing null hypotheses using Wald Z tests (with significant level of $\alpha = 0.05$) produced qualitatively similar results which we do not present here.

Results

Males in the 'eggs-removed' treatment engaged in significantly fewer zigzag dances after manipulation of their parental status than those in the 'egg-tending' (Table 1, Fig. 2) and 'courtship-only' treatments (Table 1, Fig. 2). By contrast, there was no significant difference in the number of zigzag dances between the 'egg-tending' and 'courtship-only' males (Table 1 and Fig. 2). The covariate, which was based on the number of zigzag dances performed in the baseline courtship assay, was also significant (Table 1), with more vigorously courting males in the baseline assay also courting more after manipulation of their parental status (Table 1).

Discussion

We did not find evidence of any difference in the courtship levels of males that were tending eggs and males that had been given the opportunity to court a female but not acquire eggs. This finding was surprising as we had expected male sticklebacks to elevate their courtship effort when they had obtained an initial clutch of eggs, as it is likely to be more cost-effective for males to rear multiple clutches

Table 1: Parameter estimates from a negative binomial GLMM of male zigzag dances performed after parental status manipulation. For the effects of male parental status treatments, estimated treatment–treatment differences are presented, as these are the quantities about which we wish to draw inferences. β represents fixed effect coefficients, σ represents the estimated value of standard deviations and α represents the dispersion parameter where the variance of a negative binomial distribution with mean μ is $\mu + \alpha\mu^2$.

		β	95% Credibility interval	Incidence rate ratio
Fixed effects	Courtship-only – Eggs-removed	1.052	0.082–2.065	2.86
	Egg-tending – Eggs-removed	1.675	0.678–2.712	5.34
	Egg-tending – Courtship-only ^a	0.623	–0.366–1.607	1.86
	Baseline courtship assay covariate	0.911	0.499–1.332	2.49
		σ	95% Credibility interval	Incidence rate ratio
Random effects	Male ID	1.469	1.043–1.920	4.35
		α	95% Credibility Interval	
Negative binomial dispersion parameter		1.034	0.733–1.546	

^aNote that this table presents estimates for all pairwise comparisons of treatment groups. Thus, although typically parameter estimate tables only show differences of treatments to a reference group here, we also estimate one additional parameter, the difference between egg-tending and courtship-only males. This parameter is not independent from the estimates of the difference between courtship-only and eggs-removed males and the difference between egg-tending and eggs-removed males but is shown as we are interested in the difference between all treatment groups.

simultaneously (van Iersel 1953; Perrone & Zaret 1979; Lazarus & Inglis 1986; Smith & Wootton 1995a; Manica & Johnstone 2004; cf. Jamieson & Colgan 1989). Indeed, male sticklebacks are more inclined to abort the care of young when there are fewer eggs in their nest (van den Assem 1967; but see: Mehliis et al. 2009, 2010), suggesting that the per capita cost of rearing offspring is greater for smaller clutches. So, why did we not find any difference in the courtship effort of egg-tending males and males that did not receive eggs?

The most likely explanation is that egg-tending males, as well as those that had not spawned, both stood to benefit by courting females at similar levels. In this respect, we exclude the possibility that unspawned males were simply courting at comparable levels to egg-tenders because the former had been

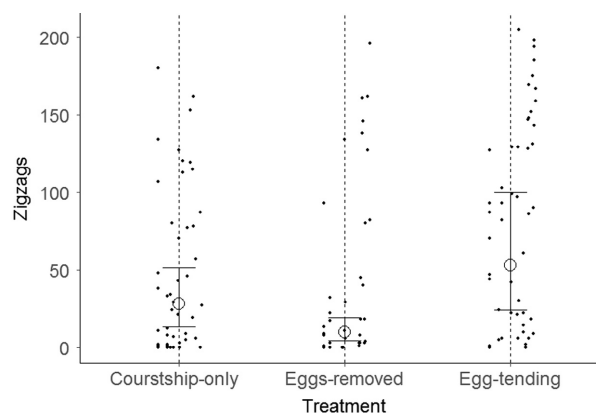


Fig. 2: Plot showing predictions from a negative binomial GLMM of the number of zigzag dances performed by male sticklebacks after manipulation of parental (open circles) and corresponding raw observed counts of zigzag dances performed by males in courtship assays (closed circles). Error bars represent 95% credibility intervals of the predicted values. Note that predicted values shown here represent the number of zigzag dances that males in each of the three treatment groups would be expected to engage in conditional on having an average courtship propensity as measured in a baseline courtship assay. Of course in the actual baseline courtship assay, individual males varied in their propensity to court females. Accordingly, on this graph, we have displaced the points showing the raw observed data (closed circles) on the horizontal axis to depict the variable propensity of males to court in the baseline assay. Those points displaced to the right of the hashed centreline for their treatment represent observed values from males that courted more vigorously in the baseline assay, whilst those points displaced to the left represent observed values from males that had less vigorous courtship in the baseline assay. Specifically, the extent of displacement is proportional to the baseline courtship assay covariate score for each male (see methods for calculation details). It should be noted that each male is represented by two data points on the above plot, as each male's courtship was assayed twice following manipulation of parental status.

denied the opportunity to spawn (Chiswell et al. 2014). This is because earlier studies have shown that male sticklebacks prevented from spawning maintain consistent courtship levels with subsequent females (van Iersel 1953; Dzieweczynski & Forrette 2015). It is important to realise, however, that courtship decisions are not only influenced by benefits. The cost of attracting additional mating opportunities can also be important. For males that have already spawned, both courtship (e.g. Kotiaho et al. 1998; Mitchell et al. 2008) and the act of mating itself (e.g. Telford & Webb 1998; Franklin et al. 2012) can be energetically demanding, which may impinge on the ability of males to provide high-quality care to their eggs. Indeed, male sticklebacks that engage in vigorous courtship are less successful at caring for their young, potentially as a result of energetic depletion (von

Hippel 2000). Young stickleback eggs do not appear to require extensive fanning until they are several days old (van Iersel 1953; Reeb et al. 1984; Smith & Wootton 1995b; Hopkins et al. 2011), thus making it unlikely that there is a substantial temporal trade-off between the need to fan and the need to court away from the nest. However, intensely courting males may risk exposing existing eggs to a heightened risk of predation (Sargent 1982 and references within) or egg stealing from rival conspecifics (Jamieson & Colgan 1992). Courting can also jeopardise an individual's own survival (Moodie 1972; Whoriskey & Fitzgerald 1985; Magnhagen 1991; Sih 1994; Candolin 1997; Candolin & Voigt 1998; but see Gwynne 1989), a risk that could be particularly costly for males that have dependent offspring. Therefore, it is possible that such costs may also constrain the courtship effort of egg-tending males. In this regard, the possibility that females prefer to spawn in nests containing eggs could also negate the need for egg-tenders to court more as the presence of eggs *per se* may improve subsequent male mating success (Ridley & Rechten 1981; Belles-Isles et al. 1990; Goldschmidt et al. 1993; but see: Jamieson & Colgan 1989; Jamieson et al. 1992; Jamieson 1994).

Whilst we did not find a difference between the courtship levels of egg-tending males and those that were not permitted to spawn, we did find that previously spawned males that had their eggs experimentally removed subsequently engaged in less courtship compared to males in the other two treatments. Although we cannot discount the possibility that courtship levels of males whose eggs were removed may have been affected by costs associated with spawning (but without the counteracting benefits of courting whilst tending eggs), lower courtship motivation might also be related to their perception of the safety of their nest site. Even though we deliberately disturbed the nests of males in all three of our treatment groups (see methods), if male behaviour is particularly sensitive to the loss of eggs, then it is possible that the act of egg removal may have affected male motivation to court. This is because, if loss of the clutch indicates that a nesting site is vulnerable to predation, then the benefits of acquiring further clutches at that site might be reduced. This pattern could also be reinforced if females avoid spawning in nest sites where eggs have recently disappeared, as has been shown, for example, in scissortail sergeant fish (*Abudefduf sexfasciatus*) (Manica 2010) and sand gobies (*Pomatoschistus minutus*) (Lindström & Kangas 1996).

In summary, our results suggest that egg-tending males are not more motivated to court than unspawned

males. The most obvious explanation for this is that both egg-tenders and unspawned males benefit from future mating success. However, the costs of seeking additional mating for egg-tending males could also be important. Further investigation into the nature of these costs is needed, but it is likely that the increased risk of young being predated or the possibility of parents being unable to care for their young as a result of predation or energetic depletion may be involved. We found the lowest courtship levels among males that had lost their clutch of eggs. This suggests that male sticklebacks are less motivated to court when they perceive their nesting location to be vulnerable to egg predators. More broadly, our findings underscore the importance of considering the impact of parental status on male courtship behaviour.

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Chapter 6

Discussion

Discussion

In species with exclusive paternal care, it is not uncommon for males to sometimes consume their own offspring (Manica 2002b). It has been theorised that this behaviour is an adaptive mechanism through which fathers are able to trade investment in existing young for benefits to future reproduction (Rohwer 1978). If this is the case, then it can be predicted that the relative contribution that existing offspring are likely to make to the overall lifetime success of their father will influence their susceptibility to being consumed (Williams 1966; Sargent and Gross 1986; Sargent 1992). Accordingly, I tested whether males display plasticity in their filial cannibalism behaviour based on the relative value of the current brood and the likelihood of future reproductive success. Specifically, this involved a literature review looking at whether mate availability influences filial cannibalism (Chapter 2), as well as experimental studies that explored the effects of brood size, rival male competition, and predation risk on filial cannibalism in the sand goby (*Pomatoschistus minutus*) (Chapters 3 and 4). Further to this, since it is often cost effective for males to rear multiple clutches simultaneously (Lazarus and Inglis 1986; Smith 1991; Smith and Wootton 1995), and because females sometimes display preferences to mate with males that are tending eggs (Ridley and Rechten 1981; Sargent 1988; Jamieson 1995; Reynolds and Jones 1999), I predicted that males may, in some circumstances, seek to capitalise on freshly spawned eggs and use them to attract additional mates. This idea was explored by looking at whether male sand gobies avoid eating their own eggs when competing for mates (Chapter 3). In addition, using the three-spined stickleback (*Gasterosteus aculeatus*), I tested whether males would elevate their courtship effort whilst egg-tending to exploit this attractive resource to help them quickly spawn again (Chapter 5).

Filial cannibalism plasticity

The first aim of this thesis was to explore whether males exhibit plasticity in filial cannibalism behaviour in relation to the likelihood of future opportunities to breed. In Chapter 2, I noted that there are multiple examples in the literature of filial cannibalism plasticity in response to prevailing mate availability conditions. Intriguingly though, it seems that the effect of mate availability varies from species to species. In some species, males

engage in more filial cannibalism when exposed to potential mates (Okuda and Yanagisawa 1996; Okuda et al. 2004; Myint et al. 2011; Takeyama et al. 2013). This aligns well with the concept that filial cannibalism is performed as an investment in future reproduction, as males that consume their young presumably benefit from doing so (likely in the form of energetic resources), and are then able to relatively easily replace the cannibalised young due to the accessibility of females. However, I also noted that, in other species, mate availability did not affect filial cannibalism (Bjelvenmark and Forsgren 2003). Indeed, evidence even suggests that mate availability can lead to reduced levels of total filial cannibalism (Pampoulie et al. 2004; Klug et al. 2005). Accordingly, to explain this latter, seemingly counterintuitive, result, I proposed several other mechanisms through which mate availability may influence filial cannibalism, including the possibility that eggs are not eaten in the presence of females as this may deter females from spawning with the male (a point I discuss in greater depth below when addressing the second aim of this thesis). Alternatively, it is possible that elevated mate availability discourages filial cannibalism since it enables males to attain multiple clutches and this incentivises parental care (due to cost efficiencies of rearing several clutches simultaneously). Concordant with this suggestion, my experimental findings in Chapters 3 and 4 show that small broods are more likely to be completely consumed. However, further studies are needed to explore whether anticipation of receiving either a small or large brood influences filial cannibalism behaviour. One way in which this might be achieved is by examining how the quality of prospective mates influences male behaviour. Do males respond differently when encountering a highly fecund mate as compared to one of below average fecundity?

Given my Chapter 2 observation that all studies so far exploring the effect of mate availability on filial cannibalism do so by manipulating female presence, in Chapter 3 I tested whether the presence of rival males would have analogous effects. Here, I found that male sand gobies did not alter their filial cannibalism behaviour in response to rival male competition. This lack of plasticity could indicate that sand gobies engage in filial cannibalism for reasons that are unrelated to current versus future reproduction trade-offs. Indeed, there is a growing body of evidence to suggest that filial cannibalism may be employed in ways that directly benefit existing young. Empirical work has shown that reduced survivorship of eggs when deposited at high density may motivate partial filial

cannibalism as a tactic to thin out the brood (Payne et al. 2002, 2004; Creighton 2005; Klug et al. 2006). Moreover, recent modelling work suggests that reduction of density dependent offspring survivorship effects alone is theoretically sufficient to lead to the evolution of filial cannibalism (Davenport 2019). In the case of sand gobies, control of the egg infecting water mould *Saprolegnia* has been recently proposed as a function of partial filial cannibalism (Lehtonen and Kvarnemo 2015a,b; Vallon et al. 2016; Vallon and Heubel 2017). More broadly, partial filial cannibalism could also be used to facilitate current reproduction by enabling parents to selectively remove low value offspring and by provisioning parents with energy for continued care of remaining young (Marconato and Bisazza 1988; Marconato et al. 1993; Gomagano and Kohda 2008; Beery and Zucker 2012). However, unlike partial filial cannibalism, total filial cannibalism is only likely to be adaptive if it facilitates future reproduction. Accordingly, lack of plasticity in total filial cannibalism in response to mating competition may indicate that costs of plasticity are high, or that the presence of rival males is not a good predictor of future reproductive success for sand gobies. The latter of these two explanations seems more likely, as the experimental results of Chapter 4 provide evidence of total filial cannibalism plasticity in sand gobies in response to another factor, predator exposure. Accordingly, this suggests that plasticity costs are unlikely to be excessive. Furthermore, the conditional nature of total filial cannibalism as a strategy is almost certain given that consumption of all offspring in all instances would be ineffectual as an evolutionary strategy.

In Chapter 4, I found that filial cannibalism was less common when apparent predation risk was high (and, thus, the likelihood of future reproduction was diminished). This result is consistent with the theory that total filial cannibalism is an adaptive behaviour enabling parents to trade current reproductive success for future reproductive success (Rohwer 1978; Sargent 1992; Manica 2002b). Here, it is thought that total filial cannibalism will be performed when the cost of caring for young is outweighed by the benefits. Concordant with this theory – as well as previous empirical observations (e.g. Kramer 1973; Pampoulie et al. 2004; Lindström and Sargent 1997; Neff 2003; Myint et al. 2011) – I observed that total filial cannibalism was most likely when males received initially small clutches. In fact, small clutch size was a much better predictor of total filial cannibalism than either rival male exposure or predator exposure. This finding may indicate that males are sensitive to the

reliability of cues regarding the relative value of future and current reproduction. Clutch size, therefore, would seem to be a very accurate indicator of the value of the current brood, whereas it is likely that the impact of mating competition and predators on future reproduction is much more probabilistic.

To a large extent, filial cannibalism plasticity in response to factors influencing the likelihood of future reproduction is thought to be about mitigating the costs of filial cannibalism. For example, as discussed in Chapter 2, filial cannibalism might be avoided when social conditions cause filial cannibalism to deter mates while filial cannibalism can be promoted when access to mates makes cannibalised offspring easier to replace. Similarly, in Chapter 4, I present results that suggest whole clutch cannibalism is more readily employed in safe environments where parents are likely to be able to live long enough to spawn again. In all of these cases, however, it is assumed that there is some other underlying benefit of filial cannibalism that might motivate the performance of this behaviour in the first place. The most well researched potential benefit is that filial cannibalism provides energy to parents (Manica 2002b). To some extent, my results from Chapter 4 support this notion, as I found that higher levels of egg consumption were linked to lower weight loss during brooding, albeit this result was not reproduced in Chapter 3. Similarly, I found that low body condition males were more likely to engage in total filial cannibalism in Chapter 3 and a similar non-significant effect in Chapter 4. However, the extent of partial filial cannibalism was not linked to male body condition. Moreover, the observation that egg consumption reduced weight loss only suggests that energy is provided, not that the acquisition of this energy is the purpose of egg consumption. In this regard, my experiments did not produce any evidence of males actually using energy acquired from egg consumption, indicating that energetic benefits might not be the principal factor motivating filial cannibalism in sand gobies. Specifically, I did not find evidence for egg consumption being associated with more extensive nest construction in Chapter 4, and, in Chapter 3, greater levels of partial filial cannibalism were not linked to more extensive nest attendance or courtship behaviour. Accordingly, it seems doubtful that filial cannibalism is performed in sand gobies for the primary purpose of providing energy to be used in nest construction, courtship or parental care. Nevertheless, I cannot rule out the possibility that increased attractiveness due to elevated body condition motivates egg consumption, as has been reported in other species

(Okuda et al. 1997). Accordingly, further study into some of the recently proposed non-energetic benefits of filial cannibalism, such as control of egg-infecting pathogens (Lehtonen and Kvarnemo 2015a,b; Vallon et al. 2016; Vallon and Heubel 2017), should be considered. Additionally, more research across a diversity of species tracking the behaviour of parents following filial cannibalism, and even manipulative studies, would be beneficial in helping to reveal where energetic gains from filial cannibalism are directed.

Use of eggs to facilitate courtship

The second aim of this thesis was to determine whether males employ specific strategies to take advantage of female preferences to spawn with egg-tending males. In this regard, in my literature review in Chapter 2, I found that several studies, including one on the sand goby, report that males are less likely to engage in total filial cannibalism when exposed to females during brooding (Pampoulie et al. 2004; Klug et al. 2005). These observations indicate that total filial cannibalism may be discouraged by female preference for egg-tending males. In other words, males may retain eggs that they might otherwise have eaten when the eggs can help the male attract a nearby potential mate. If this is indeed the case, then I expected that males should also avoid total filial cannibalism in other situations where sexual attractiveness is of elevated importance. One such situation could be where the presence of rival males creates a competitive environment that facilitates female mate choice (Noë 2017). Accordingly, in Chapter 3, I tested whether exposure to rival males would result in a lower incidence of total filial cannibalism amongst egg-tending male sand gobies. Here, I found no effect of rival male exposure on filial cannibalism, thus casting doubt on the idea that eggs are retained for mate attraction purposes. Similarly, in Chapter 5, I tested to see whether male three-spined sticklebacks might adjust their courtship effort as a result of having eggs within the nest. Here, I expected that males might elevate their courtship effort following the acquisition of eggs to exploit mate attraction benefits of egg-tending (Ridley and Rechten 1981; Sargent 1988; Jamieson 1995; Reynolds and Jones 1999), and because rearing multiple clutches together is also likely to be a cost effect means of providing parental care (Lazarus and Inglis 1986; Smith 1991; Smith and Wootton 1995). Alternatively, a decrease in courtship effort is also conceivable if the boost in attractiveness provided by eggs enables males to “rest on their laurels” (i.e. achieve sufficient mating

success despite reduced courtship effort). Again, however, my results suggested that males were relatively insensitive to the mate attraction value of eggs. Specifically, I found that egg-tending males courted with similar intensity to unspawned males. Considering both of my aforementioned experimental investigations, it remains possible that countervailing forces are present, masking effects associated with exploitation of eggs to support courtship. For example, increased vulnerability of eggs to predation during male courtship, as described by Sargent (1982), may discourage males from elevating courtship effort when egg-tending. Nevertheless, taken together, my experimental findings suggest that males do not substantially adjust their reproductive behaviour to capitalise on the value of eggs as a mate attraction resource.

There is a degree of conflict between the argument that males should maintain eggs for the purpose of attracting additional female spawning partners (Chapter 2) and observations made in Chapters 3 and 4, as well as the broader literature (e.g. Mrowka 1987; Petersen and Marchetti 1989; Lavery and Keenleyside 1990; Lissåker and Svensson 2008; Andrén and Kvarnemo 2014), that small broods frequently succumb to total filial cannibalism. This is especially pertinent in light of findings suggesting that it is in fact smaller broods that are most attractive to females (Andrén and Kvarnemo 2014). Recently, Matsumoto et al. (2018) suggested that endocrinal implications of total filial cannibalism may explain why small broods often succumb to total filial cannibalism rather than being maintained to attract mates. Specifically, they suggest that removal of all eggs from the nest is necessary for male androgen levels to return to an elevated state that enables continued courtship (Matsumoto et al. 2018; Rosenthal 2018). *Prima facie*, this idea does not accord with my findings in Chapter 5, where artificial removal of eggs from the nests of males was associated with reduced subsequent courtship. However, a more nuanced consideration of the timing at which courtship is measured following egg loss is likely required. I focused on how courtship vigour changes relatively soon after the initial spawning of males, a time when males are likely to be motivated to court additional females to add further clutches to their brood. However, several days into parental care, males of many species, including the sticklebacks I studied (van Iersel 1953; Páll et al. 2002a,b; Kent and Bell 2018), transition to what is known as the parental phase of their brood cycle whereby they cease or reduce courtship (Sikkel 1993; Sargent et al. 1995; Matsumoto et al. 2012). As such, total filial

cannibalism may be an important mechanism that enables males tending small broods to escape the parental phase and reengage in courtship activity. More research is clearly needed here, especially to explore whether this phenomenon is restricted to fish that display distinct courtship and parental phases of the brood cycle. It seems reasonable to envision that for species that maintain high levels of courtship throughout the entire brooding process, consumption of broods would not be required to restart courtship. Moreover, there is evidence that androgens do not trade-off with parental care in certain fish species (e.g. *Trichogaster trichopterus*: Kramer 1972; *Parablennius parvicornis*: Ros et al. 2004; *Lythrypnus dalli*: Rodgers et al. 2006), suggesting that these species would be able to maintain small numbers of eggs whilst maintaining high levels of courtship. Future studies might explore whether eggs are retained for courtship facilitation in these species.

Further research might also explore the timing of total filial cannibalism. Theoretically, if a brood is going to be completely consumed, the optimal time to do so will be soon after spawning, as resources expended on parental care are unlikely to be fully recouped via filial cannibalism (Sargent et al. 1995). Indeed, the majority of studies that have looked at timing report that total filial cannibalism occurs soon after spawning (Schwanck 1986; Petersen and Marchetti 1989; Petersen 1990; Manica 2002a). However, if small broods are maintained to attract additional mates and only completely consumed if this strategy fails, then I predict that total filial cannibalism will occur at a later stage. Indeed, this may offer one potential explanation for my results in Chapter 3. Specifically, I did not find any evidence of male sand gobies maintaining clutches for mate attraction purposes (via avoiding total filial cannibalism) in response to elevated mating competition. However, it remains possible that males did keep small clutches to use as mate attraction tools, but when no additional spawnings eventuated (because my experiment did not permit males further spawning), males eventually engaged in total filial cannibalism. Future work could test whether the timing of total filial cannibalism is influenced by factors that alter the value of increased attractiveness associated with egg-tending.

Conclusions

Overall my studies contribute to a body of evidence demonstrating that plasticity in filial cannibalism behaviour occurs in fish with exclusive paternal care. The main factor driving this plasticity was clutch size, with small clutches being most likely to be totally consumed. By contrast factors that affect the likelihood of future reproduction were less influential. Indeed, males did not adjust filial cannibalism behaviour in response to rival male competition, despite effects of female presence being reported in the broader literature (Pampoulie et al. 2004). These results suggest that filial cannibalism plasticity is influenced mostly by factors that have clear effects on the value of current reproduction, whereas factors that stochastically influence future reproduction are less important. In addition, my results highlight the need for future research to consider both the effects of male competition and female mating opportunities on filial cannibalism, as the effect of one is not necessarily the opposite of the other. Furthermore, I did not find clear evidence for males strategically exploiting eggs within their nests to enhance their mating success. Males did not seem to elevate courtship effort or avoid consuming their eggs to exploit female predilections to spawn in nests containing eggs. Further research exploring whether these conclusions generalise to a greater diversity of species with paternal care would be useful. Indeed, there are a large number of species that show similar patterns of paternal care to those studied in this thesis, including the majority of fish species with parental care (Blumer 1979, 1982; Gross and Sargent 1985; Reynolds et al. 2002; Mank et al. 2005). Exploration amongst other taxa with exclusive paternal care, including arthropods (Zeh and Smith 1985; Tallamy 2000, 2001; Requena et al. 2014), amphibians (Beck 1998; Summers et al. 2007; Wells 2007; Balshine 2012), and birds (Cockburn 2006), would also be desirable. This would help to elucidate more clearly what aspects of the biology of paternal caring species are linked to the various patterns of courtship, parental care and cannibalism that I have observed in my studies.

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