

EVOLUTIONARY SIGNIFICANCE OF FILIAL CANNIBALISM IN FISHES WITH
PARENTAL CARE

By

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To my family, who has always supported me.

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Parental care typically increases offspring survival, thereby increasing parental fitness. Thus, it is surprising that filial cannibalism, the consumption of one's *own* offspring, is prevalent in fishes exhibiting parental care. The most widely-accepted hypothesis of filial cannibalism suggests that males gain energy from eggs that they invest into future reproduction (energy-based hypothesis). Recently, an alternative hypothesis suggested that partial-clutch cannibalism increases oxygen availability to remaining eggs, which in turn increases overall egg survival (oxygen-mediated hypothesis). Evidence for both hypotheses is mixed and there are few alternative hypotheses. Thus, the evolutionary significance of filial cannibalism remains unclear. To enhance our understanding of filial cannibalism, I re-examined current theory (i.e., the energy-based and oxygen-mediated hypotheses), developed and evaluated an alternative hypothesis, and developed a mathematical model of filial cannibalism.

I experimentally quantified the effect of filial cannibalism on mating success of parental males in the flagfish (*Jordanella floridae*), and found that filial cannibalism always reduced lifetime reproductive success. In the sand goby (*Pomatoschistus minutus*), males that were in poorer condition consumed less of their eggs than males that were in better condition. These findings are contrary to predictions of the energy-based hypothesis.

In the sand goby, I found that egg survival is density-dependent and filial cannibalism increases when egg density is high. However, this density-dependence is not mediated by oxygen. Therefore, I did not find support for the oxygen-mediated hypothesis. I suggest a more general hypothesis of filial cannibalism mediated by density-dependent egg survival.

I hypothesize that the ability to preferentially cannibalize offspring of reduced quality might play a large role in the evolution of filial cannibalism (selective filial cannibalism hypothesis). To begin to understand the importance of selective cannibalism, I evaluated whether males cannibalize selectively in the sand goby and the flagfish. Male sand gobies cannibalized selectively with regard to egg development rate, and male flagfish cannibalized selectively with regard to egg energy and maternal size. Thus, selective filial cannibalism occurs in at least two species and this hypothesis warrants further attention.

I then developed a mathematical model of filial cannibalism to isolate factors affecting the evolution of filial cannibalism. The findings of this model highlight the plausibility of a range of alternative hypotheses. Specifically, the evolution of filial cannibalism is enhanced if (1) parents can selectively cannibalize lower quality offspring, (2) filial cannibalism increases egg maturation rate, (3) there are energetic benefits of eggs to cannibalizing males, (4) cannibalism increases a parent's reproductive rate (e.g., through mate attractiveness). Density-dependent egg survivorship alone did not favor the evolution of cannibalism. Additionally, the results of the model suggest that population-level dynamics potentially play a large role in the evolution.

Finally, I isolated and characterized six polymorphic microsatellite loci in the flagfish. These microsatellite markers will be useful in paternity assays and estimating heritability of flagfish behaviors, such as filial cannibalism.

CHAPTER 1 INTRODUCTION

Background: Theory and Empirical Evidence

Adaptive theories of evolution suggest that parents should exhibit strategies that increase offspring survival. Parental care, which is common across taxa, is one way in which parents are thought to do this (reviewed in Clutton-Brock 1991). Because parental care is assumed to increase offspring survival, it is surprising that filial cannibalism, the consumption of one's *own* offspring, may co-occur with parental care. Indeed, filial cannibalism is prevalent in a range of taxa (Polis 1981) and is particularly common in teleost fishes exhibiting paternal care (reviewed in Manica 2002). Because parental males often consume more eggs than would die naturally, filial cannibalism does not solely serve to clean the nest of dead or diseased eggs (e.g. Klug et al. 2005). Likewise, egg cannibalism cannot be attributed to the removal of eggs that were fertilized by other males (DeWoody et al. 2001; but see Neff and Sherman 2003), and filial cannibalism remains common in the absence of possible cuckolding events (Kvarnemo et al. 1998; Kume et al. 2000; Lissåker et al. 2002; Klug et al. 2005; Svensson and Kvarnemo 2007). Despite some theoretical development, the evolutionary significance of filial cannibalism remains unclear.

Early ethologists considered filial cannibalism a social pathology of little or no adaptive significance. However, more recent studies suggest that filial cannibalism reflects an adaptive trade-off between current and future reproductive success, in which males gain energy and nutrients from consumed eggs that are then reinvested into future reproduction (Rohwer 1978; Sargent 1992). According to this energy-based hypothesis, whole clutch cannibalism (i.e. the consumption of all eggs present) is expected to be more frequent within a species when clutch size is relatively small because the energy requirement of the males can be satisfied only by clutches larger than a certain size (i.e., when clutch size is small, males must consume all eggs to

satisfy their energy requirements). Empirical studies support this prediction (reviewed by Manica 2002). Theory also predicts that cannibalism should increase as food availability decreases and/or when male condition is poor (Rohwer 1978; Sargent 1992). However, evidence with regard to these predictions is equivocal. Supplementary feeding of parental males reduces partial clutch cannibalism (i.e., the consumption of only some eggs in a nest) in the common goby (*Pomatoschistus microps*, Kvarnemo et al. 1998), the scissortail sergeant (*Abudefduf sexfasciatus*, Manica 2004), and the Cortez damselfish (*Stegastes rectifraenum*, Hoelzer 1992), but food availability and/or male condition did not affect filial cannibalism in fantail darters (*Etheostoma flabellare*, Lindström and Sargent 1997) and the three-spined stickleback (*Gasterosteus aculeatus*, Belles-Isles and Fitzgerald 1991). Still other studies have quantified the energetic value of eggs to determine if eggs can provide a caring male with sufficient energy to offset the direct fitness costs of care. In one species, energy attained from partial brood cannibalism was found to be sufficient to offset costs related to care (*Apogon lineatus*, Kume et al. 2000), while in another, energy from eggs was found to be insufficient (*Gasterosteus aculeatus*, Smith 1992). Thus, there is no consistent support for the energy-based explanation of filial cannibalism.

Payne et al. (2002) recently suggested that by consuming some eggs in their nest, parental males can improve oxygen availability of the remaining eggs, thereby improving overall egg survivorship (oxygen-mediated hypothesis; Payne et al. 2002, 2004). However, there has been only limited empirical examination of this hypothesis, which does not account for the common occurrence of filial cannibalism in high oxygen environments. For example, filial cannibalism occurs when oxygen availability is relatively high in the sand goby (*Pomatoschistus minutus*, Klug et al. 2006), the flagfish (*Jordanella floridae*, Klug et al. 2005), and fantail darters (*Etheostoma flabellare*, Lindström and Sargent 1997). Additionally, Lissäker et al. (2002) found

no differences in partial or whole clutch cannibalism across oxygen levels. Thus, neither the energy-based hypothesis nor the oxygen-mediated hypothesis can explain the occurrence of filial cannibalism. Furthermore, there has been a general lack of alternative explanations for the widespread occurrence of filial cannibalism in fishes.

As an alternative to the energy-based and oxygen-mediated hypotheses, I propose the hypothesis of selective filial cannibalism (i.e., non-random consumption of offspring with regard to some aspect of offspring phenotype). Specifically, I hypothesize that the ability to cannibalize offspring selectively in relation to aspects of offspring quality can directly favor the evolution of filial cannibalism (see also Klug and Bonsall 2007 and Chapter 6). The idea of weeding out inferior offspring has been documented in other contexts (brood reduction: Forbes & Mock 1998; selective abortion in humans: Stearns, 1987; Forbes 1997; Diamond 1987; Hesketh & Xing 2006; selective abortion in plants: Burd 1998; Karkkainen et al. 1999; Melser & Klinkhamer 2001), but it has not yet been explicitly evaluated in relation to filial cannibalism (but see Mrowka 1987 and Kraak 1996 for work on consumption of unfertilized or diseased eggs). Indeed, selective elimination of lower quality offspring is thought to play a large role in the evolution of selective embryo abortion, brood reduction, and offspring abandonment (Stearns 1987; Forbes and Mock 1998; Stearns 1992). However, the relationship between offspring phenotype and filial cannibalism remains unknown (but see Chapters 4, 5, and 6), and thus, the relative importance of selective filial cannibalism is unclear.

Despite mixed empirical evidence and a lack of alternative hypotheses, the energetic hypothesis of filial cannibalism is typically accepted as a valid explanation for the prevalence of filial cannibalism in fishes (e.g. Vinyoles et al. 1999; Kume et al. 2000; Manica 2002). Overall, the support for this hypothesis is unsatisfying and it remains unclear in many systems whether or

not (and potentially how) filial cannibalism is an adaptive strategy. Despite nearly three decades of empirical and theoretical work on the subject, filial cannibalism in fishes still remains an evolutionary conundrum. Understanding the evolutionary significance of filial cannibalism requires both additional theoretical development and empirical research.

An enhanced understanding of the evolution of filial cannibalism necessitates three research strategies.

Re-Evaluation of Current Theory with an Explicit Focus on Fitness Consequences

Previous studies have failed to quantify fitness consequences of filial cannibalism (i.e., the parent and offspring survivorship and/or reproductive benefits of egg eating). Most studies of filial cannibalism have focused on the relationship between male condition and filial cannibalism, or the effect of supplemental feeding on filial cannibalism. Simply showing that males with less food eat more eggs does not demonstrate that an adaptive trade-off is occurring. Thus, there is limited support for the energy-based hypothesis, and as mentioned previously, the oxygen-mediated hypothesis has received little empirical evaluation. The first step in understanding the evolutionary significance of filial cannibalism is to explicitly evaluate the energy-based and oxygen-mediated hypotheses by focusing on potential fitness consequences of filial cannibalism (i.e., the parent and offspring survivorship and reproductive costs and benefits).

Development and Evaluation of Alternative Hypotheses

The energy-based hypothesis continues to be accepted despite mixed evidence. Thus the development and empirical examination of new hypotheses is critical. As mentioned above, I propose the alternative hypothesis of selective filial cannibalism (discussed further in Chapters 4, 5, and 6). Specifically, I hypothesize that 1) parental males might preferentially cannibalize lower quality offspring and 2) the ability to cannibalize selectively potentially plays a large role

Development of a Synthetic Model of Filial Cannibalism

The two current hypotheses (i.e., the energy-based and oxygen-mediated) are currently presented as mutually exclusive ideas, leading to a debate that has resulted in very little resolution. Instead, I argue that the prevalence of filial cannibalism cannot be explained by single factors (i.e., energy or oxygen). A model incorporating a variety of trade-offs associated with current and future reproductive success (i.e., a multivariate approach) is essential to identify and evaluate the plausibility of a range of alternative hypotheses.

Summary of Dissertation Objectives

The goals of my dissertation are three-fold, and consist of four experiments and one mathematical model.

First, I re-evaluate current theory by focusing on fitness consequences of cannibalism. In my first experiment, I evaluate the reproductive fitness consequences of filial cannibalism. To evaluate the energy-based hypothesis, I quantify the effect of filial cannibalism on long-term mating success of parental males (i.e., current and future reproductive success) and determine whether energy consumed from eggs is directly translated into future reproduction in the flagfish. In my second experiment, I examine the relationship between partial clutch cannibalism and egg survivorship in relation to oxygen availability. I evaluate the oxygen-mediated hypothesis by quantifying the effect of oxygen and egg density on filial cannibalism and net egg survival.

Second, I develop and evaluate an alternative hypothesis. In my third and fourth experiments, I assess the relative importance of aspects of egg phenotype on filial cannibalism in the sand goby and flagfish. To begin to evaluate the hypothesis of selective filial cannibalism proposed above, I assess whether parental males preferentially consume eggs with regard to

some aspect of offspring phenotype. Specifically, I focus on the relationship between filial cannibalism and egg size or energetic content, because egg size and energetic content have been correlated with post-hatching survival and growth in fishes (Kamler 2005).

Finally, I fully develop a mathematical model incorporating a range of costs and benefits associated with filial cannibalism (i.e., the multivariate approach). I use this model to isolate the pivotal factors affecting the evolutionary dynamics of filial cannibalism, and I evaluate the plausibility of a range of non-mutually exclusive alternative hypotheses.

Study Systems

Filial cannibalism likely functions differently among systems, and because there are potentially multiple explanations for the occurrence of filial cannibalism, I focused on two distinct systems: the flagfish (*Jordanella floridae*) and the sand goby (*Pomatoschistus minutus*). Both systems are exemplary of care in fishes: (i) males provide care (i.e., nest guarding, fanning, and cleaning), (ii) filial cannibalism is prevalent, and (iii) they live approximately one year, allowing fitness measurements quantified over one breeding season to be representative of lifetime fitness. However, the species have different life histories (egg laying patterns, nest structure, rates of mating), thus making them suitable for testing particular hypotheses related to filial cannibalism.

Flagfish males defend open nests consisting of filamentous algae or bare substratum. Male flagfish fan eggs but fanning is not necessary for egg survival, and flagfish eggs are not clumped together (Mertz & Barlow 1966). Thus, limited oxygen at the nest is not a main source of egg mortality, and there is no a priori expectation in flagfish that filial cannibalism leads to increased survivorship of remaining eggs through increased oxygen availability. Unlike flagfish, sand goby males build nests under shells and cover the nest with sand, leaving only a small (~1cm) opening. Sand goby eggs are clumped and oxygenation of the eggs by male fanning is required

for egg survival. Thus, the sand goby is an ideal system to test the hypothesis of oxygen-mediated filial cannibalism. Males of both species sequentially receive eggs from multiple females, increasing the possibility that eggs vary in quality.

Overview of Dissertation Chapters

Reproductive Fitness Consequences of Filial Cannibalism in the Flagfish

In Chapter 2, I investigate the effects of filial cannibalism on components of fitness in the flagfish. Specifically, I expect filial cannibalism to increase future reproductive success. To quantify the reproductive fitness consequences of filial cannibalism, I experimentally manipulate (1) the diet of parental males (i.e., males either receive a high quality or low quality diet) and (2) the ability to practice filial cannibalism (i.e., males either have full access to eggs or access to eggs is prevented by a nest cover). Each male experiences a single experimental treatment (i.e., high food, access to eggs; high food, no access to eggs; low food, access to eggs; low food, no access to eggs) for the duration of the experiment. Specifically, I follow males over 90 days, approximately one breeding season (i.e., the expected reproductive lifetime of flagfish), and consider three components of fitness: 1) the total number of eggs received, 2) the number of spawnings, and 3) the frequency of spawning. Contrary to predictions, filial cannibalism reduces male reproductive success. While an enhanced diet increases the number of eggs received, the number of spawnings, the frequency of spawning, and male weight gain, there is no effect of filial cannibalism on any component of reproductive success or male weight. Thus, in the flagfish there is no evidence that energy or nutrients gained from filial cannibalism are directly translated into increased future reproductive success. See also Klug and St. Mary (2005).

Parents Benefit from Eating Offspring: Density-Dependent Egg Survivorship Compensates for Filial Cannibalism

In Chapter 3, I evaluate the hypothesis of oxygen-mediated filial cannibalism in the sand goby by 1) examining the effect of oxygen and egg density on the occurrence of filial cannibalism, 2) evaluating the effects of partial clutch cannibalism on the survivorship of the remaining eggs, and (3) comparing potential costs and benefits of filial cannibalism related to the net number of eggs surviving. I find that oxygen level and egg density affect the occurrence of cannibalism and that simulated partial clutch cannibalism improves survivorship of the remaining eggs. Additionally, because increased egg survivorship, stemming from partial egg removal, compensates for the cost of cannibalism (i.e., number of eggs removed) at a range of cannibalism levels, filial cannibalism potentially results in no net losses in reproductive success. However, oxygen does not affect egg survivorship. Thus, in this chapter, I suggest a more general hypothesis of filial cannibalism mediated by density-dependent egg survivorship. See also Klug et al. 2006.

Selective Filial Cannibalism in the Sand Goby

In Chapter 4, I evaluate the novel hypothesis of selective filial cannibalism. Specifically, I examine the relationship between aspects of egg phenotype and partial clutch filial cannibalism in the sand goby. Males are either allowed to spawn with one or two females, and I then evaluate cannibalistic preferences in relation to the order in which eggs were spawned and egg size. I focus on egg size because egg size has been correlated with post-hatching survival and growth in a range of fishes (Kamler 2005). In this experiment, I find that males selectively cannibalize eggs with respect to egg phenotype, but only in some cases. When males mated with two females sequentially, they preferentially consume the larger eggs of the second female. Because egg size is correlated with development time (and because female 2's eggs were slightly younger), the

patterns of cannibalism appear to represent a strategy that reduces the duration of care necessary for the current brood. By reducing the duration of care required for each brood, it is possible that males can attain additional brood cycles during their breeding season, thereby increasing their reproductive success. This work highlights the potential role of selectivity in understanding the adaptive significance of filial cannibalism.

Selective Filial Cannibalism in the Flagfish

In Chapter 5, I examine the relationship between maternal size and condition, egg energetic content, and filial cannibalism. Both egg energetic content and maternal size have been correlated with post-hatching survival in a range of fishes (Kamler 2005). In this experiment, I find that males exhibit preferential cannibalism with regard to mean energetic content per egg and maternal size. However, the patterns of selective cannibalism differ between whole and partial clutch cannibalism. Specifically, males cannibalize the whole clutch more often when the mean per-egg energetic content is relatively high. Because I find no relationship between mean egg energy and egg number, the increase in whole clutch cannibalism when mean egg energetic content is relatively great is not explained by any differences in egg number. In contrast, there is a negative relationship between mean egg energy content and the number of eggs consumed for the case of partial clutch cannibalism. Similarly, maternal size is negatively correlated with the proportion of and the number of eggs consumed. Because female size has been positively related to post-hatching survival in other fishes, it seems that for the case of partial clutch cannibalism, males in this experiment preferentially cannibalize offspring that have lower survival post-hatching. In contrast, when they practice whole clutch cannibalism, they appear to be maximizing their energetic gain. The findings in this chapter (in combination with those of Chapter 4) suggest that males practice selective filial cannibalism with regard to aspects of offspring phenotype.

A Model of the Evolution of Parental Care and Filial Cannibalism

In Chapter 6, I evaluate the importance of a range of factors on the evolution of parental care and filial cannibalism using an evolutionary ecology approach (see also Klug and Bonsall 2007). Parental care, no care/total abandonment, and filial cannibalism evolve and often co-exist over a range of life-history strategies (i.e., strategies associated with a wide range of adult death rates, egg death rates, egg maturation rates, population carrying capacities, juvenile survival rates). While no single benefit is essential for the evolution of filial cannibalism, benefits associated with adult or offspring survival and/or reproduction facilitate the evolution of cannibalism. This model highlights the plausibility of a range of alternative hypotheses. Specifically, the evolution of filial cannibalism is enhanced if 1) parents can selectively cannibalize lower quality offspring, 2) filial cannibalism increases egg maturation rate, 3) there are energetic benefits of eggs to cannibalizing males, 4) cannibalism increases a parent's reproductive rate (e.g., through mate attractiveness). Density-dependent egg survivorship alone does not favor the evolution of cannibalism. When egg survivorship is density-dependent, parents are expected to simply lay eggs at densities that maximize offspring survival. While density-dependent egg survival does not directly favor the evolution of filial cannibalism in the model, density-dependent egg survival does not preclude the evolution of filial cannibalism entirely. For the case of density-dependent egg survival, filial cannibalism evolves more often when the density-dependence is relatively more intense (i.e., when there is a relatively large increase in offspring mortality with increasing density). Additionally, the evolution of filial cannibalism and/or parental care is highly sensitive to population carrying capacity in the model, and care and/or cannibalism are more likely to evolve if they allow an organism to use resources more effectively. These results suggest that population-level resource competition potentially plays an important role in the evolution of both parental care and filial cannibalism.

Conclusions

In this final chapter, I summarize the major conclusions of my dissertation. I discuss my findings in relation to previous theory, and highlight future directions of research on filial cannibalism.

Isolation and Characterization of Microsatellite Markers in the Flagfish

In the Appendix (Klug, St. Mary and Clark, in preparation), I describe six polymorphic microsatellite loci in the flagfish. These microsatellite markers will be useful in future behavioral research on the flagfish for estimating paternity, reproductive success, and heritability.

CHAPTER 2
REPRODUCTIVE FITNESS CONSEQUENCES OF FILIAL CANNIBALISM IN THE
FLAGFISH, *JORDANELLA FLORIDAE*

Introduction

Parental care, which is assumed to increase the fitness of a parent by increasing survival or quality of the offspring (Clutton-Brock 1991), is common across animal taxa (reviewed in Clutton-Brock 1991; Rosenblatt & Snowdon 1996). In fishes care is typically paternal, and includes territory guarding and nest care (Gross and Sargent 1985). Because parental care is assumed to increase the survival of offspring, it is surprising that filial cannibalism, the consumption of one's own offspring, is prevalent in fishes exhibiting parental care (reviewed in Manica 2002). Since parental males often consume more eggs than would die naturally, filial cannibalism does not solely serve to clean the nest of dead or diseased eggs (e.g., Klug et al. 2005). While early ethologists considered filial cannibalism a social pathology with little or no adaptive significance, filial cannibalism is currently thought to reflect an adaptive trade-off between current and future reproductive success (Rohwer 1978).

Whole clutch cannibalism (i.e., the consumption of all eggs present) and partial clutch cannibalism (i.e., the consumption of some eggs present) are thought to occur for different reasons. Whole clutch cannibalism theoretically represents a termination of parental care (Rohwer 1978; reviewed in Manica 2002). Because the net reproductive gain associated with caring for a small clutch is expected to be less than that of a large clutch, whole clutch cannibalism is expected to be more frequent when clutch size is relatively small. Indeed, in many systems with paternal care, smaller clutches are subject to whole clutch cannibalism more frequently than larger clutches (reviewed in Manica 2002).

The most widely accepted explanation for partial-clutch filial cannibalism is that it provides a male with energy or limited nutrients allowing him to care for the remaining brood or

to increase future reproduction (Rohwer 1978; Sargent 1992). According to this energy-based hypothesis of filial cannibalism, food availability and male condition should affect the occurrence of filial cannibalism (Rohwer 1978; Sargent 1992; Sargent 1997). Evidence regarding these predictions is mixed. Contrary to the theory, neither initial male condition nor food availability predicted the number of eggs consumed in fantail darters, *Etheostoma flabellare* (Lindström and Sargent 1997). Similarly, food availability was not related to the occurrence of filial cannibalism in the three-spined stickleback *Gasterosteus aculeatus* (Belles-Isles and Fitzgerald 1991). However, evidence in other species suggests food availability does affect filial cannibalism. Kvarnemo et al. (1998) found that starved male common gobies consumed more of their eggs than males whose diet was supplemented with either mussel meat or both mussel meat and the eggs of conspecifics. Similarly, Manica (2004) found that supplementary feeding significantly reduced partial clutch filial cannibalism in the scissortail sergeant (*Abudefduf sexfasciatus*). In the Cortez damselfish (*Stegastes rectifraenum*), supplementation of a male's diet with conspecific eggs reduced cannibalism but did not fully inhibit it (Hoelzer 1992). Other studies have quantified the energetic value of eggs to determine if eggs can provide a caring male with sufficient energy to offset the direct fitness costs of cannibalism. In one species energy attained from partial brood cannibalism was found to be sufficient to offset costs related to care (*Apogon lineatus*, Kume et al. 2000), while in another, energy from eggs was found to be insufficient (*Gasterosteus aculeatus*, Smith 1992). Thus, there is a lack of consistent support across fish species for the energy-based hypothesis of filial cannibalism. Despite the mixed empirical support, the energy-based hypothesis of filial cannibalism is generally accepted as valid (e.g. Manica 2002), and it remains unclear in many systems whether (and potentially how) filial cannibalism is an adaptive strategy. While previous studies have focused on testing some of

the assumptions of energy-based models, simply showing that males with less food eat more eggs does not demonstrate that an adaptive trade-off is occurring. A thorough examination of current theory instead necessitates an explicit examination of the fitness consequences of filial cannibalism (i.e., the survivorship and/or reproductive consequences of egg eating).

According to the energy-based explanation of filial cannibalism (Rohwer 1978), we would expect cannibalism to increase lifetime reproductive success, and in a short-lived species we might expect filial cannibalism to increase reproductive success over the course of one breeding season. The present study quantified reproductive fitness consequences of filial cannibalism over approximately one breeding season in a short-lived species of fish exhibiting filial cannibalism. Specifically, I was interested in whether males that eat eggs experience an increase in reproduction. The flagfish, *Jordanella floridae*, is an ideal subject for such a study because 1) males show care behavior, i.e., nest guarding, fanning, and cleaning (Mertz and Barlow 1966), 2) filial cannibalism is prevalent (Mertz and Barlow 1966; Foster et al. 1969; Klug et al. 2005), and 3) they live approximately one year (H. Klug, unpublished data), allowing fitness measurements quantified over one breeding season to be representative of lifetime fitness.

In order to evaluate the effect of filial cannibalism on reproductive output, it is necessary to compare the reproductive success of males who are able to consume eggs and males that are prevented from consuming eggs. To do so effectively, males should be the only egg consumers and thus the experimental design must limit the access of potential egg predators, even females, to the eggs. Males not allowed to cannibalize must be excluded from their eggs yet still encouraged to provide parental care. Thus, these males must have access to their nest (with eggs covered) and yet not be allowed to continue spawning (as they would then have the opportunity to eat some eggs). Additionally, such a study must be designed so that males are energy-limited

and consume a substantial number of eggs in order to adequately evaluate benefits of egg consumption. The evaluation of the effect of filial cannibalism on male survivorship requires additional environmental controls; such a study must be done as above (to control egg consumption) but also in the presence of predators of the male and with other natural stressors. Because of the difficulty of evaluating the survivorship effects of filial cannibalism, I focus here on the reproductive effects of filial cannibalism.

I explore the reproductive fitness consequences of filial cannibalism in the flagfish by comparing two cannibalism treatments, one in which males have the opportunity to consume their eggs and another in which filial cannibalism is prevented, over 90 days, the approximate duration of a flagfish breeding season in north central Florida (Hale, unpublished data). Three components of reproductive fitness were considered: 1) total number of eggs received, 2) total number of spawnings, and 3) the frequency of spawning. Specifically, I evaluated whether energy gained from the consumption of eggs was directly translated into an increase in the total number of eggs received by a male. In addition, I examined the effect of filial cannibalism on components of male condition. While I only focus on reproduction here, systematically quantifying specific effects of filial cannibalism on components of fitness will provide key insight into the validity of current models of filial cannibalism.

Methods

Study Species

Flagfish live approximately one year, and flagfish males care for their nest by guarding, cleaning, and fanning. The incubation period of eggs is typically less than one week, and males are able to feed on vegetation and invertebrates, which are common near nesting sites. Flagfish females spawn with multiple males, and brood cycling (i.e., the alteration of courtship and mating periods with periods of full brood care) is absent in this species. Nesting males

potentially receive eggs continuously but may also care for only a single brood. In north central Florida, I have observed flagfish breeding approximately May through September. Flagfish have been successfully used in laboratory studies before (e.g., Mertz and Barlow 1966; Hale et al. 2003; St. Mary et al. 2001; Klug et al. 2005) and readily adapt to being housed in aquaria.

Experimental Design and Data Collection

The experiment was conducted in Gainesville, Florida beginning in May and ending in November 2002. Due to space restrictions, two blocks of the experiment were completed, the first beginning in May and the second beginning in September. To replicate peak breeding season conditions in both blocks, the experiment was conducted in an environmentally-controlled room where temperature and lighting could be held constant. The two blocks did not differ significantly (i.e., there were no significant block effects in any of the analyses) so the data were pooled for all analyses. Males were used only once in the experiment and were euthanized after the experiment. Flagfish were collected from the Otter Creek/ Waccasassa River drainage just prior to use and both sexes were housed in separate 150 l freshwater holding tank maintained at approximately 28°C prior to use. During this time the fish were fed *ad libitum* a diet consisting of algae tablets and frozen brine shrimp.

In all cases the experiment began by placing one male and three females in a 36 l freshwater aquarium (measuring 26 cm x 30 cm x 30 cm) equipped with air-driven, activated carbon and Dacron floss filtration, a spawning mat, and three artificial *Ludwigia* plants. The mat consisted of a 100 cm² tile covered with heavy, green acrylic felt carpet. The fish experienced a regular 14-hour daylight period and temperature was maintained at a constant 29°C. All males were randomly assigned to a treatment. Each male was allowed to spawn 90 days from his initial spawning date (i.e., date of first spawning for each male). I crossed two filial cannibalism treatments (access and no access to eggs) with two feeding regimes (low and high food). Thus,

there were four treatments: 1) high food and no filial cannibalism (HF NFC), 2) high food and filial cannibalism (HF FC), 3) low food and no filial cannibalism (LF NFC), and 4) low food and filial cannibalism (LF FC). Fish in a low food treatment were fed one algae tab weighing approximately 0.29 g every second day. Fish in a high food treatment received one algae tab weighing approximately 0.52 g and 1.2 g (wet weight) of frozen brine shrimp daily. During the experiment, fish were fed at approximately 1500 hrs daily. As mentioned above, males either had access to their eggs or access was denied by covering the eggs with a screen nest cover. The nest covers used in this experiment were 182.5 cm² and consisted of plastic netting with 1mm mesh. Males continue to actively care for the nest despite the addition of the cover.

I checked the nests for eggs four times each day at approximately 8am, 11am, 3pm, and 7pm. They were frequently checked in excess of four times daily, and if it was not possible to check them at least three times on a given day, a clear acrylic partition was placed in each tank separating males and females to prevent any undetected spawning. There were six days during the first block of the experiment and five days during the second block during which I was unable to check the nests at least three times per day.

When eggs were discovered (day 0), I removed the nest from the tank, counted the eggs, and recorded the developmental stage to ensure eggs were discovered soon after spawning. I am confident that in all cases eggs were discovered immediately after spawning. In all treatments, I then placed a clear acrylic divider containing nine holes in the rear half of the tank immediately after eggs were discovered, physically separating males and females while still allowing them to remain in visual and chemical contact, thus allowing males to continuously court females. Physically separating males and females with the partition (which was done in all treatments) was necessary to prevent females from consuming eggs. I then returned the eggs to the male, and

if the male was in a no filial cannibalism treatment (i.e., NFC, no access to eggs), I immediately placed the mesh nest cover over the eggs. In all treatments, nests with eggs were briefly removed from the tank each day in order to count the eggs. On day five (all eggs either hatched or were consumed by day 5), I removed the nest cover and/or the partition, allowing males the opportunity to spawn again. This procedure was repeated each time a male spawned for the duration of the 90 days.

Males remained in the same aquaria during the entire experiment. Females were used repeatedly throughout the experiment, but were frequently and randomly moved amongst the tanks to ensure that all females 1) experienced similar feeding regimes and 2) spent approximately equal amounts of time with each male (to limit any female-specific effects). Males were weighed at several intervals during the experiment.

Statistical Analyses

I used a 2-way ANOVA to examine the effect of food and filial cannibalism on correlates of fitness and male weight and length. These analyses were performed in SYSTAT 9.0 (SPSS, Inc.). I used logistic regression to evaluate the effect of food on proportion of eggs consumed; this analysis was performed using SAS 8.2 (SAS institute). I performed all analyses including and excluding data from males that died during the 90 days. Since the findings did not differ for any of the comparisons, I only present results excluding dead males. Because filial cannibalism treatment could not have affected the first clutch received, I evaluated the effect of filial cannibalism on total number of eggs received both including and excluding the first clutch received. The findings did not differ qualitatively, so results including all clutches are presented.

In order to explicitly evaluate whether cannibalistic males experienced a net gain in reproductive success, I compared the observed number of eggs cannibalistic males received with the number of eggs they were expected to receive to achieve, as a minimum, no net loss in

offspring produced. Specifically, I expected males that consumed eggs to receive, on average, the same number of eggs as non-cannibalistic males plus at least the number of eggs that were consumed. Thus, the expected egg benefit necessary for males to receive no reduction in reproductive output is defined as the mean number of eggs consumed by FC males, and the observed egg benefit is defined as the difference between the mean number of eggs received by FC males and the mean number of eggs received by NFC males. I used two-sample, one-tailed t-tests to compare the expected and observed egg benefit for high food and for low food males.

Results

Occurrence of Filial Cannibalism

Filial cannibalism was prevalent when males had access to eggs. Indeed, when food was high males consumed approximately 95% +/- 3.9% (\bar{X} +/- SE) of their eggs and when food was low males consumed approximately 84% +/- 3.6% (\bar{X} +/- SE) of their eggs. Such high rates of cannibalism gave me confidence that in all cases where access to eggs was allowed, I would expect to see benefits of filial cannibalism if they exist.

Effect of Diet on Filial Cannibalism

Diet significantly affected the proportion of eggs consumed (logistic regression food effect: $X_1^2 = 7.11, P = 0.008$). Specifically, males in the low food treatment consumed a smaller proportion of eggs than males in the high food treatment.

Costs and Benefits of Filial Cannibalism for Reproduction

I compared the difference between the mean number of eggs received for FC males and NFC males (i.e. the observed egg benefit) and the mean number of eggs consumed by FC males (i.e., the minimum expected egg benefit) (Figure 2-1). For high food males, the egg benefit of filial cannibalism necessary for filial cannibalism to result in no reduction in reproductive output

was 205 eggs; surprisingly, high food FC males received approximately 40 fewer eggs than high food NFC males (Figure 2-1). Consequently, high food males received significantly fewer eggs than what was necessary to achieve no reduction in net eggs received (2-sample t test: $t_{10} = 7.889$, $P < 0.0001$). Similarly, the egg benefit necessary for low food males to break even was 107 eggs, but they received only 38 more eggs than low food NFC males. Again, low food males received significantly fewer eggs than was necessary for no reduction in fitness (2-sample t test: $t_{10} = 2.504$, $P = 0.016$).

Effects of Food and Access to Eggs on Components of Fitness

Reproduction: There was a significant effect of food on all components of fitness I measured. In comparison to males receiving the low food diet, high food males received significantly more eggs (2-way ANOVA, food: $F_{1,23} = 10.047$, $P = 0.005$), spawned more times over the 90 day period ($F_{1,23} = 11.861$, $P = 0.002$), and had a greater frequency of spawning ($F_{1,23} = 11.250$, $P = 0.003$). In contrast, there was no effect of filial cannibalism on any of these variables (2-way ANOVA, FC: $F_{1,23} = 0.001$, $P = 0.975$; $F_{1,23} = 0.533$, $P = 0.474$; $F_{1,23} = 1.103$, $P = 0.306$, respectively) and no interaction ($F_{1,23} = 0.911$, $P = 0.351$; $F_{1,23} = 0.035$, $P = 0.853$; $F_{1,23} = 0.559$, $P = 0.463$, respectively) (Figure 2-2).

Male weight and length: There was no significant difference in initial male weight between the treatment groups (2-way ANOVA: food, $F_{1,23} = 0.200$, $P = 0.659$; FC, $F_{1,23} = 0.743$, $P = 0.398$; food x FC, $F_{1,23} = 0.416$, $P = 0.526$). During the experiment, high food cannibalistic males gained 1.73 ± 0.73 g ($\bar{X} \pm \text{SD}$), high food non-cannibalistic males gained 1.75 ± 0.47 g ($\bar{X} \pm \text{SD}$), low food cannibalistic males gained 0.79 ± 0.60 g ($\bar{X} \pm \text{SD}$), and low food non-cannibalistic males gained 1.15 ± 0.77 g ($\bar{X} \pm \text{SD}$). Although males in the high food treatment gained significantly more weight than low food males ($F_{1,23} = 8.538$, $P = 0.008$), there was no

effect of filial cannibalism ($F_{1,23} = 0.532$, $P = 0.474$) and no interaction between diet and cannibalism ($F_{1,23} = 0.429$, $P = 0.520$) on weight gained.

Additionally, there was no significant difference in initial male standard length between the treatment groups (2-way ANOVA: food, $F_{1,25} = 0.075$, $P = 0.786$; FC, $F_{1,25} = 0.402$, $P = 0.533$, food x FC, $F_{1,25} = 0.288$, $P = 0.597$), and there was no significant effect of food or filial cannibalism on change in male standard length (food, $F_{1,23} = 1.881$, $P = 0.185$; FC, $F_{1,23} = 0.105$, $P = 0.749$; food x FC, $F_{1,23} = 0.105$, $P = 0.749$).

Discussion

Parental investment, and parental care in particular, is expected to increase offspring survival (Trivers 1972; Sargent 1988; Clutton-Brock 1991; Balshine et al. 2002). Indeed, care has been shown to increase parental and offspring fitness in various animal taxa (Forester 1979; Dominey 1981; Simon 1983; Fairbanks and McGuire 1986; discussed in Balshine et al. 2002). Thus, the ambiguity regarding the adaptive significance of filial cannibalism coupled with the prevalence of filial cannibalism in fishes exhibiting parental care is surprising. Indeed, previous research in the flagfish suggests that the offspring survivorship benefits of parental care may be offset by the occurrence of filial cannibalism (Klug et al. 2005). If filial cannibalism is an adaptive trade-off between current and future reproductive success (Rohwer 1978), filial cannibalism should lead to an increase in net reproductive success. One way that an increase in net reproductive output could occur is through an increase in number of eggs fertilized (e.g., if males reinvest energy from cannibalism into increased courtship behavior).

Contrary to the expectation that filial cannibalism will increase male mating success, I found that the number of additional eggs received by males who cannibalized never compensated for the loss resulting from cannibalism. Among males on the high food diet, those that were allowed to cannibalize eggs actually received fewer eggs from females than those that were not

allowed to cannibalize eggs. For males on the low food diet, those that were allowed to cannibalize eggs received more eggs from females than those that were not allowed to cannibalize eggs, but the number of extra eggs received never compensated for the number lost to cannibalism. Since the flagfish life span is approximately one year in the wild, such a reduction in the number of eggs over the course of one breeding season likely has a large impact on lifetime reproductive success. In order to explain these findings in the context of the current energy-based explanation of filial cannibalism (Rohwer 1978; Sargent 1992), egg cannibalism would need to have a substantial positive effect on male survivorship, the survivorship of the eggs that remain in the nest, or on the survivorship of any future eggs that a male receives.

In contrast to cannibalism, food availability greatly affected correlates of fitness. Indeed, an enhanced diet was related to an increase in eggs received, spawning frequency, number of clutches received, and increased weight gain. Thus, I have evidence that males in my study were energy-limited and that food and/or nutritional level affects reproductive success. The finding that food availability affects reproductive success coupled with the lack of benefits of filial cannibalism suggests that eggs do not have substantial energetic or nutrient content relative to the costs of reproduction. This finding is also inconsistent with the energy-based hypothesis of filial cannibalism (Rohwer 1978; Sargent 1992). Furthermore, I found that males in the low food treatment consumed significantly fewer eggs than males in the high food treatment, which further contradicts the predictions of energy-based hypothesis (Rohwer 1978; Sargent 1992). However, reduced consumption of eggs by males in the low food treatment is consistent with life history theory if low food males have a reduced expectation of future reproduction and thus invest more in current reproduction. A similar trend (i.e., increased investment in current clutch as expected future reproduction declines) has been associated with seasonal patterns of

cannibalism in the cardinal fish (*Apogon doederleini*). Takeyama et al. (2002) found that 1-year old males cannibalised less at the end of the breeding season.

There were several limitations stemming from the controlled nature of the present study. In order to experimentally manipulate cannibalism while still allowing males to care for eggs I used a nest cover. After eggs were discovered, males and females were separated for 4 days in all treatments, thus preventing continuous spawning. Such separation was necessary to prevent NFC males and females from consuming eggs. Not allowing males to receive eggs continuously possibly led to clutch sizes that were small in comparison to those found in nature, and relatively small clutches, which have been associated with increased whole clutch cannibalism in other species (reviewed in Manica 2002), likely contributed to the high rates of cannibalism observed. Indeed, I do not believe that such rates of cannibalism are necessarily representative of natural filial cannibalism rates. Due to the nature of the spawning substrate in the field, it's currently impossible to accurately measure clutch size in the wild, and thus, I do not have reliable estimates of natural rates of filial cannibalism. Regardless, such high rates of cannibalism should result in even greater fitness effects of cannibalism and thus gave me confidence that I would be able to detect any benefits of filial cannibalism. Yet, I found no net benefits related to reproduction and I have no reason to believe that there would be any benefit at lower levels of filial cannibalism. Additionally, I only evaluated one major component of reproductive success and therefore, cannot evaluate alternative ways in which filial cannibalism could affect lifetime fitness. For example, separating males and females after spawning prevented me from assessing the effect of filial cannibalism on the number of simultaneous broods a male would subsequently receive, which may be an important component of reproductive success. Similarly, I did not measure hatching success, predation, and other potentially important components of reproductive

success. Further work is clearly needed to evaluate the adaptive significance of filial cannibalism in the flagfish. Nonetheless, experimentally manipulating cannibalism while still allowing males to care for eggs allowed me to evaluate key predictions of energy-based explanations of filial cannibalism. Indeed, this study is the first to experimentally manipulate filial cannibalism while still allowing males to care for eggs, thus allowing for the specific examination of some longer-term fitness consequences of filial cannibalism in relation to the energetic hypothesis (Rohwer 1978).

The hypothesis that filial cannibalism in fishes reflects an adaptive trade-off in which energy or nutrients gained from eggs is invested into future reproduction is widely accepted as valid (e.g. Manica 2002) and has rarely been questioned since it was first proposed 25 years ago (but see Smith 1992). While whole clutch cannibalism may be explained as the termination of care, it does not appear that we have an adequate explanation for the widespread occurrence of partial clutch cannibalism. In the present study, flagfish males consumed a large number of their eggs and no benefits related to increased reproduction or physical condition were observed. Thus, with regard to the flagfish, there is no evidence that Rohwer's (1978) hypothesis provides adequate explanation for partial clutch filial cannibalism. More generally, there is mixed support for Rohwer's theory of partial clutch cannibalism, as is evident from the inconsistent results of studies examining the effect of food availability and parental condition on filial cannibalism (as discussed above). In the case of flagfish, food sources other than eggs are available and the incubation period is relatively short (less than 4 days at 29°C), making it even more difficult to understand why males would consume eggs purely for caloric or nutritional purposes. Thus, future experiments should evaluate further specific ways in which energy gained from eggs could be translated into net fitness benefits (i.e., male survivorship and increased quality of

parental care). Furthermore, I suggest alternatives to Rohwer's (1978) energy-based hypothesis should be considered.

Currently, I can envision several adaptive explanations for why parental flagfish males would consume eggs; 1) energy or nutrients from egg may increase male survival (consistent with Rohwer 1978), 2) partial clutch cannibalism may improve survival of the remaining clutch (e.g. Payne et al. 2002), and 3) males may selectively cannibalize eggs with reduced survivorship or quality. These alternatives have received relatively little attention. Currently, the effect of filial cannibalism on male survival remains untested and further research is needed to evaluate this hypothesis. The effect of cannibalism on survival should be evaluated in the presence of predators and other natural stressors. In the present study, I did not measure the effect of filial cannibalism on offspring survival, and this idea should also be explicitly examined in separate experiments. Recently, Payne et al (2002) suggested that partial clutch cannibalism increases survivorship of remaining eggs through increased oxygen availability. This idea has received support in one system (*Stegastes leucostictus*, Payne et al. 2002) but not in another (*Pomatoschistus minutus*, Lissäker et al. 2002). However, it is possible that partial clutch cannibalism improves survivorship of remaining offspring through other mechanisms. For instance, if density-dependent egg predation exists, partial clutch cannibalism might reduce the male's risk of losing some or all of his eggs to egg predators. It is also possible that parental males use energy attained from eggs to increase the quality and/or quantity of parental care, thereby increasing remaining offspring survivorship or quality. This idea is still consistent with Rohwer's hypothesis (1978) but has not yet been evaluated. The idea that males may selectively cannibalize eggs has rarely been considered. Indeed, males of many species eat more eggs than would die naturally (e.g. Klug et al. 2005), but survival is typically measured only to hatching. It

is possible that males consume eggs with decreased post-hatching survivorship. Finally, it is possible that filial cannibalism is maladaptive. This idea has been dismissed in recent literature, but the validity of this dismissal remains unclear. In general, future work should focus on developing and examining alternatives to Rohwer's energy-based explanation of filial cannibalism.

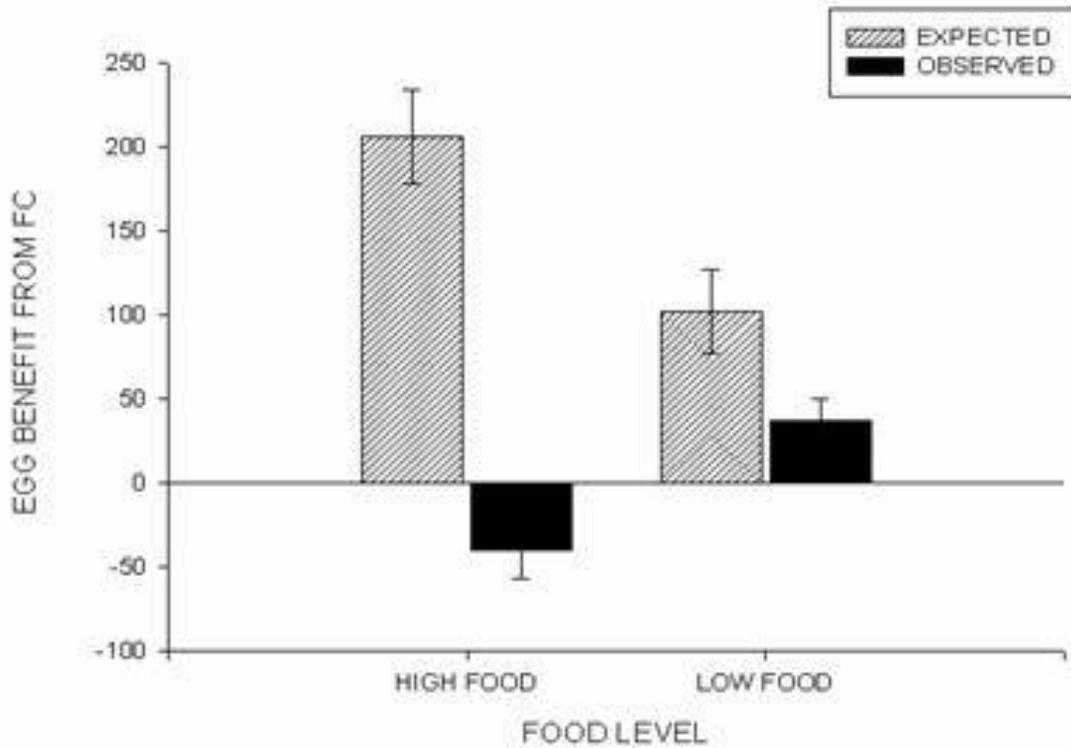


Figure 2-1. Expected and observed benefit of filial cannibalism in eggs received by males. The minimum expected benefit (hatched bars) of filial cannibalism necessary to overcome the loss resulting from the consumption of eggs is defined as the number of eggs consumed by FC males; the observed benefit (solid bars) of filial cannibalism is the difference in the mean number of eggs received by FC males and the mean number of eggs received by NFC males. Bars represent mean number of eggs and error bars are standard error.

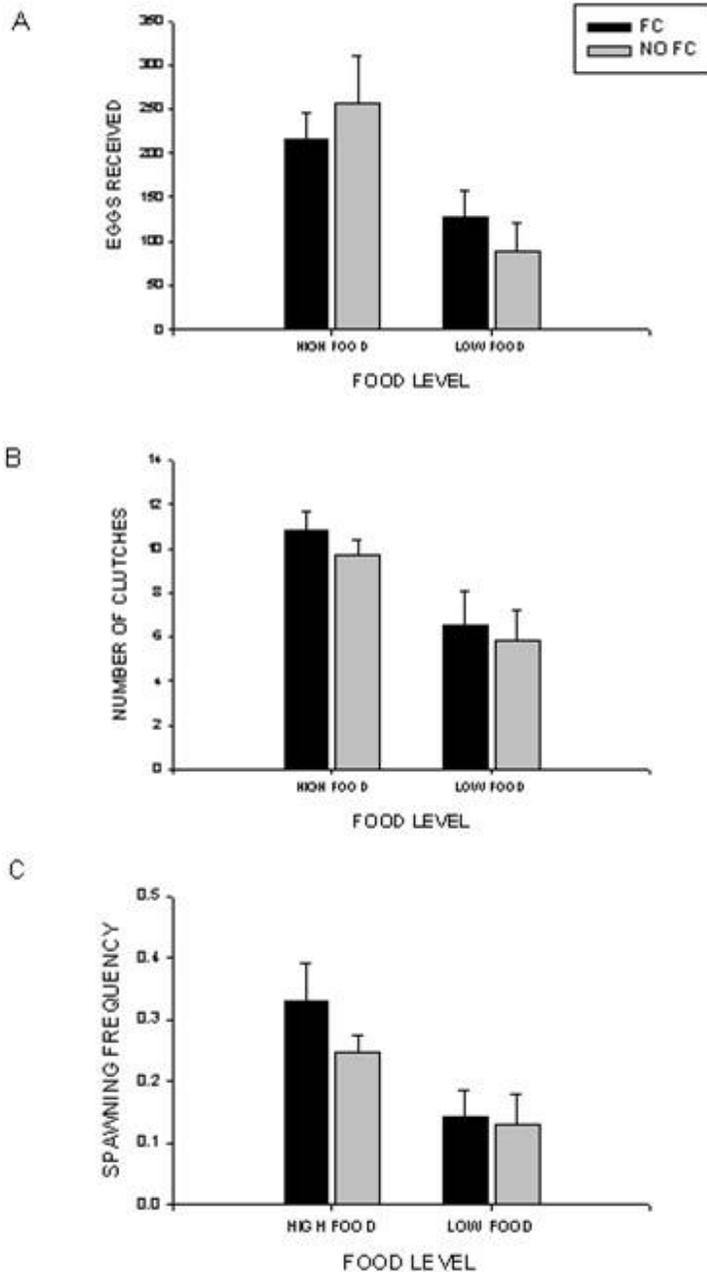


Figure 2-2. Effect of filial cannibalism on components of fitness. A) The mean total number of eggs received over 90 days for males in each of the four treatments. The treatments were high food and FC (i.e. access to eggs), high food and NO FC (i.e. no access to eggs), low food and FC, & low food and NO FC. B) The total number of clutches received over the 90 days across treatments. C) The frequency of spawning during the 90 days across treatments. Bars represent means and error bars are standard error.

CHAPTER 3
PARENTS BENEFIT FROM EATING OFFSPRING: DENSITY-DEPENDENT EGG
SURVIVORSHIP COMPENSATES FOR FILIAL CANNIBALISM

Introduction

Filial cannibalism is an evolutionary conundrum. How is eating one's own offspring ever an adaptive strategy? Indeed, it is hard to imagine many circumstances in which regularly consuming one's own offspring leads to increased net reproductive success. Thus, it is surprising that filial cannibalism, which occurs in a range of taxa (Polis 1981), is particularly common in fishes exhibiting paternal care (reviewed in Manica 2002), a behavior assumed to increase an individual's fitness through increased offspring survivorship or quality (Clutton-Brock 1991). While early ethologists considered filial cannibalism to be a rare behavior with little or no evolutionary significance, filial cannibalism in fishes has now been well documented in both the laboratory and the field (reviewed in Manica 2002), and currently, filial cannibalism in fishes is thought to represent an adaptive strategy in which males maximize lifetime reproductive success.

Specifically, filial cannibalism is thought to reflect a trade-off between current and future reproductive success, in which males gain energy and nutrients from eggs that are reinvested into current and future reproduction (the energy-based hypothesis; as articulated by Rohwer 1978 and Sargent 1992). According to this hypothesis, whole clutch cannibalism (i.e., the consumption of all eggs present) is expected to be more frequent when clutch size is relatively small because the energy requirements of caring males can be satisfied only by clutches larger than a certain size (Rohwer 1978). Specifically, this hypothesis suggests that males should consume some specific number of eggs to satisfy their energetic needs, and when initial clutch size is smaller than this critical number, males should consume the whole clutch. Consistent with this prediction, several studies have found that whole clutch cannibalism is more frequent when clutch size is relatively small (reviewed in Manica 2002; but see Payne et al. 2003, who found that smaller clutches were

not preferentially eaten). The energy-based hypothesis also predicts that cannibalism should increase as food availability decreases and/or when male condition is poor (Rohwer 1978; Sargent 1992). Evidence regarding these predictions is equivocal. Consistent with the energy-based hypothesis, supplementary feeding parental males reduced filial cannibalism in the common goby (*Pomatoschistus microps*, Kvarnemo et al. 1998), the scissortail sergeant (*Abudefduf sexfasciatus*, Manica 2004), and the Cortez damselfish (*Stegastes rectifraenum*, Hoelzer 1992), and in some cases (e.g., Manica 2004) males do appear to simply be cleaning the nest of dead eggs (i.e., mortality resulting from filial cannibalism is similar to background mortality) when food is abundant. Contrary to predictions of the energy-based hypothesis, there was no relationship found between cannibalism and food availability and/or male condition in fantail darters (*Etheostoma flabellare*, Lindström and Sargent 1997) and the three-spined stickleback (*Gasterosteus aculeatus*, Belles-Isles & Fitzgerald 1991). Furthermore, male flagfish (*Jordanella floridae*) with reduced food availability actually consumed *fewer* eggs than males with high food availability (Klug and St. Mary 2005 and Chapter 2).

Other studies have taken a different tack and examined the energetic content of eggs-- one study suggested that energy from partial clutch cannibalism could potentially offset costs related to care (*Apogon lineatus*, Kume et al. 2000), while another claimed that energy from eggs would be insufficient (*Gasterosteus aculeatus*, Smith 1992). Also inconsistent with the energy-based hypothesis, Payne et al. (2002) found that filial cannibalism increased in the later stages of egg development, when egg energetic value is much lower. Thus, there is a lack of general support for the energy-based explanation of filial cannibalism (Rohwer 1978; Sargent 1992) and at best current theory can only explain cannibalism in some cases. Despite such mixed evidence and a lack of many alternative hypotheses, the energy-based hypothesis of filial cannibalism is often

accepted as valid, and filial cannibalism is commonly considered an adaptive strategy (e.g., Vinyoles et al. 1999; Kume et al. 2000; Manica 2002). Overall, the support for this hypothesis is unsatisfying and it remains unclear in many systems if (and potentially how) filial cannibalism is an adaptive strategy.

Recently, Payne et al. (2002) proposed an alternative hypothesis suggesting that filial cannibalism is an adaptive strategy in which partial clutch cannibalism improves survivorship of remaining eggs by increasing oxygen availability to remaining eggs. In several systems low dissolved oxygen levels have been related to increased egg mortality (Kamler 1992), and according to the oxygen-mediated hypothesis of filial cannibalism (as articulated by Payne et al. 2002, 2004), males potentially improve overall clutch survivorship by removing some of their eggs. Through a reduction in egg density, cannibalism can increase the surface area of the developing embryos exposed to the water, thereby improving oxygen exchange and overall survivorship of the remaining eggs. In other words, when egg density is relatively low, each individual egg is expected to have greater oxygen availability than when egg density is high. This hypothesis has received relatively little empirical examination. In their initial paper proposing the idea of oxygen-mediated filial cannibalism, Payne et al. (2002) found that reducing egg density in the beaugregory damselfish (*Stegastes leucostictus*) increased developmental rate of embryos and that partial clutch cannibalism was significantly reduced when oxygen levels were high. However, the reefs inhabited by beaugregory damselfish have undergone significant environmental changes, particularly in relation to oxygen levels, over the past twenty years, and beaugregory damselfish do not oxygenate their eggs by fanning; thus, with respect to other systems, it is unclear how general we would expect oxygen-mediated cannibalism to be, particularly in species that are thought to oxygenate their eggs by fanning. In

the sand goby (*Pomatoschistus minutus*), a system in which males fan eggs, Lissåker et al. (2002) found no differences in whole clutch or partial clutch cannibalism across oxygen levels, although the aim of that study was not to explicitly evaluate oxygen-mediated filial cannibalism. Thus, the importance of oxygen-mediated cannibalism remains unclear.

Effectively evaluating the importance of oxygen-mediated filial cannibalism necessitates both an evaluation of predictions of the oxygen-mediated hypothesis of filial cannibalism (i.e., does cannibalism vary across oxygen/egg density levels) and an examination of potential fitness consequences of filial cannibalism (i.e., does the potential benefit of cannibalism in terms of additional number of eggs surviving outweigh the cost in number of eggs consumed by the male). Thus, the goals of my study were two-fold. First, I evaluated the effect of oxygen, egg density, and male condition on the occurrence of filial cannibalism and compared my findings to predictions of both the energy-based and oxygen-mediated hypotheses of filial cannibalism. Specifically, the oxygen-mediated hypothesis predicts that: 1) cannibalism will increase as oxygen decreases (because of reduced egg survivorship when oxygen is relatively low); 2) cannibalism will increase as egg density increases (because of decreased oxygen availability and survivorship when egg density is high); and 3) there is no *a priori* expectation that male condition will affect the occurrence of filial cannibalism. Likewise, the energy-based hypothesis predicts that 1) cannibalism will increase as oxygen decreases (because energetic costs increase when oxygen is low due to increased male fanning and increased metabolic costs to the males, Jones and Reynolds 1999); 2) there is no *a priori* expectation that egg density will affect cannibalism; and 3) cannibalism is expected to increase as initial male condition decreases. Secondly, by experimentally manipulating cannibalism, I evaluated the effect of simulated partial clutch cannibalism on egg survivorship and quantified the net benefits of partial clutch

cannibalism. If partial clutch cannibalism is an adaptive mechanism in which removing some eggs improves overall egg survivorship, we would expect partial clutch cannibalism to be related to no net reduction in offspring produced. The sand goby, *Pomatoschistus minutus*, is an ideal system for evaluating the oxygen-mediated hypothesis of filial cannibalism because eggs are laid in a dense layer, nests often have relatively low oxygen availability, and egg development is dependent on male fanning (and therefore thought to be highly oxygen dependent); thus, if oxygen-mediated filial cannibalism occurs generally, I would expect to find evidence of it in a system such as the sand goby.

Methods

Study Species and Experimental Site

Sand goby males care for their eggs through guarding, cleaning, and fanning. Males build nests under suitable substrates and cover the nest with sand, leaving only a small (~1cm) opening. Sand goby eggs are clumped and male fanning is required for egg development and survival. I conducted this study at Tvärminne Zoological Station, University of Helsinki, in southern Finland. Sand gobies were collected in shallow brackish water using a seine, and males and females were housed in separate holding tanks (100 l) with continuous seawater flow prior to use. During this time the fish were fed *ad libitum* live Mysid shrimp and frozen Chironomidae larvae. The experiment was conducted during the sand goby breeding season (June and July) of 2004.

Experimental Design

Experiment 1: Effect of oxygen and egg density on filial cannibalism: I crossed two oxygen treatments (high and low oxygen concentration) with two egg density levels (high and low egg density) to evaluate the effect of oxygen and egg density on the occurrence of filial cannibalism. Thus, there were four treatments: 1) high oxygen, high egg density, 2) high oxygen,

low egg density, 3) low oxygen, high egg density, 4) low oxygen, low egg density. I used natural variation in initial male condition (measured as $K=100*\text{weight}/\text{length}^3$; Williams 2000) to evaluate the relationship between parental condition and the occurrence of filial cannibalism.

Each experimental tank was 60 l and equipped with continuous seawater flow through. The tanks contained either a large (8 cm diameter) or a small (4 cm diameter) half-flowerpot, which served as an artificial nest site. The two nest size treatments corresponded to my two experimental egg density levels: high and low. Because females spawn their eggs in a monolayer on the ceiling of the half-flowerpot and because egg number is approximately equal amongst females, egg density in small nests can be much greater than egg density in large nests (K. Lindström, personal observation). I fitted the inside of each nest with a transparent piece of plastic onto which females spawn their eggs; the transparent plastic allowed me to remove and photograph the clutch, when necessary, without disturbing the eggs. Specifically, there were 1.8 ± 0.05 eggs per mm^2 ($\bar{X} \pm \text{SE}$) in small, high density nests and 1.4 ± 0.12 eggs per mm^2 in the large, low density nests, and this difference was significant (2-tailed t-test, $t=-3.09$, $df=38$, $p=0.004$). These egg density measurements are comparable to those observed in the wild (egg density of nests in nature: range = 0.79 - 2.8 eggs per mm^2 , $\bar{X} \pm \text{SE} = 1.77 \pm 0.26$ eggs per mm^2 , $N = 9$).

I began each experimental by placing one male and one female in a tank with the randomly assigned egg density treatment (small nest or large nest). After spawning occurred, I removed the nest from the tank and photographed the eggs using a digital camera such that individual eggs could be counted. I subsequently quantified initial egg numbers using these digital images. I then transferred the clutch, on its plastic sheet, to a nest of intermediate size (6 cm diameter) and returned the nest with eggs to the male. Transferring the eggs to a nest of intermediate size

ensured that males in both egg density treatments fanned nests of similar size and thus had similar costs of care, which allowed me to isolate effects of egg density from effects of nest size. Immediately after returning the eggs to the male, I randomly assigned an oxygen treatment (high or low). In the low oxygen treatment, low oxygen water constantly flowed directly into the male's nest, reducing the oxygen concentration inside the nest to approximately 32.2 +/- 10.1 % (i.e., 3.2 +/- 1.0 mg/L at 14.3°C, \bar{X} +/- SE) of fully air-saturated water. This was done by continuously bubbling nitrogen gas into a covered holding tank; using airline tubing, the reduced-oxygen seawater was then allowed to flow continuously in through the rear of the male's nest. In the high oxygen treatment, high oxygen water (from a flow through seawater system) was continuously allowed to flow into the rear of the male's nest; in this case oxygen concentration in the males nest was maintained at approximately 96.1 +/- 1.4% (i.e., 9.3 +/- 0.18 mg/L at 14.7°C, \bar{X} +/- SE) of fully air-saturated water. Because oxygen concentration was only manipulated in the nest and because all tanks had continuous flow through of sea water, oxygen concentration outside of the nest was approximately the same for both high and low oxygen treatments. I quantified the oxygen levels in the high and low oxygen nests for a sample of the males in the experiment using an ISO2 oxygen meter equipped with an OXELP oxygen electrode (World Precision Instruments); oxygen levels inside the high oxygen treatment nests were significantly greater than those in the low oxygen treatments (two-tailed t-test, $t = -4.7$, $df = 9$, $p=0.001$).

I followed eggs until hatching and visually inspected nests daily by shining a light into the nest. When eye shine was visible in the nest (approximately 1-3 days prior to hatching), I removed the nest, photographed the plastic transparency with eggs, and later counted the number of eggs using the digital photograph. Male and female weight and standard length were measured

at the beginning and end of each replicate, and the condition measure K (Williams 2000) was used as an indicator of male condition.

Experiment 2: Effect of simulated filial cannibalism on egg survivorship: I examined the effect of two levels of simulated filial cannibalism (egg removal and no egg removal) in high and low oxygen environments. In this experiment, one male and one or two females were placed in an aquarium (described above) with an intermediate-size artificial nest (described above) containing a transparent plastic sheet for spawning; after spawning occurred, I removed the nest from the tank. I then cut the plastic sheet into four approximately equal pieces and each quarter was randomly assigned to one of the four treatments: 1) high oxygen, egg removal, 2) high oxygen, no egg removal, 3) low oxygen, egg removal, 4) low oxygen, no egg removal.

In the egg removal treatments, I simulated filial cannibalism by using a pair of fine forceps to haphazardly remove some proportion of the eggs corresponding to actual levels of filial cannibalism observed in experiment 1 (simulated cannibalism: 10 - 66% of eggs removed, $39.6 \pm 2.5\%$ = mean \pm SE; observed partial cannibalism: 6 - 93%, $37.5 \pm 7.9\%$). In the no egg removal treatments, I removed a trivial number of eggs (approximately 5-10 eggs) from the nest and gently touched a proportion of the remaining eggs (corresponding to the approximate number of eggs that were removed in the egg removal treatment) with the forceps. Digital images were then taken of the transparencies and I later counted the eggs. Each transparency with eggs was then placed in either a high oxygen water or low oxygen water container, each approximately 18 cm x 13 cm x 3.5 cm. Specifically, using a pin, I attached the transparencies with eggs to a styrofoam lid designed to snugly fit on each of the containers. I then placed the lid on the container so that the eggs were always in water. Because eggs are dependent on fanning, an air stone continuously bubbled air approximately 5 cm directly below the eggs at all times in both treatments. This

method allows eggs to develop at rates comparable to those observed when males fan the eggs (Maria Järvi-Laturi, personal communication). The high oxygen water contained a second air stone that continuously bubbled air into the water. This air stone was placed in the corner of the container so that the bubbles did not directly hit the eggs, and the oxygen concentration was maintained at 93.0 +/- 3.1% (i.e., 8.9 +/- 0.28 mg/L, \bar{X} +/- SE) of fully saturated water. Likewise, in the low oxygen treatment, I placed a second air stone in the corner of the tank and nitrogen was continuously bubbled into this container through this air stone. Again, the bubbles from the second air stone did not directly flow onto the eggs, and thus, I eliminated any potential effects of direct contact of nitrogen gas with the eggs. Oxygen concentration in this tank was maintained at approximately 24.9 +/- 6.4% (i.e., 2.4 +/- 0.61 mg/L, \bar{X} +/- SE) of fully saturated water when the probe was placed 5cm above the air stone bubbling air (i.e., where the eggs were placed and in direct flow of the air bubbles). I checked eggs and oxygen concentration daily by briefly removing the lids of the containers. When measuring oxygen level, the Styrofoam lid was carefully raised and the probe was placed against the Styrofoam near the eggs, directly in the flow of the air bubbles. Despite bubbling air underneath the eggs in all treatments, oxygen concentration was significantly greater in the high oxygen containers than in the low oxygen containers (two-tailed t-test, $t = -8.5$, $df = 5$, $p < 0.001$), and I am thus confident that eggs in the two oxygen treatments experienced very different oxygen levels. I recorded the proportion of the clutch surviving until eye shine was present, the day on which eye shine was visible, and the proportion of the clutch covered in fungus. Three to six clutches were placed in a container at one time and four replicates were completed.

Data Analysis

Experiment 1: Effect of oxygen and egg density on filial cannibalism: I analyzed the effect of oxygen and egg density on the occurrence of whole clutch cannibalism using a stepwise

logistic regression (remove if $p > 0.15$); oxygen and egg density were treated as categorical variables, and date of spawning, initial male condition, change in male condition, and initial egg number were used as covariates in the analysis. I analyzed the effect of oxygen and egg density on the day of whole clutch cannibalism, egg survivorship, and male condition using stepwise ANCOVA (remove if $p > 0.15$), and thus, for simplicity's sake, I only present significant effects of the final model, unless otherwise stated. In all analyses, I initially evaluated all two-way interactions between factors and covariates and found them to be non-significant. I then removed these factor-covariate interactions and proceeded with the stepwise ANCOVA. For day of whole clutch cannibalism and egg survivorship analyses, oxygen and egg density were treated as categorical fixed factors, and initial egg number, date of spawning, initial male condition, and change in male condition were used as covariates. The interaction between oxygen and egg density was also included in the model. For male condition analyses (i.e., change in condition and final condition), oxygen and egg density were again treated as categorical fixed factors, and date of spawning, initial male condition, and number of eggs consumed were used as covariates, and again, the interaction between oxygen and egg density was included. For analyses of survivorship, proportion surviving was first arcsin square root transformed.

Additionally, whole clutch cannibalism and partial clutch cannibalism likely have distinct biological significance; whole clutch cannibalism is a termination of care and benefits of whole clutch cannibalism can only be seen in future reproductive success, whereas benefits of partial clutch cannibalism are potentially related to current and/or future reproductive success. Thus, I performed analyses both including and excluding cases of whole clutch cannibalism, when applicable.

Experiment 2: Effect of simulated filial cannibalism on egg survivorship: I evaluated the effect of egg removal and oxygen on survivorship of remaining eggs using a completely randomized block design. For the analysis of survivorship, the proportion of the clutch surviving was first arcsin square root transformed. I treated oxygen and egg removal as fixed factors, and clutch (i.e., the original clutch eggs were from) was treated as a random factor. Blocking by clutch allowed me to account for inherent differences among clutches (e.g., effects of parents) and also implicitly accounts for any effect of time (i.e., replicate); thus, blocking by replicate (i.e., time) is unnecessary (G. Wallace, University of Florida Statistics Department, pers. comm.). I compared the number of eggs surviving with and without simulated cannibalism in order to explicitly evaluate whether the potential benefit of cannibalism (i.e., increased survivorship of remaining eggs stemming from egg removal) outweighed the associated cost (i.e., number of eggs removed). For cannibalism to result in no net reduction in current reproductive success, the total number of eggs surviving with cannibalism must, on average, be greater than or equal to the total number of eggs surviving without cannibalism. As above, I analyzed this data as a completely randomized block design, and treated oxygen and egg removal as fixed factors and clutch as a random factor. All analyses were performed both including and excluding cases of whole clutch death.

Results

Experiment 1: Effect of Oxygen, Egg Density, and Male Condition on Filial Cannibalism

Occurrence of whole clutch cannibalism: Whole clutch cannibalism was more prevalent when oxygen was low and/or egg density was high (stepwise binary logistic regression, oxygen effect, $X_1^2 = 3.81$, $p = 0.05$; egg density effect, $X_1^2 = 3.78$, $p = 0.05$; Figure 3-1). Similarly, smaller clutches were subject to whole clutch cannibalism more frequently than larger

clutches (initial egg number effect, $X_1^2 = 4.43$, $p = 0.035$). It is important to note that there was no significant difference in initial egg number between the oxygen or egg density treatments (2-way ANOVA, oxygen effect, $F_{1,39} = 0.1$, $p = 0.75$, egg density effect, $F_{1,39} = 0.001$, $p = 0.98$). While there was a trend for whole clutch cannibalism to decrease as the breeding season progressed, there was no significant effect of the date of spawning on whole clutch cannibalism ($X_1^2 = 3.20$, $p = 0.07$). Also noteworthy in relation to the energy-based hypothesis, there was no effect of initial male condition or change in male condition on the occurrence of whole clutch cannibalism ($p > 0.15$). Specifically, the initial condition (K) of males that cannibalized their whole clutch was 0.64 ± 0.014 g/cm³ ($\bar{X} \pm$ SE), and the initial condition of males that did not practice whole clutch cannibalism was 0.63 ± 0.024 g/cm³ ($\bar{X} \pm$ SE).

To further analyze patterns of whole clutch cannibalism, I examined the day on which whole clutch cannibalism occurred. The timing of whole clutch cannibalism occurred earlier as the breeding season progressed ($F_{1,24} = 9.85$, $p = 0.005$) and when initial egg number was relatively small ($F_{1,24} = 4.559$, $p = 0.05$). Additionally, males in poorer condition cared for their clutches longer before cannibalizing them entirely (initial condition effect, $F_{1,24} = 7.27$, $p = 0.01$). There was significant interaction between the date spawning occurred and the initial number of eggs received ($F_{1,24} = 17.6$, $p < 0.001$).

Egg survivorship: High oxygen tended to increase egg survivorship (oxygen effect, $F_{1,37} = 3.62$, $p = 0.06$; Figure 3-2), and egg survivorship also increased as initial egg number increased (initial egg number effect, $F_{1,37} = 7.96$, $p = 0.008$); however, there was no significant effect of initial condition, egg density, or spawning date on egg survivorship ($p > 0.15$ for all). Because the trend for oxygen and initial egg number to affect egg survivorship was almost certainly the result of whole clutch cannibalism (which was affected by oxygen and initial egg number), I then

repeated the analysis excluding cases of whole clutch cannibalism. In this case, I found a significant effect of oxygen ($F_{1,12} = 9.9$, $p = 0.02$) and spawning date ($F_{1,12} = 6.1$, $p = 0.05$). Additionally, egg survivorship was higher for males that were initially in poorer condition (initial condition effect, $F_{1,12} = 15.0$, $p = 0.008$; Figure 3-3 A), and there was also a relationship between change in male condition and egg survivorship ($F_{1,12} = 15.5$, $p = 0.008$). Specifically, males that were in poorer condition to begin with ate a smaller proportion of (and fewer) eggs than males in better condition (Figure 3-3 A), and males that did eat eggs had less of a decline in condition (Figure 3-3 B). Again, there was no effect of egg density. However, it's important to note this analysis is, in a sense, not performed on a random sample of eggs; males have already decided whether or not to cannibalize the whole clutch, and potentially, they have decided to continue to care for eggs that they expect to have the greatest survivorship. For example, only one male in the low oxygen, high egg density did not cannibalize his entire clutch. We have no idea what survivorship of the other low oxygen, high egg density clutches would have been. Effectively analyzing the direct effects of oxygen and egg density on egg survivorship necessitates that this is done in the absence of whole clutch cannibalism (as in Experiment 2).

Male condition: When males consumed their entire clutch (i.e., including only cases of whole clutch cannibalism), there was a significant effect of initial condition on final condition ($F_{1,24} = 49.5$, $p < 0.001$) but not on change in male condition ($p > 0.15$). Additionally, final male condition worsened as the breeding season progressed (spawning date effect, $F_{1,24} = 4.5$, $p = 0.05$).

When I considered only partial clutch cannibalism, providing care in low oxygen nests resulted in a poorer final condition and a greater decrease in condition, in comparison to providing care in high oxygen nests (final condition, $F_{1,12} = 19.4$, $p = 0.003$; change in condition,

$F_{1,12} = 16.4, p = 0.007$). Additionally, condition worsened as the breeding season progressed (final condition, $F_{1,12} = 10.6, p = 0.01$; change in condition, $F_{1,12} = 9.3, p = 0.02$). The number of eggs a male consumed was positively related to condition, suggesting that eggs provide energetic benefits to caring males (final condition, $F_{1,12} = 17.2, p = 0.004$; change in condition, $F_{1,12} = 11.0, p = 0.02$).

Experiment 2: Effect of Simulated Filial Cannibalism on Egg Survivorship

Effect of oxygen and egg removal on remaining egg survivorship: Egg removal significantly improved egg survivorship ($F_{1,33} = 4.64, p=0.04$; Figure 3-4 A). Additionally, there were significant differences among clutches in egg survivorship (i.e., eggs from particular clutches had higher egg survivorship than eggs from other clutches, regardless of treatment; $F_{1,16} = 4.02, p = 0.004$) and significant interaction between the clutch that eggs were from and oxygen (i.e., some clutches did better in the low oxygen environment, while others did better in the high oxygen environment; $F_{16,33} = 5.06, p < 0.001$). Surprisingly, there was no effect of oxygen on egg survivorship. This analysis was performed including cases in which the whole clutch died. In all cases in which the whole clutch died, fungus had taken over the nest. However, in the presence of the male, fungus is never observed to attack the entire clutch. Thus, I repeated this analysis excluding whole clutch death, which might be more representative of natural conditions. The results were unchanged; egg removal increased egg survivorship ($F_{1,10.1} = 13.83, p = 0.004$; Figure 3-4 B) and there was a significant interaction between clutch and oxygen ($F_{8,6} = 9.36, p = 0.007$), but again, there was no effect of oxygen on egg survivorship.

Effect of oxygen and egg removal on total number of eggs surviving: I compared the number of eggs surviving with and without cannibalism to evaluate potential fitness consequences of cannibalism. Regardless of whether I included or excluded cases of whole clutch death, I found no effect of oxygen or egg removal on the number of eggs surviving

(Figure 3-5). In both cases, there is a significant interaction between oxygen and the clutch that the eggs were from (including whole clutch death, $F_{17,33} = 4.60$, $p < 0.001$; excluding whole clutch death, $F_{18,16} = 3.89$, $p = 0.004$).

Discussion

Here, I present evidence that filial cannibalism can potentially be an adaptive mechanism associated with density-dependent egg survivorship. When I simulated partial clutch cannibalism by removing eggs, the survivorship of the remaining eggs increased, and more importantly, egg removal at a range of cannibalism levels (10 – 66 % of clutch) did not reduce the total number of offspring produced. Indeed, my results show that males can consume, on average, 40% of their eggs with no reduction in current reproductive success! Thus, partial clutch filial cannibalism is potentially a mechanism by which males improve survivorship of remaining eggs. This finding is consistent with the theoretical predictions of Payne et al. (2004), whose modeling results suggest that under some conditions, males can consume up to 80% of their clutch without a reduction in reproductive output. Under this scenario, males potentially also gain energy from eggs with no net loss in reproductive success. My results and previous work in the sand goby (Lindström 1998) suggest that consuming eggs is energetically beneficial. Additionally, actual partial clutch cannibalism is likely to be much more precise and selective than my simulated cannibalism and males can potentially track the conditions in their nest, suggesting that partial clutch cannibalism may be even more efficient at enhancing the survival of the remaining brood.

Consistent with previous theory (Rohwer 1978; Sargent 1992), I found that whole clutch cannibalism in the sand goby is more prevalent when initial clutch size is relatively small. However, male condition did not affect the occurrence of whole clutch cannibalism; this finding is inconsistent with the current energy-based hypothesis, which suggests that whole clutch cannibalism should be more frequent when clutch size is relatively small because the energy

requirement of males can be satisfied only by clutches larger than a certain size (Rohwer 1978). My results suggest that whole clutch cannibalism depends on costs and expected benefits of care, as suggested by Manica (2004). Parental care in fishes is often assumed to be shareable among offspring in a nest (i.e., a unit of parental care may be given to one or several offspring; Wittenberger 1981, Williams 1975). Thus, the costs of care for small and large clutches is assumed to be comparable, whereas the benefit (i.e., offspring produced) of caring for a large clutch is assumed to be much greater than that of a small clutch. In my study, whole clutch cannibalism increased as the expected benefit of care decreased (i.e., as initial egg number decreased) and as the cost of care increased (i.e., with decreasing oxygen). This finding that low oxygen led to more whole clutch cannibalism is consistent with both the previous energy-based hypothesis (Rohwer 1978; Sargent 1992) (because cost of care to the male increases as oxygen decreases) and with the oxygen-mediated hypothesis (Paynet et al 2002; 2004) (because the expected benefit would be less when oxygen is low, according to this hypothesis). However, the finding that males altered their whole clutch cannibalism according to egg density is only consistent with the oxygen-mediated hypothesis (since the benefit from a high density clutch would be less than that of a low density clutch, assuming egg numbers are equal, Figure 3-4) and is not predicted by the energy-based hypothesis.

The observed patterns of filial cannibalism, and in particular partial clutch cannibalism, are thus consistent with cannibalism mediated by density-dependent egg survivorship (e.g., the oxygen-mediated hypothesis, Payne et al 2002) and inconsistent with the energy-based hypothesis (Rohwer 1978; Sargent 1992). For example, the energy-based hypothesis assumes that there is an adaptive trade-off occurring between current and future reproductive success, in which males gain energy for future reproduction at a cost to current reproductive success. In the

sand goby, I found that there is no cost to current reproduction (i.e., no trade-off between current and future reproductive success) because density-dependent egg survivorship compensates for filial cannibalism. Furthermore, the energy-based hypothesis predicts a negative relationship between male condition and filial cannibalism. Contrary to this prediction, I found that males in poorer condition actually consumed *fewer* of their eggs than males in better condition. A similar finding in the flagfish was reported by Klug and St. Mary (2005; Chapter 2), who suggested that males in poor condition possibly have reduced expected future reproduction and thus invest more into their current clutch. While inconsistent with the current energy-based hypothesis, my findings are similar to those in some other systems (e.g., Belles-Isles and Fitzgerald 1991; Lindström and Sargent 1997; Klug and St. Mary 2005), but contrary to results in others (e.g., Hoelzer 1992; Kvarnemo et al. 1998; Manica 2004). However, my results are also, in part, contrary to oxygen-mediated filial cannibalism. Although whole clutch cannibalism was affected by oxygen and egg density, and egg removal improved egg survivorship, oxygen did not affect egg survivorship in the simulated cannibalism experiment. Thus, it does not appear that partial clutch cannibalism in the sand goby improves egg survivorship by increasing oxygen availability of remaining eggs. Indeed, partial clutch cannibalism does appear to be a mechanism in which the consumption of some eggs improves survivorship of remaining eggs; however, the cause of density dependent egg survivorship is unknown in this system. Additionally, the lack of an effect of oxygen on egg survivorship also indicates that male fanning might not primarily serve to oxygenate eggs, as is typically assumed.

I therefore suggest a general explanation of filial cannibalism that is mediated by density-dependent egg survivorship, but that is not solely related to oxygen, as in current theory (Payne et al. 2002, 2004). There are many ways in which density-dependent egg survivorship can occur.

For example, in systems such as the sand goby in which eggs are clumped, it is plausible that waste from developing embryos negatively affects the development and/ or survival of other embryos, and that decreased egg density reduces the negative effects of such waste. In species whose eggs are not highly clumped (e.g., flagfish) other density-dependent factors, such as density-dependent egg predation might affect egg survivorship. For instance, if male nest size has some limit and predators are attracted to nests with more eggs, a male might reduce the probability of losing some or all of his eggs to predators by consuming some proportion of them. In systems such as beaugregory damselfish, the system on which Payne et al. (2002) based their hypothesis of oxygen-mediated cannibalism, which lack male fanning of eggs, it does seem likely that density-dependent egg survivorship is due to limited oxygen availability. Specifically, the reefs inhabited by beaugregory damselfish recently underwent changes in oxygen levels, and thus it seems likely that males cannibalize their eggs to increase oxygen availability of remaining eggs. More work is needed to assess the relative importance of the evolution of filial cannibalism and fanning, and future work should focus on systems with different fanning and parental care strategies. Indeed, the actual costs and benefits of fanning and filial cannibalism are unknown in many systems. More generally, other hypotheses associated with filial cannibalism mediated by density-dependent egg survivorship should be explored further.

Regardless of the mechanism, filial cannibalism mediated by density-dependent egg survivorship raises an interesting question: why don't females just lay fewer eggs? If egg survivorship is density dependent and laying tightly packed eggs reduces overall egg survivorship, why haven't females been selected to lay less dense clutches? In the sand goby, it seems unlikely that laying dispersed egg batches would be an evolutionarily stable strategy. If a female were to lay fewer, more dispersed eggs, it is likely that the remaining space would be

taken up by another female's eggs, resulting in the same amount of cannibalism. If all nests (or nests of high quality males) were full of sparsely laid eggs, a female would likely increase her fitness by laying a denser clutch in a nest already containing eggs, as opposed to not laying at all or laying eggs with a low quality male. Additionally, it is important to note that females do, to some extent, mediate the egg density of their clutch; in the present study, egg density in larger nests was significantly less than egg density in smaller nests. Thus, females do reduce the egg density of their clutch when it is possible to do so. Why females lay many, densely packed eggs is a complex problem, and necessitates consideration of many factors affecting egg survivorship, including the costs associated with density-dependent egg survivorship and the costs and benefits associated with mate quality. However, it does not appear that selection will necessarily favor females laying clutches with fewer, less tightly packed eggs when egg survivorship is density-dependent.

In conclusion, alternative explanations of filial cannibalism need to be explored further, and new hypotheses should be developed and evaluated. For example, selective filial cannibalism seems plausible. Numerous studies show that males consume healthy and viable eggs (discussed in Manica 2002). However, if variation in offspring quality exists and if care is not entirely shareable among offspring, or if egg survivorship is density-dependent, males could potentially benefit by consuming viable eggs of reduced quality (e.g., eggs with reduced post-hatching survival; see also literature on selective embryo abortion in plants, e.g., Burd 1998). To more explicitly evaluate the potential fitness consequences of cannibalism, it would be useful to estimate the average offspring fitness in nests in which males have removed eggs and nests in which experimenters have removed eggs, to determine if males are eating poor-quality eggs. Furthermore, the future benefit of eating eggs in this system remains unclear and should be

evaluated in an experiment specifically designed to quantify future reproductive and survivorship benefits of cannibalism. Eating eggs clearly provides a male with some energetic gain, but the relative importance of this benefit for future reproduction is unknown in this system. Finally, the evolutionary significance of filial cannibalism is likely not due solely to one factor (e.g., energetic benefit of eggs, density-dependent egg survivorship), and once the current and future costs of filial cannibalism are better understood, a more synthetic model of filial cannibalism will be necessary.

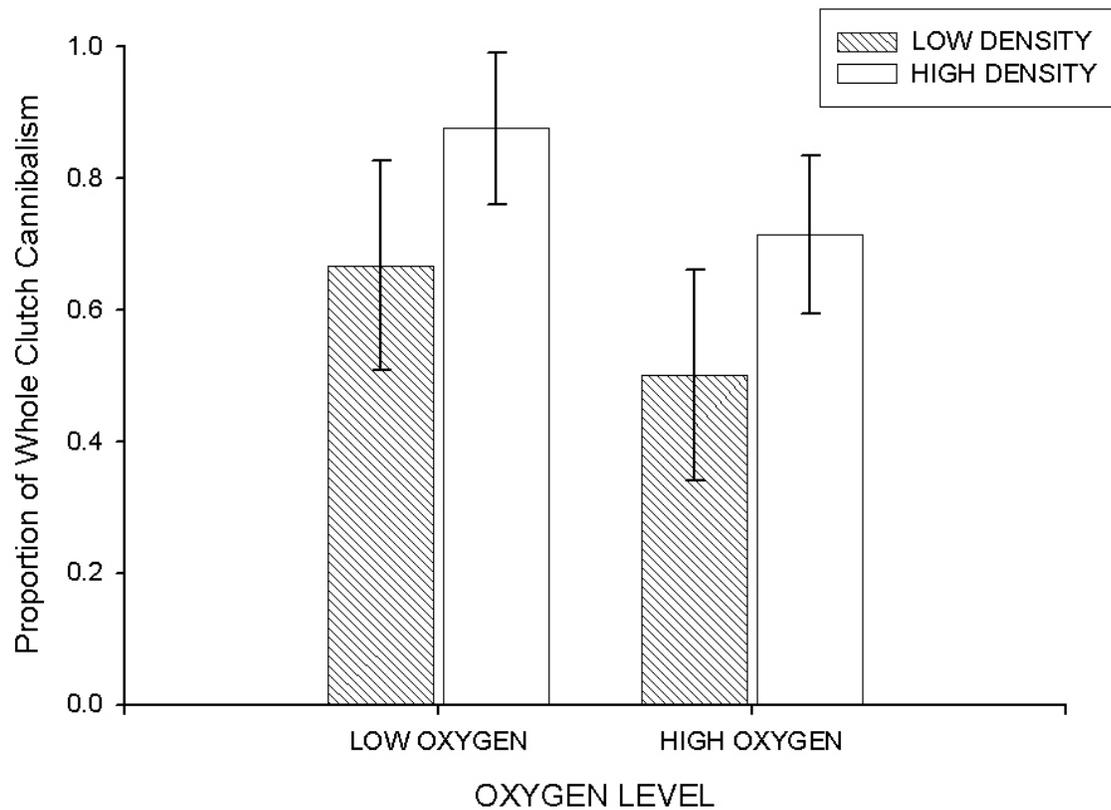


Figure 3-1. Effect of oxygen and egg density on the prevalence of whole clutch cannibalism by parental males. Bars represent the proportion of clutches in which the male consumed the entire clutch, and error bars are standard error based on a binomial distribution.

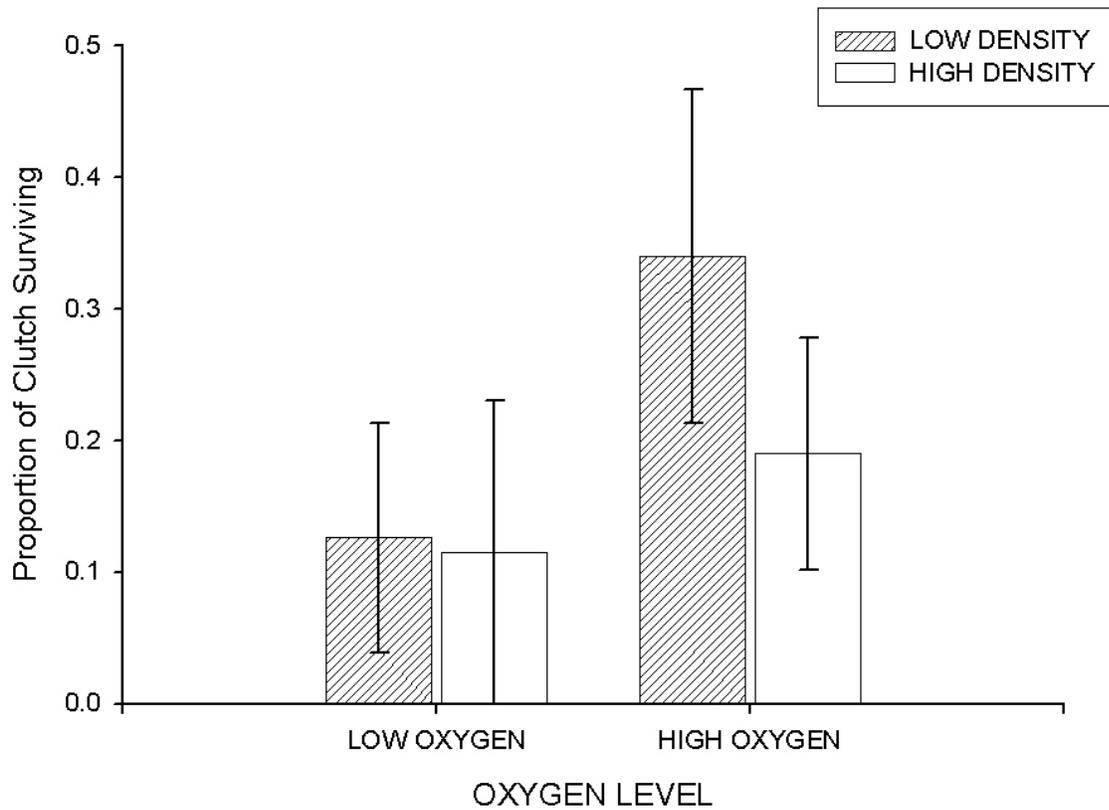


Figure 3-2. Effect of oxygen and egg density on the mean (\pm SE) egg survivorship (i.e., proportion of the clutch that survived until hatching) when males were present with eggs, including cases of both whole and partial clutch cannibalism. It is important to note that in the low oxygen, high egg density treatment, only 1 male cared for his clutch until hatching; the other 8 males in this treatment cannibalized their whole clutch.

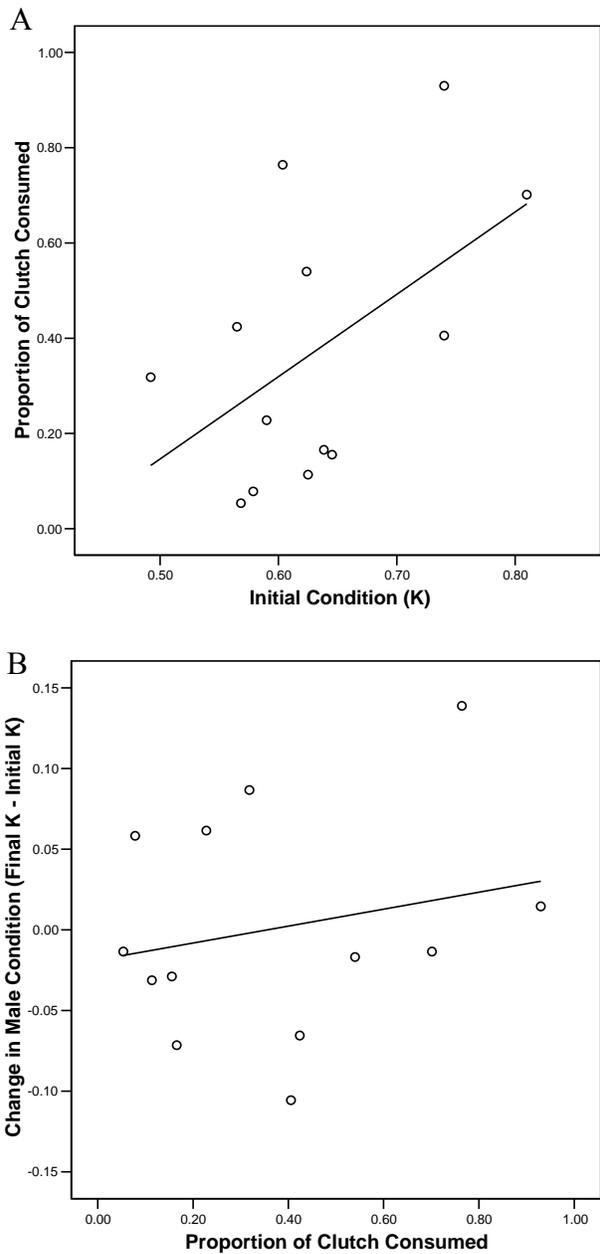


Figure 3-3. Relationship between A) male condition (i.e., $K=100 \cdot g/cm$) and the proportion of the clutch consumed by parental males, and B) partial clutch cannibalism and change in male condition.

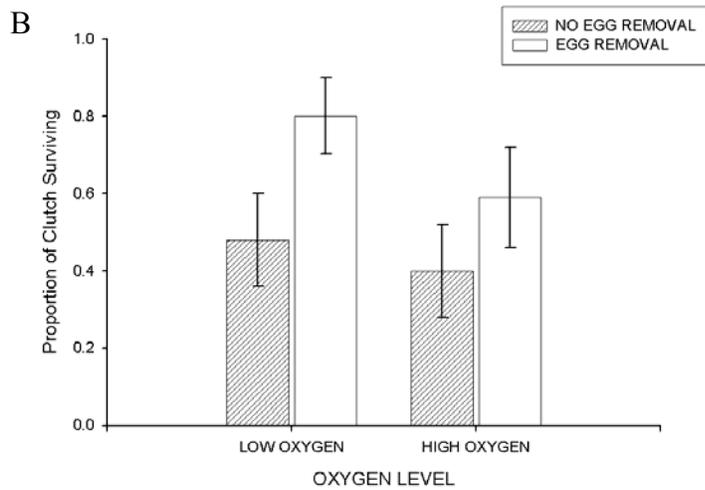
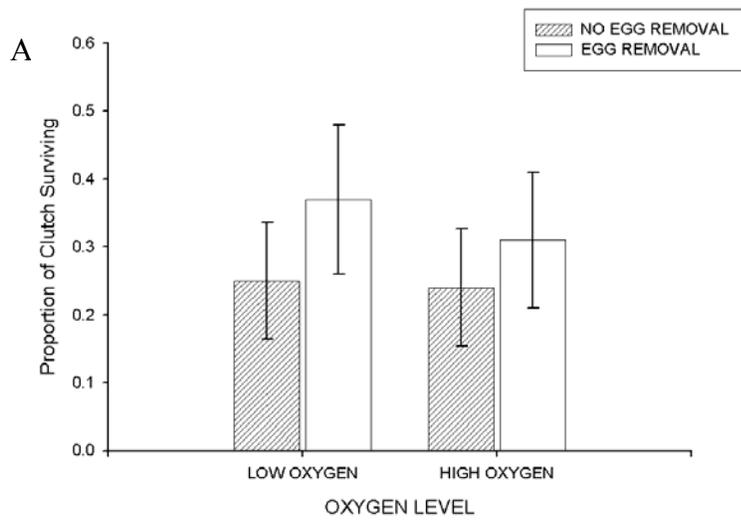


Figure 3-4. Effects of simulated filial cannibalism. A) The effect of oxygen and egg removal on egg survivorship (i.e., the mean \pm SE proportion of the clutch surviving), including cases of both whole and partial clutch death. B) The effect of oxygen and egg removal on egg survivorship (i.e., the mean \pm SE proportion of the clutch surviving), excluding cases of whole clutch death.

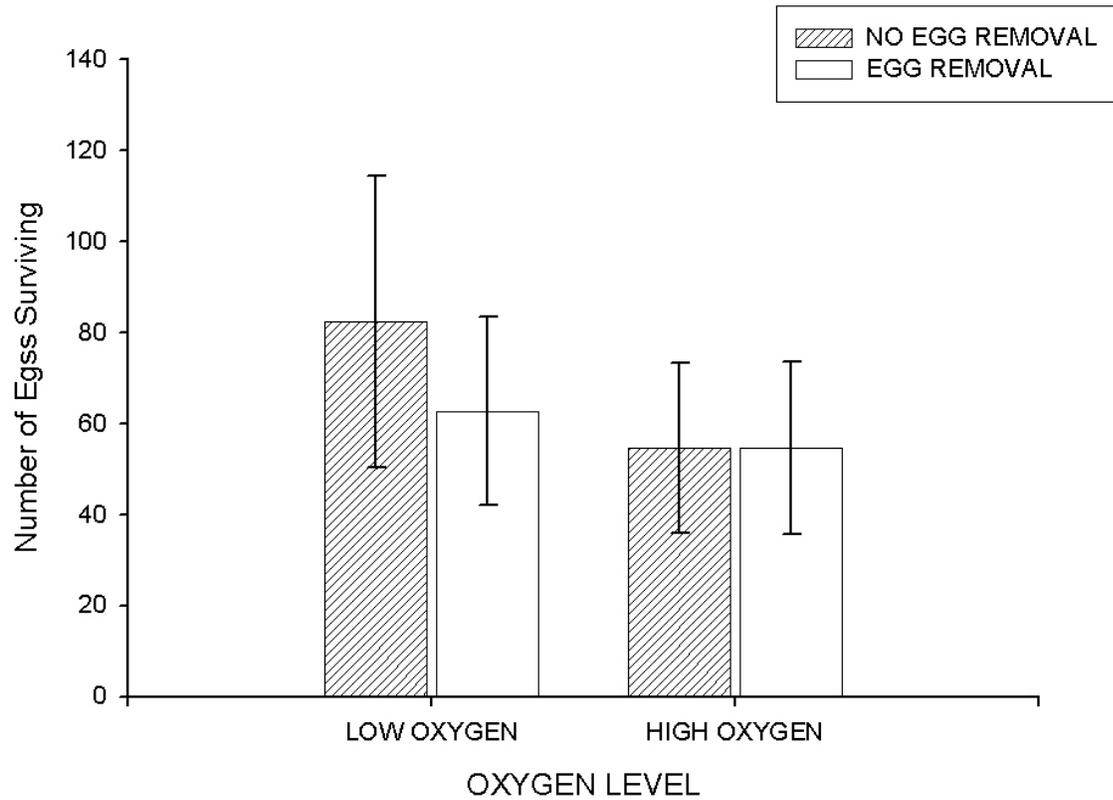


Figure 3-5. Simulated filial cannibalism: The effect of oxygen and egg removal on the total number of eggs surviving, including cases of both whole and partial clutch death. Egg removal did not significantly reduce the total number of eggs surviving. Bars represent means and error bars are standard error.

CHAPTER 4 SELECTIVE FILIAL CANNIBALISM IN THE SAND GOBY

Introduction

Filial cannibalism is an evolutionary mystery. It is difficult to imagine how regularly consuming one's own viable young represents an adaptive strategy, yet filial cannibalism is prevalent in a range of animals, particularly fishes exhibiting paternal care of eggs (discussed in Manica 2002; Klug and Bonsall 2007). Typically, filial cannibalism is viewed as an adaptive trade-off in which energy gained from eggs is used to better care for remaining offspring, or for increasing future reproduction (Rohwer 1978; Sargent 1992; Manica 2002). Because energy is such an obvious and direct benefit of filial cannibalism, much of the work aimed at understanding the adaptive significance of filial cannibalism has focused on energetic benefits (reviewed in Manica 2002). However, some have suggested that energetic benefits alone are unlikely to explain the prevalence of filial cannibalism in natural systems (e.g. Smith 1992; Payne et al. 2002; Klug et al. 2006 and Chapter 3).

Recent theoretical work suggests that the ability to cannibalize offspring selectively in relation to aspects of offspring phenotype (e.g., quality or egg maturation rate) can directly favor the evolution of filial cannibalism (Klug and Bonsall 2007 and Chapter 6). While the idea of weeding out inferior offspring has been documented in other contexts (Forbes & Mock 1998; e.g. selective abortion in humans: Stearns, 1987; Forbes 1997; Diamond 1987; Hesketh & Xing 2006; selective abortion in plants: Burd 1998; Karkkainen et al. 1999; Møller & Klinkhamer 2001), it has not yet been explicitly evaluated in relation to filial cannibalism (but see Mrowka 1987 and Kraak 1996 for work on the consumption of unfertilized or diseased eggs, and Neff and Sherman 2003 regarding egg cannibalism of non-kin). Indeed, the relationship between offspring phenotype and filial cannibalism remains unknown. One study found preferential cannibalism of

younger eggs when within-brood variation in egg age existed (Salfert and Moodie 1985), but in general, little is known about the specifics of which eggs are consumed when a parent does decide to cannibalize. Hence, the importance of selective filial cannibalism remains unknown.

To begin to understand the potential importance of selectivity in filial cannibalism, I evaluated patterns of within-brood cannibalism in the sand goby, *Pomatoschistus minutus*, a fish in which males alone provide parental care and practice filial cannibalism during the egg stage. My primary goal was to determine if males practice selective cannibalism (i.e., non-random consumption of eggs with regard to some aspect of egg phenotype). Specifically, I focused on the relationship between egg size and partial clutch filial cannibalism (i.e., the consumption of some eggs present during a given reproductive bout) by males. Egg size is correlated to larva size in this species (H.K., unpublished data) and has been correlated with post-hatching survivorship in a range of fishes (discussed in Kamler 2005). I considered cases in which males received eggs from one or two females. For the case in which males had eggs from only one female, I asked whether males exhibited a preference for eggs of a particular size range. When males had eggs from multiple females, I was interested in whether males 1) preferentially consumed eggs of the first or the second female that they spawned with, and 2) showed any preference with regard to egg size for each of the clutches in a nest (i.e., female 1's and female 2's clutches). I also compared the size of female 1's and female 2's eggs to determine if any differences in egg size existed between the females, and if so, whether these differences might explain the patterns of cannibalism observed.

Materials and Methods

Experimental Design

I evaluated selective filial cannibalism in the sand goby using data from two years. In both years adult sand gobies were collected in shallow brackish water using a seine near Tvärminne

Zoological Station (University of Helsinki) in southern Finland. All fish were fed *ad libitum* live Mysid shrimp and frozen *Chironomidae* larvae throughout the studies.

Multiple-female set-up: In 2006, I initiated each replicate by placing a single male and a single female (female 1) in an aquarium equipped with continuous flow-through seawater system. Each nest contained a half-flowerpot (8 cm diameter) which served as the nesting site. The inside of each nest was fitted with a transparent piece of plastic onto which females spawn their eggs. The transparent plastic allowed me to remove and photograph the eggs, when necessary. The male-female pair was allowed to spawn, and immediately after spawning, I removed the nest with eggs, digitally photographed the eggs, and cut out and removed a small subset of eggs (20-30 eggs) from the plastic transparency. I reared the subset of eggs in the absence of the male (described below) to determine if any size-specific patterns of egg mortality existed. I then returned the nest with eggs to the male, and a second female (female 2) was placed in the tank. The male and second female were then allowed 24 h to spawn (only clutches in which the second female spawned within 24 h of the first spawning were used in this experiment). After spawning, I again removed and photographed the eggs, and I removed a small subset of eggs. The nest with eggs was then returned to the male. Only cases of partial-clutch cannibalism were considered in the present study, as I was interested in within-brood patterns of cannibalism. I followed all eggs until hatching and visually inspected the nests daily by shining a light into the nest. Just prior to hatching (i.e., 1-3 days before hatching), eye shine (i.e., reflection from a flashlight) becomes visible in the developing embryos, and this is an indication that the eggs are about to begin hatching. When eye shine was visible in the eggs, I removed the nest and photographed the plastic transparency with eggs.

The subsets of removed eggs were reared in individual plastic containers, each equipped with an airstone. Water in the plastic containers was changed daily using water from the flow-through system, and the water temperature in these containers was maintained at approximately 16°C.

Single-female set-up: For the single male-single female trials, I retrospectively analyzed digital images collected from a previous experiment conducted in 2004 (Klug et al. 2006 and Chapter 3) in the same location using the same population of fish. In this case, I placed a male and female in an aquarium equipped with continuous sea water flow-through and a half flowerpot nest (8 cm diameter) equipped with a plastic transparency. Immediately after spawning, the nest and eggs were removed and photographed. In this case, I then transferred the clutch, on its plastic sheet, to a nest of intermediate size (6 cm diameter) and returned the nest with eggs to the male (see Chapter 3 for additional details). I only used clutches from the low density, high oxygen treatments (Klug et al. 2006 and Chapter 3) in the present study, as this set-up was most comparable to the design used in 2006 (described above). Again, only cases of partial clutch cannibalism were considered. I followed all eggs until hatching, and I visually inspected the eggs daily by shining a light into the nest. When eye shine was visible in the nest, I removed the nest and photographed the plastic transparency with eggs.

Image Analysis

For each male's eggs in 2006 (the multiple-female scenario), I superimposed the image immediately following female 1's spawning and the image immediately following female's 2. I then identified all eggs and labeled them as belonging to either female 1 or female 2. The image following female 2's spawning (in which all eggs have now been identified) was then superimposed with the final image taken just before hatching. I then determined the specific eggs that had been consumed. Using Sigma Scan Pro 5.0 (SPSS, Inc.) and the image containing the

spawn of female 1 and 2, I quantified the initial diameter of 1) a random subset of female 1's eggs and female 2's eggs (range: 25-75 eggs of each female) and 2) a subset of the specific eggs consumed (range: 5-45 eggs of each female). For each male's eggs in 2004 (the single-female scenario), I superimposed the initial and final image to determine which eggs had been consumed. I then used Sigma Scan Pro 5.0 (SPSS, Inc.) to quantify the initial diameter of 1) a random subset of the eggs (range: 35-80 eggs) and 2) a subset of the specific eggs consumed (range: 10-38 eggs). These data allowed me to quantify the initial size distributions of 1) all eggs in a nest and 2) the eggs that were consumed. This, in turn, allowed me to estimate cannibalistic preference for eggs of varying size classes (described below), while taking into account the initial abundance of eggs of varying sizes.

Preference Calculation

I was interested in whether males preferentially consumed 1) eggs of female 1 or female 2 (for the multiple-female data), and/or 2) eggs of a particular size class (for both the multiple- and single-female data). To assess whether males consume eggs in some non-random way, I used the preference measure α (with the i^{th} component α_i ; Manly et al. 1972; Chesson 1983). This preference measure has been used widely in studies of foraging (discussed in Chesson 1983). It is an ideal measure of preference for my purposes because it allowed me to account for 1) the initial abundance of eggs of varying sizes and 2) the depletion of eggs of varying size due to cannibalism. I calculated measures of egg preference in relation to preference for female 1's eggs and for female 2's eggs, and for eggs of given size classes. Preference for each egg type (i) was calculated as follows:

$$\hat{\alpha}_i = \frac{\ln((n_{i0} - r_i)/(n_{i0}))}{\sum_{j=1}^m \ln((n_{j0} - r_j)/(n_{j0}))} - \frac{i}{m}, \text{ where } i = 1, \dots, m \quad (4-1)$$

where n_{i0} is the number of eggs of type i present initially, r_i is the number of eggs of type i consumed by the male, and m is the total number of different egg types present (modified from Manly et al. 1972 and Chesson 1983). For this measure of preference, 0 indicates no preference (i.e. consumption is equivalent to what is expected if males randomly consume eggs), a positive value reflects consumption that is greater than would be expected from random consumption (i.e. a preference for that egg type exists), and a negative value suggests that consumption is less than what would be expected from random consumption.

Based on my data (i.e., the range in observed egg size and patterns of consumption), I had sufficient resolution to identify 4 size classes for each brood of eggs. I calculated four equal size classes (i.e., small, small-medium, medium-large, and large) for each brood by dividing the range in egg diameter for a given brood by four. For the single-female data, I calculated preference for each of the 4 size classes ($\hat{\alpha}_{small}$, $\hat{\alpha}_{small-medium}$, $\hat{\alpha}_{medium-large}$, and $\hat{\alpha}_{large}$). In this case, if there was no preference for any particular size class of eggs, I would expect

$\hat{\alpha}_{small} = \hat{\alpha}_{small-medium} = \hat{\alpha}_{medium-large} = \hat{\alpha}_{large} = 0$. For the 2006 data, I estimated preference for 4 size classes for each of the two females, and thus, there were a total of 8 egg types. Again, if there was no preference for eggs of a particular female or egg size, I would expect

$$\hat{\alpha}_{fem.1small} = \hat{\alpha}_{fem.1small-medium} = \hat{\alpha}_{fem.1medium-large} = \hat{\alpha}_{fem.1large} = \hat{\alpha}_{fem.2small} = \hat{\alpha}_{fem.2small-medium} = \hat{\alpha}_{fem.2medium-large} = \hat{\alpha}_{fem.2large} = 0$$

Statistical Analyses

I analyzed all preference data using non-parametric Friedman ANOVA. I used t-tests to examine differences in mean egg diameter between female 1 and female 2 in 2006, and to compare mean egg diameter in 2004 versus 2006. Given the differences in experimental set-up

between years, I compared mean egg density between 2004 and 2006 using a t-test. Linear regressions were used to examine the relationship between mean egg diameter and egg survival, and between mean egg diameter and egg development rate (i.e. time from spawning until hatching) for the subsets of eggs reared in the absence of males. For the regression between egg diameter and development time, one clutch contained visible fungus and was excluded from this analysis, as fungus increases the rate of egg development in this species (H. Klug, personal observation). In both cases, means were taken for the subsets from female 1 and female 2 for a given male to avoid pseudoreplication.

Results

Differences in Egg Size, Egg Density, and Cannibalism Rates between Years

There was no significant difference between the mean egg diameter of female 1 and of female 2 in 2006 (paired t-test, $t = -0.51$, $df = 6$, $p = 0.62$; female 1 mean \pm SE egg diameter: 0.61 ± 0.013 mm; female 2 mean \pm SE egg diameter: 0.62 ± 0.011 mm). Eggs tended to be slightly larger in 2006 in comparison to 2004 (2004 mean \pm SE egg diameter: 0.58 ± 0.018 mm; 2006 mean \pm SE egg diameter: 0.62 ± 0.011 mm), but this difference was not significant (independent samples t-test, $t = -1.79$, $df = 10$, $p = 0.10$). Additionally, egg density did not differ significantly between years ($t = -0.12$, $df = 10$, $p = 0.91$; 2004 mean \pm SE: 1.42 ± 0.27 eggs/mm²; 2006 mean \pm SE: 1.45 ± 0.12 eggs/mm²). In 2004 males consumed 32.1 ± 0.12 % (mean \pm SE) of their eggs, and in 2006 males consumed 36.2 ± 0.079 % (mean \pm SE) of their eggs. There was no significant difference in the proportion of eggs cannibalized between the years (t-test, $t = -0.30$, $df = 10$, $p = 0.77$).

Egg Size, Survivorship, and Development Time in Eggs Reared in the Absence of Males

There was no relationship between egg size and egg survivorship (linear regression, $F_{1,8} = 0.14$, $p = 0.72$). However, egg size was positively correlated with development time, suggesting that larger eggs take longer to develop (linear regression, $F_{1,5} = 13.85$, $p = 0.02$; Figure 4-1).

Cannibalistic Preferences by Males

In the single-female scenario, males exhibited no significant size preferences ($\chi^2 = 2.25$, $df = 3$, $p = 0.522$; Figure 4-2 A). In other words, for each given size class (i.e. small, small-medium, medium-large, and large), the relative abundance of eggs consumed was comparable to the initial relative abundance of eggs of that size class (Figure 4-3 A), and this pattern of cannibalism is consistent with random consumption of eggs with regard to size. However, males exhibited significant preferences in the multiple-female scenario ($\chi^2 = 15.13$, $df = 7$, $p = 0.034$; Figure 4-2 B), and specifically, males exhibited a significant preference for the larger eggs of female 2 (Figure 4-2 B). In this case, the relative abundance of female 2's medium-large and large eggs that were consumed was greater than the relative abundance of those eggs that were present initially (Figure 4-3 B).

Discussion

Male sand gobies cannibalized eggs selectively, but only in some cases. When males received eggs sequentially from two females, they preferentially consumed the larger eggs from the second female only. Thus, my results suggest that sand goby males exhibit non-random preferences for eggs when they spawn sequentially with two females. These patterns raise several questions. First, why do males prefer larger eggs in some cases, but not others, and in particular, what distinguishes female 2's larger eggs from those of female 1?

It is possible that energetic benefits play a role in cannibalistic preferences-- larger eggs likely provide a male with more energy (Kamler 2005), and filial cannibalism is thought to be a

way in which caring parents attain energy to offset costs of care (Rohwer 1978; Manica 2002). Thus, it wouldn't be surprising if males maximized their per-offspring energetic gain. However, males didn't always consume larger eggs-- they exhibited no size preference for female 1's eggs in either 2004 or 2006. If males were attempting to maximize their per-offspring energetic gain, we would have expected them to consume larger eggs in all cases. This was not the case, and thus, it does not appear that energetic gain alone can explain the patterns of cannibalism observed in the sand goby.

Alternatively, it is possible that the preference for the larger eggs of female 2 is associated with decreased duration of care and the ability to re-enter the mating pool sooner. Larger eggs took longer to develop, and the eggs of female 2 were already several hours (i.e., up to 24 h) behind those of female 1. Thus, the larger eggs of female 2 would likely hatch later and require a longer duration of care than female 1's eggs and the smaller eggs of female 2. Perhaps consuming the larger eggs of female 2 allows a male to decrease time spent caring for the current brood, thereby allowing him to re-enter the mating pool sooner. This hypothesis seems particularly relevant for sand gobies, which live only one year and have multiple brood cycles over a six-week period. During a given brood cycle, males receive eggs for just a few days and then enter a 'care-only' phase during which they do not receive additional eggs until their current brood hatches (typically 7 - 15 days from spawning). Indeed, my results suggest that preferentially consuming larger eggs potentially reduces the duration of care for a given clutch by several days (Figure 4-1). It is easy to imagine how even a small reduction in the duration of care over multiple brood cycles might allow a male an additional brood cycle, which in turn might increase the total number of eggs he receives over the breeding season. This hypothesis is consistent with some theoretical work (Chapter 6 and Klug and Bonsall 2007), which suggests

that parental fitness is highly sensitive to the maturation rate of eggs. Specifically, I suggest (Chapter 6 and Klug and Bonsall 2007) that males potentially benefit by consuming eggs that take longer to develop, and that the consumption of slower developing eggs can directly facilitate the evolution of filial cannibalism. However, consuming larger eggs likely comes at a cost, as egg size is correlated with larva size in the sand goby and larger eggs have been shown to have higher post-hatching survival in a range of fishes (Kamler 2005). These ideas warrant further attention, and in particular, more work is needed to understand factors affecting the optimal duration of care in this species and others.

In summary, I have demonstrated that male sand gobies can cannibalize eggs selectively with regard to the order in which those eggs are laid and the size of eggs in some contexts. However, in this case, size *per se* does not appear to be the factor influencing cannibalism. Rather, males seem to be sensitive to the expected development rate of eggs. More work is needed to further understand specific costs and benefits of consuming eggs of a particular size and expected developmental rate. Additionally, it will be important to assess the relationship between other aspects of egg phenotype and filial cannibalism in this and other species.

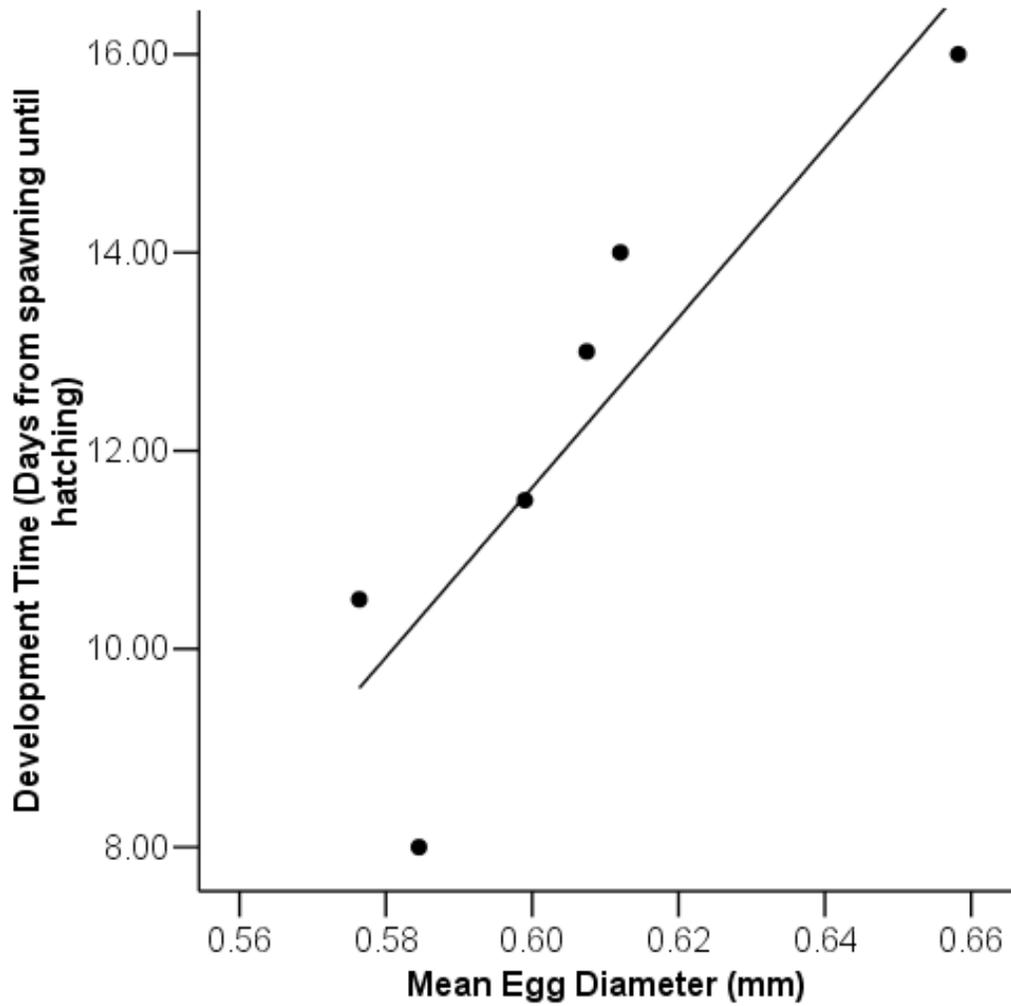


Figure 4-1. Relationship between initial egg size and development time (i.e. the number of days from spawning until hatching) in eggs reared in the absence of males.

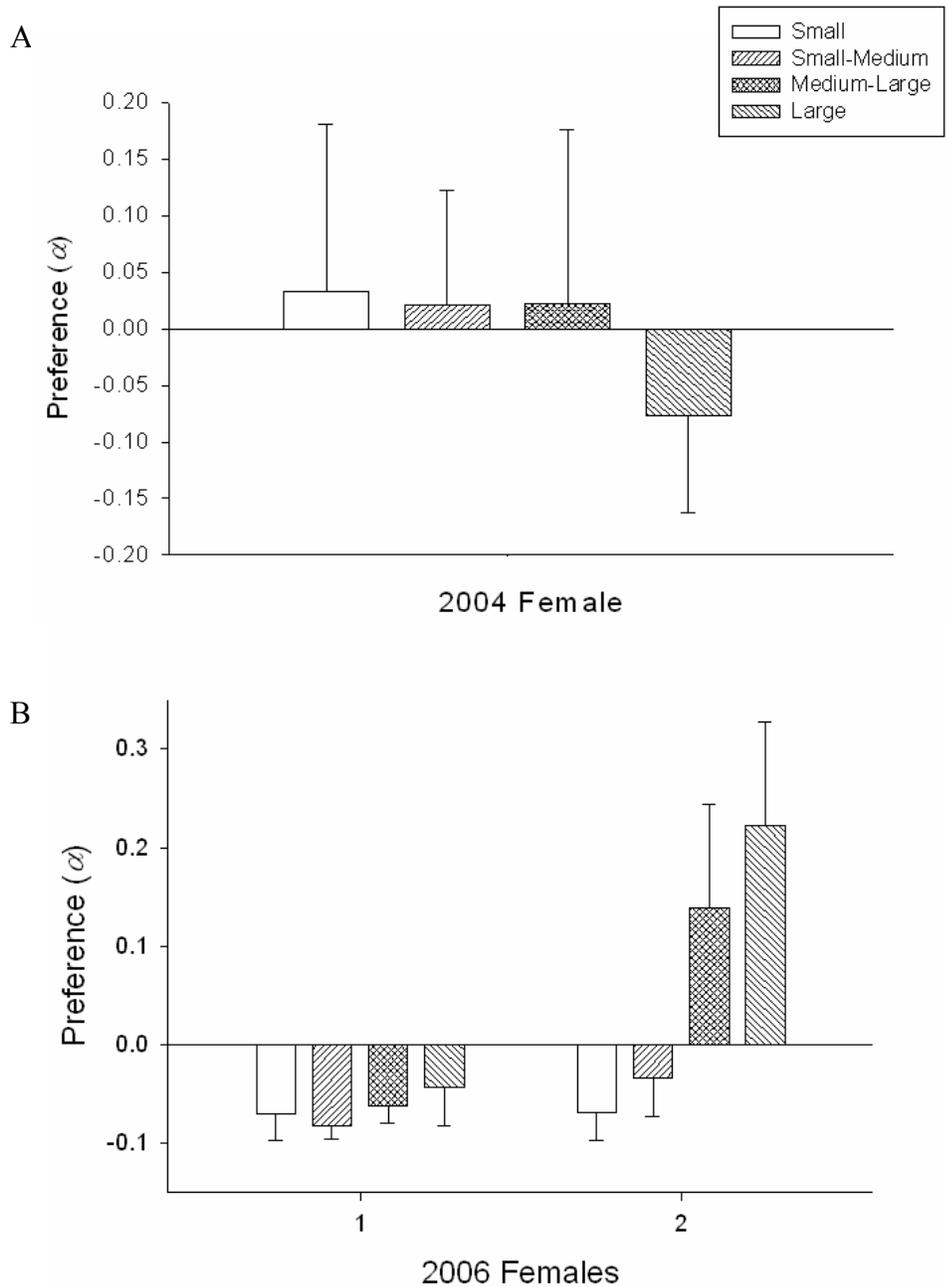


Figure 4-2. Preferences ($\hat{\alpha}$) in egg consumption by parental males. Male preferences for A) 4 size classes of eggs (labeled here as small, small-medium, medium-large, and large) when each male mated with a single female in 2004 and B) 4 size classes of eggs from two females when males mated sequentially with 2 females in 2006. Bars represent means and error bars are standard error.

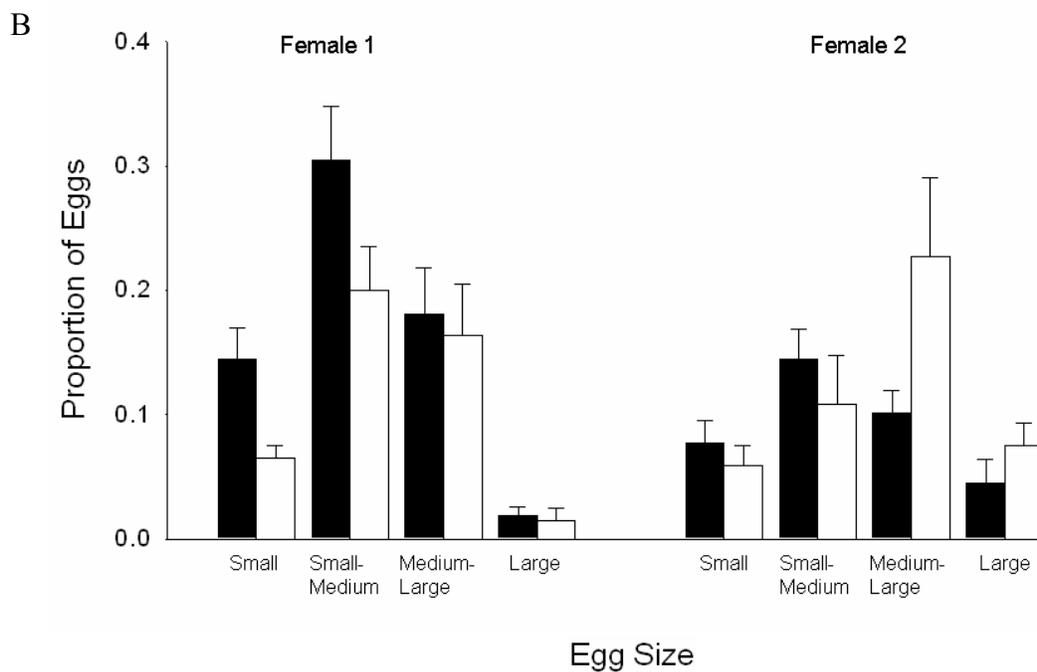
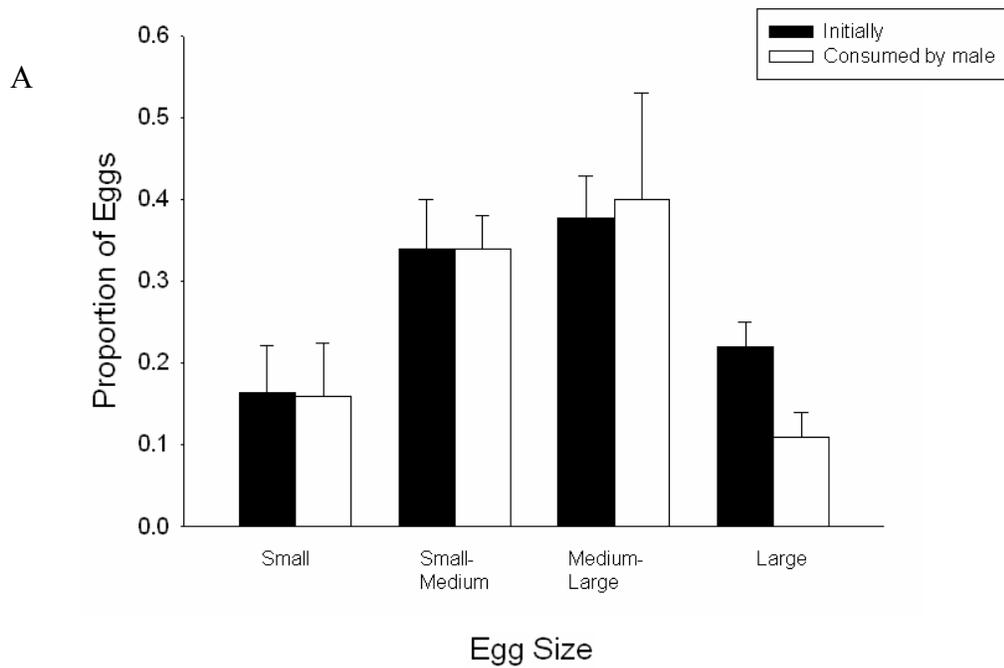


Figure 4-3. Distribution of egg size initially and in the male diet. The mean (\pm S.E.) proportion of eggs that were either small, small-medium, medium-large, or large initially, i.e. on Day 1 of each replicate (filled bars), and the mean (\pm S.E.) proportion of eggs consumed by males (open bars) that were either small, small-medium, medium-large, or large in A) 2004 and B) 2006.

CHAPTER 5 SELECTIVE FILIAL CANNIBALISM IN THE FLAGFISH

Introduction

Filial cannibalism commonly co-occurs with parental care in many animals and has been particularly well-documented in fishes exhibiting paternal care during the egg stage (Polis 1981; Manica 2002). While parental care typically increases offspring survival (discussed in Clutton-Brock 1991), filial cannibalism involves the killing of one's own young. It is difficult to imagine how such a behavior could represent an adaptive strategy. Indeed, prior to the 1970s filial cannibalism was dismissed as a rare behavior with little or no evolutionary significance (discussed in Manica 2002). However, filial cannibalism has now been well-documented in nature, and in many species caring parents consume more offspring than would die naturally. In recent years, much empirical and theoretical work has focused on understanding the adaptive significance of filial cannibalism (reviewed in Manica 2002). Currently, filial cannibalism is thought to be an adaptive strategy, and specifically, some have suggested that filial cannibalism involves an adaptive trade-off in which parents gain energy or nutrients from eggs, which they then use to better care for their remaining offspring or re-invest in future reproduction (energy-based hypothesis: Rohwer 1978; Sargent 1992; reviewed in Manica 2002). According to this hypothesis, whole clutch cannibalism (i.e., the consumption of all offspring present during a given reproductive bout) represents an investment in future reproduction, whereas partial clutch cannibalism (i.e., the consumption of only some offspring present) can either be an investment in future or current reproduction. Alternatively, others have suggested that by reducing egg density in the nest, partial clutch filial cannibalism can improve egg survivorship of remaining offspring, thereby increasing overall egg survival (oxygen-mediated hypothesis: Payne et al. 2002, 2004; density-dependent egg survival hypothesis: Klug et al. 2006). However, neither energetic need

nor density-dependent egg survival can explain the prevalence of filial cannibalism in natural systems. Indeed, filial cannibalism is not affected by energetic need in some species (Belles-Isles and Fitzgerald 1991; Lindström and Sargent 1997) and continues to occur when egg density is relatively low in others (Klug et al. 2006 and Chapter 3). Thus, the evolutionary significance of filial cannibalism remains unclear in many systems.

Alternatively, recent theoretical work suggests that the ability to selectively cannibalize offspring that have reduced phenotypic quality can independently facilitate and play a key role in the evolution of filial cannibalism (Klug and Bonsall 2007 and Chapter 6). The elimination of lower quality offspring has been demonstrated in relation to selective embryo abortion in humans and plants (Forbes 1997; Diamond 1987; Burd 1998; Karkkainen et al. 1999), brood reduction (Mock and Forbes 1995; Mock and Parker 1997; Forbes and Mock 1998), and parents allowing or encouraging siblicide of low quality offspring (Mock and Parker 1997; Stearns 1987). Because the elimination of low quality offspring is thought to play a central role in explaining the evolutionary significance of offspring abandonment and brood reduction (e.g., Stearns 1987, 1992; Forbes and Mock 1998), it is surprising that the relationship between offspring quality and filial cannibalism has received little attention. While some studies have found a relationship between filial cannibalism and uncertainty of paternity (Neff 2003; Gray et al. 2007; Frommen et al. 2007) or egg age (Salfert and Moodie 1985; Sikkell 1994), little is known about the relationship between offspring quality and filial cannibalism of viable young (see also Kraak 1996, for discussion of cannibalism of diseased eggs). Thus, the general importance of selective filial cannibalism remains unclear.

The first step in understanding the potential importance of selective filial cannibalism is to determine whether parents that provide care preferentially consume eggs with regard to some

aspect of offspring quality. Here, I examine the relationship between one aspect of offspring quality, egg energy content, and filial cannibalism in the flagfish (*Jordanella floridae*). Egg energy content was used as a proxy for quality because energy content and size have been strongly and positively correlated with post-hatching survival and growth (and hence fitness) in a range of fish species (reviewed in Kamler 1992, 2005; Keckeis et al. 2000; Brownman et al. 2003). In addition, I examined the relationship between filial cannibalism and maternal condition and size, because maternal effects on egg quality have been well-documented (Kamler 2005), and specifically, because a positive relationship between female size and offspring quality has been found previously in fishes (reviewed in Kamler 2005).

Methods

Study Species

Flagfish males alone provide parental care of eggs (including nest guarding, cleaning, and fanning), filial cannibalism is prevalent (Klug & St. Mary 2005), and parental males are known to consume more eggs than die naturally (i.e., the rate of filial cannibalism is greater than the mortality rate; Klug et al. 2005). Thus, filial cannibalism does not function solely to clean the nest of dead or diseased eggs. Indeed, egg survival in the absence of parental males and predators is very high (> 90% egg survival), and thus, most egg mortality can be attributed to parental males. Flagfish typically live only one year in the wild, and both males and females mate multiply during a several month breeding season. Additionally, eggs are spawned and fertilized individually, and sneaking is not thought to occur in this species.

Experimental Design

The study was conducted April - July 2005 in Gainesville, Florida. All fish were collected from the Otter Creek/Waccasassa River drainage in Levy County, Florida within 20 days of the experiment. Fish of both sexes were housed in separate freshwater holding tanks. All

experimental aquaria were 36 L and equipped with air-driven filtration, a spawning mat (i.e. a 100 cm² ceramic tile with heavy, green acrylic felt carpet glued to the top of the tile), and three artificial plants. Throughout the experiment, all fish were fed *ad libitum* a diet consisting of algae tablets and frozen brine shrimp. During the experiment, all fish experienced a 14h:10h light:dark cycle and temperature was maintained at 26°C.

I initiated each replicate by randomly selecting and placing one male and one female in an aquarium. The male and the female were allowed to spawn, and immediately following spawning, I briefly removed the nest with eggs from the tank. I counted the number of eggs, and for a subset of the clutches (N = 18), I removed three eggs from the nest and used them in subsequent energy assays. No eggs were removed from the nests of six males, which allowed me to evaluate whether there was an effect of egg removal on filial cannibalism. In all cases, a clear acrylic divider containing multiple holes was used to physically separate the male and female following spawning, which ensured that all cannibalism was done by the male. After counting the eggs, I returned the nest with eggs to the male, who was allowed to care for the eggs until hatching. I counted the eggs daily by visually inspecting the nest. Eggs usually began to hatch on day four, and thus I measured egg survivorship through day three of each replicate. Eggs never became diseased or infected with fungus during the course of the study. I weighed and measured all experimental fish just prior to the start of each replicate. For five replicates, I did not obtain reliable weight measurements, and thus these fish were excluded from analyses involving parental condition or size. I used the condition measure K (where $K=100*\text{weight}/(\text{length})^3$; Williams 2000), which provides a size-independent estimate of physical condition, to evaluate the relationship between parental condition and the occurrence of filial cannibalism. I also

estimated the relationship between parental size and filial cannibalism, and weight and standard length (which were highly correlated) were used as estimates of size.

Energy Assays

I used dichromate oxidation technique (modified from McEdward and Carsons 1987) to quantify total energy content (i.e. J egg⁻¹) of each sampled egg. Egg energy content was compared to a glucose standard (1 - 4 J mL⁻¹). Specifically, I incubated each egg in 0.5 mL 70% phosphoric acid at 105°C for 15 min. I allowed the solution to cool to room temperature, and then oxidized the sample with 1 mL of 0.3% potassium dichromate in concentrated sulphuric acid at 105°C for 15 min. Samples were then diluted with 3.5 mL distilled water and I measured absorbance using a spectrophotometer (λ 440 nm). I calculated total energy by comparing the absorbance of each sample with that of the glucose standards. I performed energy assays on eggs from 18 clutches. Only intact eggs were used for the energy assays, and I was able to quantify the total energy of one egg in 12 clutches, two eggs in three clutches, and three eggs in two clutches. While it would have been ideal to measure a larger sample from each clutch, this was impossible because flagfish spawn relatively few eggs (typically < 100) and I wanted to minimize any effects of egg removal. Additionally, because there was greater variation in the per-egg energy content between clutches than within clutches (discussed in Results), a small within clutch sample of egg energetic content provided an estimate of the mean energy content of eggs within a given clutch.

Statistics

I used linear regression to evaluate the relationship between male and female condition (i.e. K) and size (i.e. weight and length); the relationship between the mean energy content per egg within a clutch and the number of eggs spawned; the relationship between the number of

eggs spawned or received and female and male condition and size; and the relationship between mean egg energy content and male and female condition and size.

Whole clutch cannibalism represents a termination of current reproduction, and therefore any benefit of whole clutch cannibalism is associated with future reproductive success. In contrast, benefits of partial clutch cannibalism can be associated with either increased current or future reproductive success. Because whole and partial clutch cannibalism likely represent different biological phenomena, I analyzed these data separately. First, I used stepwise logistic regression (remove if $p > 0.15$) to evaluate the relationship between whole clutch cannibalism and 1) male condition (i.e. K), 2) male size (i.e. weight), 3) female condition (i.e. K), 4) female size (i.e. weight), 5) the number of initial eggs present, and 6) mean energetic content per egg within a clutch. I then considered only cases of partial clutch cannibalism and used stepwise linear regression (remove if $p > 0.15$) to evaluate the relationship between the proportion of eggs consumed and 1) male condition (i.e. K), 2) male size (i.e. weight), 3) female condition (i.e. K), 4) female size (i.e. weight), 5) mean egg energy, and 6) the initial number of eggs present. To meet assumptions of normality, the proportion of eggs consumed was arcsin square root transformed. Data associated with the number of eggs consumed could not be transformed to meet assumptions of normality. Thus, I used spearman rank correlation tests to evaluate the relationship between the number of eggs consumed and male and female size (i.e. weight) and condition (i.e. K), mean egg energy, and the initial number of eggs present.

Results

Of the 24 males, 10 exhibited whole clutch cannibalism, 12 exhibited partial clutch cannibalism, and 2 males consumed no eggs. Excluding cases of whole clutch cannibalism, the mean (+/- SE) percentage of eggs cannibalized was 38.7 +/- 0.097 % (or 45.2 +/- 0.10 % excluding males who didn't exhibit any cannibalism). As mentioned previously three eggs were

removed from the nests of 18 males and no eggs were removed from the nests of 6 males. There was no effect of egg removal (i.e., removal of 3 eggs for subsequent energy assays) on whole clutch cannibalism (logistic regression, $\chi^2 = 0.523$, $df = 1$, $p = 0.465$) or partial clutch cannibalism (ANCOVA, $F_{1,12} = 2.20$, $p = 0.164$). On average, eggs contained $1.94 \pm 0.57 \text{ J egg}^{-1}$ (mean \pm SD). As mentioned previously, energy measurements were taken for multiple eggs for 5 clutches. In these cases, the mean energy content (\pm SD) was $2.01 \pm 1.07 \text{ J egg}^{-1}$. The standard deviation within a clutch ranged between 0.0094 to 0.089 J egg^{-1} , and was on average 0.042 J egg^{-1} . In all cases, the within clutch variation in energy content was much less than the between clutch variation in energy content.

Parental Condition and Size, Egg Energetic Content, and Egg Number

There was no significant relationship between male and female condition ($F_{1,19} = 1.84$, $p = 0.19$) or male and female size (weight: $F_{1,19} = 0.91$, $p = 0.35$; length: $F_{1,19} = 0.97$, $p = 0.34$). Additionally, there was no significant relationship between mean energy content of eggs and the number of eggs spawned ($F_{1,16} = 0.84$, $p = 0.37$), suggesting that there was not a clear trade-off between the number of offspring produced and the mean energy invested into those offspring within a given reproductive episode in this experiment.

There was no significant relationship between female condition and mean egg energy content (linear regression, $F_{1,25} = 0.37$, $p = 0.55$) or the number of eggs spawned ($F_{1,19} = 1.92$, $p = 0.18$). Likewise, there was no significant relationship between female size and the number of eggs spawned (weight: $F_{1,19} = 1.69$, $p = 0.21$; length: $F_{1,19} = 0.88$, $p = 0.36$). However, there was a significant relationship between female size and the mean egg energy content (weight: $r^2 = 0.41$, $F_{1,11} = 7.63$, $p = 0.02$; length: $r^2 = 0.42$, $F_{1,11} = 7.92$, $p = 0.02$; Figure 5-1 A).

There was no significant relationship between male condition and mean energetic content of eggs received (linear regression, $F_{1,11} = 0.08$, $p = 0.78$) or the number of eggs received ($F_{1,19} =$

0.53, $p = 0.53$). Likewise, male size was unrelated to the number of eggs received (weight: $F_{1,19} = 0.70$, $p = 0.41$; length: $F_{1,19} = 1.35$, $p = 0.26$). However, larger males received eggs that were on average more energetic (weight: $r^2 = 0.27$, $F_{1,11} = 5.33$, $p = 0.041$; length: $r^2 = 0.33$, $F_{1,11} = 7.29$, $p = 0.021$; Figure 5-1 B). As mentioned above, there was no relationship between male and female size, and thus, assortative mating does not explain these patterns.

Whole Clutch Cannibalism

There was no significant effect of initial egg number, male condition, male size, or female condition on the occurrence of whole clutch cannibalism, i.e., the proportion of clutches that were entirely eaten (stepwise logistic regression, $p > 0.15$ in all cases). However, whole clutch cannibalism was more frequent when the mean energetic content of eggs was relatively great (logistic regression, $\chi^2 = 6.71$, $df = 1$, $p = 0.01$; Figure 5-2 A) and when female size was greater ($\chi^2 = 4.73$, $df = 1$, $p = 0.03$; Figure 5-2 B).

Partial Clutch Cannibalism

When only cases of partial clutch cannibalism were considered, there was no relationship between male condition and the proportion of eggs surviving ($p > 0.15$), or the number of eggs consumed ($df = 10$, $t = -0.41$, $p > 0.05$). However, larger males tended to consume a smaller proportion of eggs ($F_{1,8} = 3.90$, $p = 0.10$; Figure 5-3 A), and they consumed significantly fewer eggs than smaller males (weight: $df = 10$, $t = -13.54$, $p < 0.01$; length: $df = 10$, $t = -2.45$, $p < 0.05$; Figure 5-3 B). Female condition was unrelated to the proportion of ($p > 0.15$) or the number of eggs consumed by males ($df = 10$, $t = -0.72$, $p > 0.05$). However, female size was negatively correlated with the proportion of eggs consumed (weight: $F_{1,8} = 11.77$, $p = 0.009$; Figure 5-4 A) and the number of eggs consumed (weight: $df = 10$, $t = -8.36$, $p < 0.01$; length: $df = 10$, $t = -5.21$, $p < 0.01$; Figure 5-4 B).

For cases of partial clutch cannibalism, egg energy was unrelated to the proportion of eggs consumed ($p > 0.15$), but there was a negative relationship between mean egg energy and the number of eggs consumed ($df = 8$, $t = -6.49$, $p < 0.01$; Figure 5-5). There was no significant relationship between the number of eggs initially present and the proportion of eggs ($p > 0.15$) or the number of eggs ($df = 12$, $t = 0.0266$, $p > 0.05$) consumed.

Discussion

Male flagfish preferentially cannibalized eggs laid by females of larger body size and when the mean energy content of eggs was high for cases of whole clutch cannibalism. Because egg size, egg energy, and maternal size are correlated with post-hatching survival and growth in fishes (reviewed in Kamler 2005), it appears that males are sacrificing high quality offspring for a relatively large energetic gain when they practice whole clutch cannibalism. With regard to partial clutch cannibalism, the number of eggs consumed increased as the mean energy content of eggs decreased. The energy-based hypothesis of filial cannibalism (Rohwer 1978; Sargent 1992) suggests that partial clutch cannibalism is a way in which males attain energy to offset costs of care (Manica 2002). If the function of filial cannibalism is to attain energy that can be reinvested in increased current or future reproduction (which I did not evaluate here), it seems likely that a male's energetic need can be satisfied by consuming a smaller number of eggs when those eggs have a relatively high energetic content. However, males in this experiment received food (i.e., algae and brine shrimp) *ad libitum*, and thus energetic need alone cannot explain the filial cannibalism observed in the present study. Alternatively, because egg energy content is likely correlated with subsequent offspring survival (Kamler 2005), it is possible that the negative relationship between the number of eggs consumed and mean energetic content of eggs suggests that males are investing more into offspring of relatively high quality. Similarly, males consumed a greater proportion of eggs spawned by relatively small females. While female size

was correlated with mean egg energy content, egg energy alone did not explain the proportion of eggs cannibalized. Because female body size is positively correlated with egg size and resistance to starvation and predation in a range of fishes (reviewed in Kamler 2005), it appears that males consumed a greater proportion of relatively low quality eggs when they practiced partial clutch cannibalism.

In summary, this experiment suggests that at least some aspects of offspring quality (i.e. egg energy, maternal size) affect both whole and partial clutch filial cannibalism, albeit in different ways. With regard to partial clutch cannibalism, males consume more of the lower quality offspring. This finding is consistent with previous work on the elimination of offspring via abandonment, siblicide, or infanticide, which focuses on the removal of low quality offspring (e.g., Mock and Parker 1997; Forbes and Mock 1998). Additionally, this finding is consistent with theoretical work suggesting that selective filial cannibalism of low quality offspring is beneficial to caring parents (Klug and Bonsall 2007 and Chapter 6).

However, with regard to whole clutch cannibalism, males are more likely to cannibalize higher quality offspring. This finding suggests that males are sensitive to the nutritional benefits of cannibalism, which is consistent with the idea that cannibalistic parents use eggs as an alternative food source (Rohwer 1978; Manica 2002). However, the specific finding that males sacrificed their higher quality offspring for increased energetic gain is not explicitly predicted by current theory. Indeed, previous work in the flagfish (Klug and St. Mary 2006 and Chapter 2) suggests that the energetic benefits of consuming eggs to male size or reproduction are relatively small in comparison to those of food. Thus, additional theoretical and empirical work is needed to better understand the expected trade-offs associated with filial cannibalism. In future studies,

it will be important to consider within-clutch patterns of cannibalism to better understand patterns of parental investment and filial cannibalism.

Finally, there was no relationship between initial egg number and whole clutch cannibalism in the present study. This finding is in contrast to some previous theoretical predictions (Rohwer 1978) and empirical findings (reviewed in Manica 2002) suggesting that whole clutch cannibalism is more common when clutch size is relatively small (but see Payne et al. 2003, who found that smaller clutches were not preferentially consumed). Similarly, there was no clear trade-off between the number of eggs spawned and the mean energetic content of those eggs. This trade-off is a key assumption of life-history evolution (Stearns 1987). However, it is likely that the scale of the present experiment, as well as other sources of variation, made it difficult to detect such a trade-off if one does indeed exist in the flagfish. Indeed, better understanding of female investment will necessitate an experiment specifically designed to assess such trade-offs over a longer time frame.

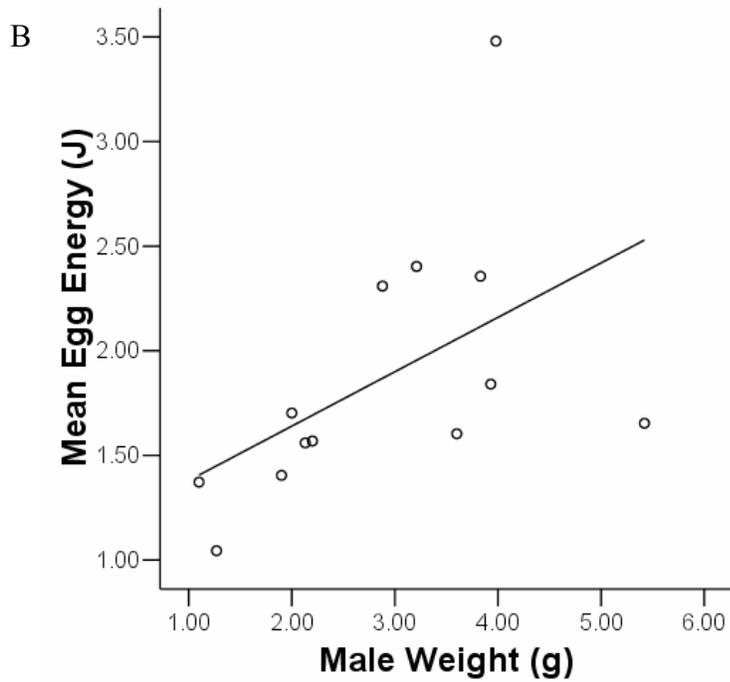
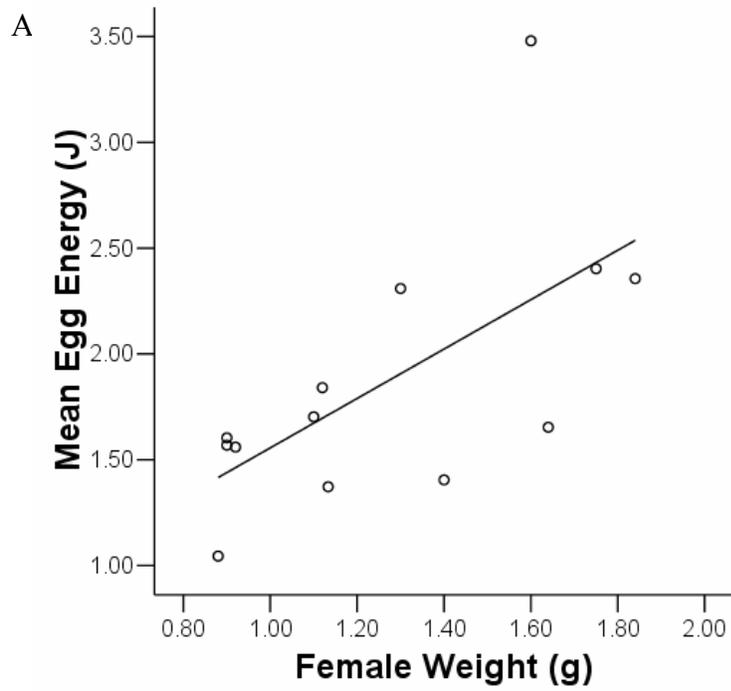


Figure 5-1. Relationship between the mean energy per egg (J egg^{-1}) within a clutch and A) female weight and B) male weight.

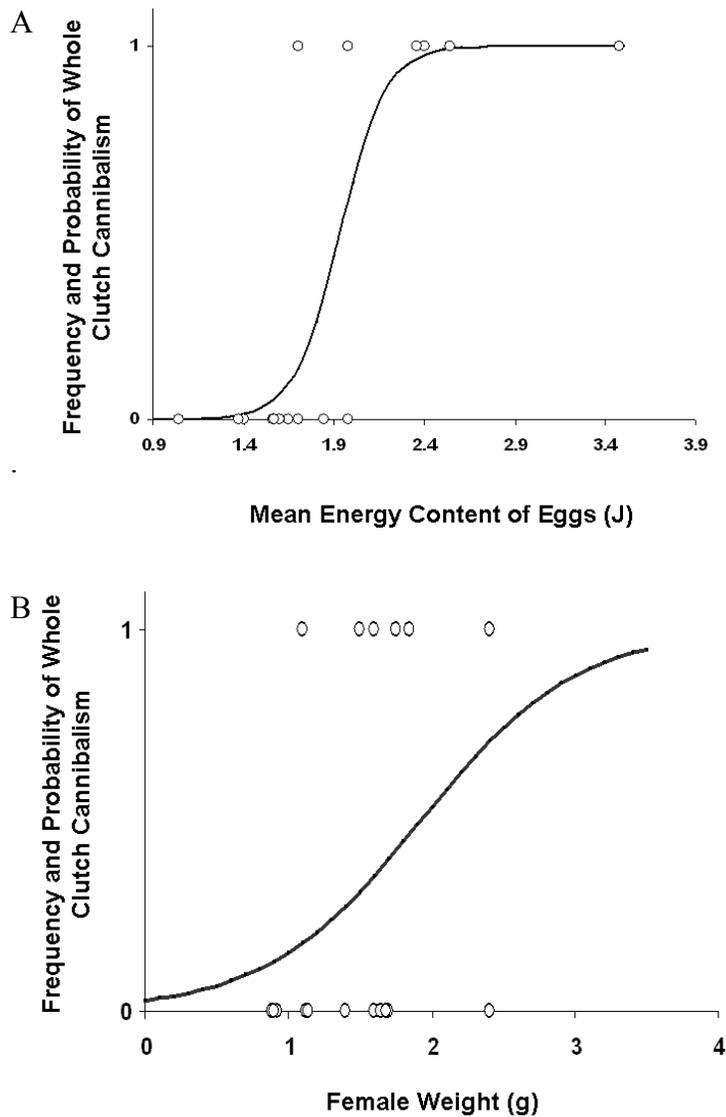


Figure 5-2. Relationship between the frequency of whole clutch cannibalism and A) the mean energy per egg (J egg^{-1}) within a clutch and B) female weight. Lines represent the predicted probability of whole clutch cannibalism as a function of A) mean egg energy or B) female weight, as determined by a logistic regression; for A) $y = 1 - \frac{1}{1 + e^{-15.38 + 7.97 \cdot x}}$ and (B) $y = 1 - \frac{1}{1 + e^{-3.58 + 71.86 \cdot x}}$, where y is equal to the probability of whole clutch cannibalism and x is equal to either mean egg energy A) or female weight B).

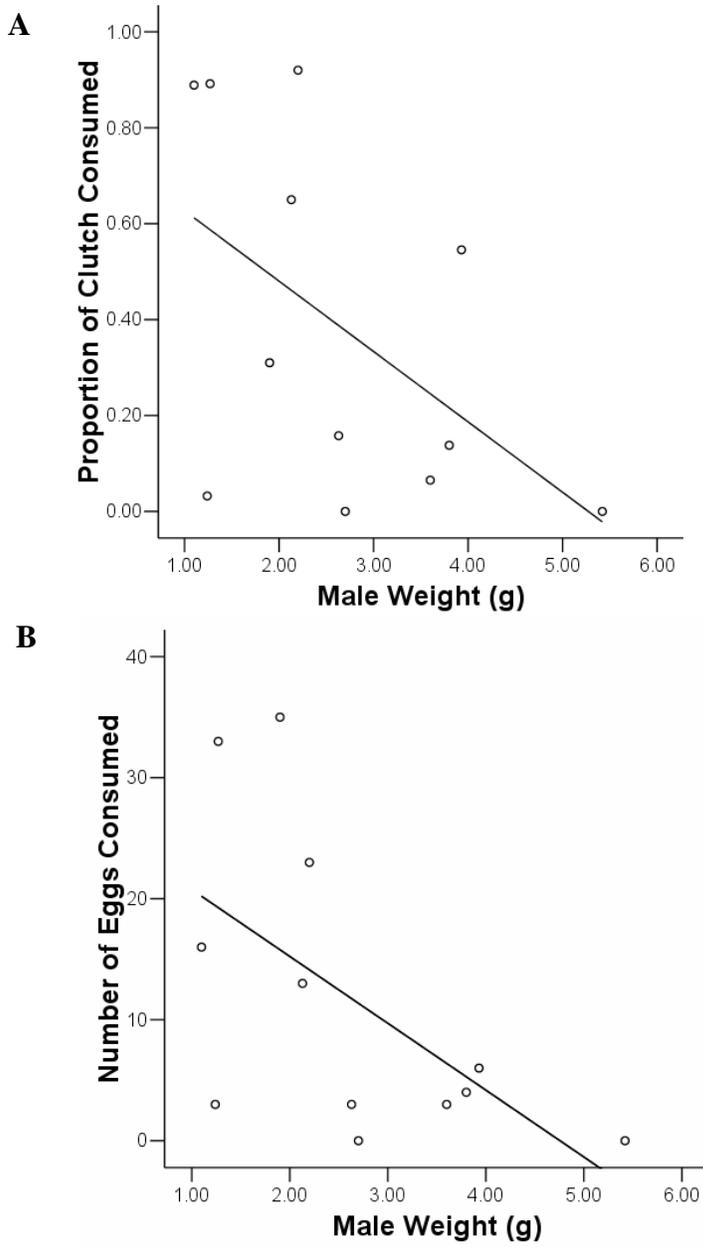


Figure 5-3. Relationship between male weight and A) the proportion and B) the number of eggs consumed for cases of partial clutch cannibalism.

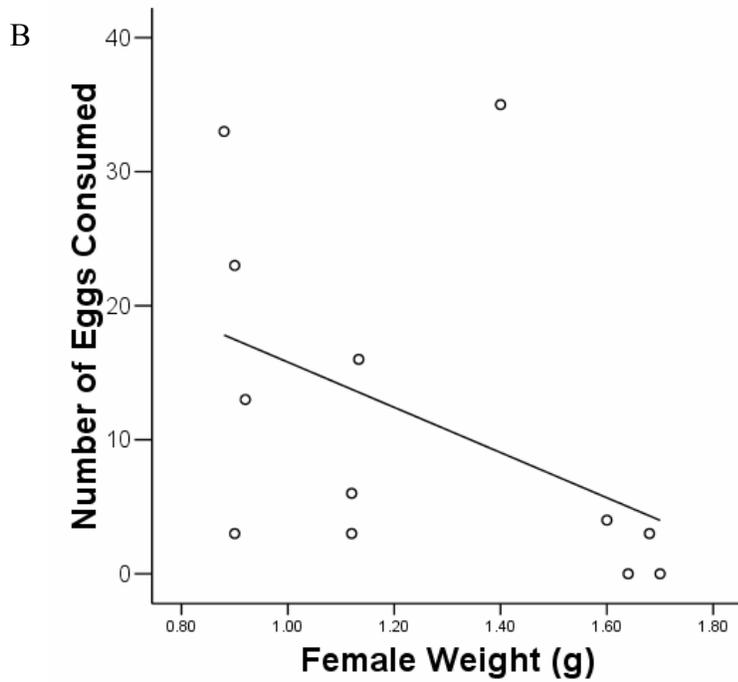
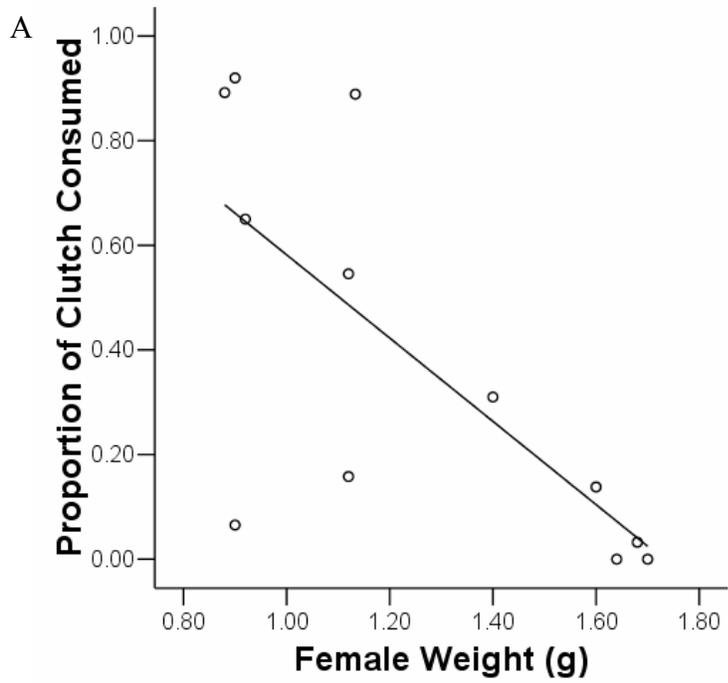


Figure 5-4. Relationship between female weight and A) the proportion and B) the number of eggs consumed for cases of partial clutch cannibalism.

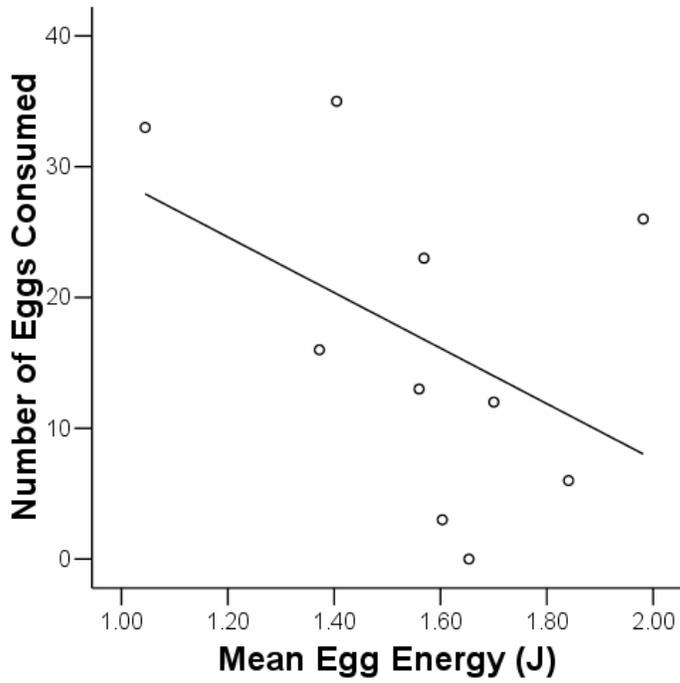


Figure 5-5. Relationship between the mean energy per egg (J egg^{-1}) within a clutch and the number of eggs consumed for cases of partial clutch cannibalism.

CHAPTER 6
WHEN TO CARE FOR, ABANDON, OR EAT YOUR OFFSPRING: A MODEL OF THE
EVOLUTION OF PARENTAL CARE AND FILIAL CANNIBALISM

Introduction

Adaptive theories of evolution typically suggest that parents should exhibit strategies that increase offspring survival, and parental care is one way in which parents are thought to achieve this (reviewed by Clutton-Brock 1991). Although parental care is assumed to increase offspring survival, filial cannibalism, the consumption of one's own viable offspring, commonly co-occurs with parental care. Indeed, filial cannibalism is prevalent in a range of taxa exhibiting parental care (Polis 1981; Elgar and Crespi 1992). For example, caring females consume some of their young in the bank vole (*Clethrionomys glareolus*, Klemme et al. 2006), the house finch (*Carpodacus mexicanus*, Gilbert et al. 2005), and the wolf spider (*Pardosa milvina*, Anthony 2003), and both parents of the burying beetle (*Nicrophorus orbicollis*) are known to consume their offspring (Bartlett 1987). Filial cannibalism has been particularly well-documented in fish species with paternal care during the egg stage (reviewed in Manica 2002). Indeed, because of its prevalence in fish systems, most theoretical and empirical work on filial cannibalism has focused on fish (but see Bartlett 1987, Thomas and Manica 2003, Creighton 2005). While early ethologists considered filial cannibalism a social pathology with little or no evolutionary significance, filial cannibalism is now typically thought to reflect an adaptive trade-off between current and future reproductive success (e.g., Manica 2002, 2004). However, despite much theoretical development and empirical work over the last few decades, the evolutionary significance of filial cannibalism remains unclear in many systems.

The most widely accepted hypothesis of filial cannibalism as an adaptive strategy suggests that energetic need is the primary factor leading to filial cannibalism, and that a caring parent gains energy and nutrients from consuming their offspring that are then reinvested into future

reproduction, thereby increasing net reproductive success (Rohwer 1978; Sargent 1992). Specifically, whole-clutch cannibalism (i.e., the consumption of all offspring during a given reproductive bout) is assumed to be an investment in future reproduction, whereas partial-clutch cannibalism (i.e., the consumption of only some offspring present) can represent an investment in either current or future reproduction. This energy-based hypothesis predicts that cannibalism will increase as food availability decreases and when parental condition is poor (Rohwer 1978; Sargent 1992). While food availability and/or parental condition affect the amount of cannibalism in some species (e.g., *Stegastes rectifraenum*, Hoelzer 1992; *Pomatoschistus microps*, Kvarnemo et al. 1998; *Abudefduf sexfasciatus*, Manica 2004), it has no effect in others (e.g., *Gasterosteus aculeatus*, Belles-Isles and Fitzgerald 1991; *Etheostoma flabellare*, Lindström and Sargent 1997), and in two systems cannibalism declines as male condition or food availability decreases (*Pomatoschistus minutus*, Klug et al. 2006 and Chapter 3; *Jordanella floridae*, Klug and St. Mary 2005 and Chapter 2). Other studies have examined whether eggs can provide a caring parent with sufficient energy to offset the costs of care. Again, the evidence is mixed-- two studies concluded that energy attained from filial cannibalism is sufficient to offset costs related to care (Kume et al. 2000; Thomas and Manica 2003), while in another, energy from eggs was found to be insufficient (Smith 1992). Thus, parental energetic need alone cannot explain the prevalence of filial cannibalism.

Alternatively, Payne et al. (2002) and Klug et al. (2006 and Chapter 3) suggested that filial cannibalism is mediated by density-dependent egg survivorship, and that by consuming some eggs in their nests, caring parents can improve the survivorship of the remaining eggs and increase their net reproductive success. Such density-dependent egg survivorship is potentially related to the physical environment (e.g., oxygen availability, Payne et al. 2002) or increased

benefits of parental care to the remaining offspring. The hypothesis of filial cannibalism mediated by density-dependent egg survivorship has received support in two marine fish species (*Stegastes leucostictus*, Payne et al. 2002; *Pomatoschistus minutus*, Klug et al. 2006 and Chapter 3), but has in general received little further empirical or theoretical examination (but see Payne et al. 2004). Likewise, some have suggested that filial cannibalism is a mechanism by which parents reduce brood size in response to anticipated resource competition amongst their adult offspring (Bartlett 1987; Creighton 2005) or kill offspring of reduced quality (Forbes and Mock 1998; see also Kozlowski and Stearns 1989). While the former hypothesis has received some attention in the burying beetle (Creighton 2005), neither of these hypotheses of filial cannibalism has been explicitly evaluated.

Because of the mixed empirical support for the energy-based hypothesis and the lack of empirical evidence regarding alternative hypotheses, filial cannibalism remains an evolutionary conundrum. Indeed, previous work suggests that a parent's energetic need (Rohwer 1978; Sargent 1992; Manica 2002), expectations regarding offspring survival or reproductive value (Payne et al. 2002; Neff 2003; Klug et al. 2006 and Chapter 3), competition for mates (Sikkel 1994; Kondoh and Okuda 2002), and anticipated offspring resource competition (Creighton 2005) are potentially important factors for explaining the adaptive significance of filial cannibalism. However, previous theory has tended to focus on each of these factors in separate theoretical contexts (e.g., energetic benefits of consuming offspring: Rohwer 1978; Sargent 1992; expectations regarding offspring survivorship: Payne et al. 2004; variation in offspring quality: Forbes and Mock 1998; mate availability: Kondoh and Okuda 2002), despite empirical evidence suggesting that it is unlikely that any single factor alone can explain the prevalence of filial cannibalism (e.g., Manica 2004; Klug et al. 2006 and Chapter 3).

Here, I develop a model of parental care, total offspring abandonment (i.e., no care), and filial cannibalism to begin to isolate the pivotal factors affecting the evolution of care and filial cannibalism. First, I determine the general conditions under which we would expect these strategies (i.e., care, no care/total abandonment, filial cannibalism) to evolve alone or in combination. I then evaluate the plausibility of multiple alternative hypotheses within a single theoretical context by assessing the importance of a range of potential costs and benefits of care and cannibalism. Specifically I focus on costs and benefits related to energetics, offspring survival and quality, mate competition, and general resource competition.

Methods

The model is set up as an ecological problem in which a rare mutant with a unique life-history strategy is allowed to invade a resident population (e.g., Vincent and Brown 2005). Specifically, the resident strategy represents the strategy that is currently exhibited by individuals in a population, and the mutant strategy is some alternative strategy not currently exhibited by individuals in the population. I assume that the resident strategy is in equilibrium (i.e., it is the strategy that currently prevails in the population) and that an alternative mutant strategy invades from rare into the population.

Because the general characteristics of an organism in one life-history stage (e.g., maturation rate, juvenile survival, adult mortality during the egg, juvenile, and adult stages) potentially affect the costs and benefits of strategies occurring in another life-history stage, I assume a stage-structured system in which individuals develop through an egg stage and a juvenile stage, and then mature and reproduce as adults. While in the egg stage, individuals can either be abandoned by parents, receive parental care, suffer filial cannibalism, or receive parental care and suffer filial cannibalism (Figure 6-1). Below, I outline the dynamics of a system in which a mutant with care and/or cannibalism invades a resident population that either

lacks or provides parental care. I then use mutual invasion analysis to explore the effects of costs and benefits of varying strategies on lifetime fitness and the evolution (i.e., invasion from rare and subsequent fixation) of parental care and/ or filial cannibalism.

Model Dynamics

I consider a stage-structured system (which is appropriate for many fish, bird, and insect systems) in which individuals pass through an egg (E), juvenile, and adult stage (A). The number of eggs increase as adults reproduce and decrease as eggs mature and as eggs die, such that:

$$\frac{dE}{dt} = r \cdot A(t) \cdot \left[1 - \frac{A(t)}{K} \right] - d_E \cdot E(t) - m_E \cdot E(t), \quad (6-1)$$

where r represents the rate of egg fertilization (i.e., a proxy for mean reproductive rate of adults), d_E represents death rate of eggs, and m_E is the rate at which eggs mature. I assume logistic population growth, where K represents population carrying capacity, and density-dependence associated with resource competition affects adult reproduction (i.e., the rate of fertilization). Adults in the population increase as eggs mature and survive the juvenile stage, and decrease as adults die, such that:

$$\frac{dA}{dt} = m_E \cdot E(t - \tau) \cdot \sigma_J - d_A \cdot A(t), \quad (6-2)$$

where τ is a time delay representing the juvenile stage, σ_J is survival rate through the juvenile stage, and d_A is the death rate of adults (Figure 6-1).

As mentioned above, I assume that the population exhibiting the resident strategy is in equilibrium. Specifically, the resident strategy is assumed to be fixed in the population (and on average, all individuals therefore have relative fitness equal to 1). Because 1) the resident strategy is fixed and 2) the resident population (which exhibits the strategy of interest) is regulated by density-dependence, the resident population is assumed to be in ecological

equilibrium (i.e., the population density is not increasing or decreasing). Because we know that a population in equilibrium is not increasing or decreasing (i.e. $A(t)$ and $E(t)$ both equal zero), I can analytically solve for the equilibrial densities by setting $A(t)$ equal to $E(t)$, and then algebraically solving for the adult and egg densities at equilibrium (A^* and E^*) The equilibrial densities in this model are thus

$$E^* = \frac{d_A \cdot A^*}{m_E \cdot \sigma_J} \quad (6-3)$$

$$A^* = K \cdot \left[1 - \left(\frac{\frac{d_E \cdot d_A}{m_E \cdot \sigma_J} + \frac{d_A}{\sigma_J}}{r} \right) \right]. \quad (6-4)$$

Resident and Mutant Trade-Offs

To explore the fixation of different strategies, I allowed rare mutants with different life histories to invade a resident population. I considered the following cases: 1) a rare mutant who provides parental care invades a resident population with no care (and no cannibalism), 2) a rare mutant who practices filial cannibalism invades a resident population with no care (and no cannibalism), 3) a rare mutant who provides parental care and practices filial cannibalism invades a resident population with no care and no cannibalism, and 4) a rare mutant who provides parental care and practices filial cannibalism invades a resident population that provides parental care (but does not cannibalize). The different life-history strategies are represented through the incorporation of appropriate trade-offs into the model (described below and in Table 6-1), and the model was analyzed using linear additive trade-offs and non-linear trade-offs (Table 6-1).

In cases in which parental care was provided (either by individuals in the resident population and/or by the rare mutant), I assumed that parental care increases the survivorship of eggs (i.e., as d_E decreases, parental care increases) and that receiving parental care during the

egg stage increases an individual's likelihood of surviving through the juvenile stage (i.e., the level of care received as an egg affects quality such that σ_J increases as d_E decreases). Providing parental care is assumed to be costly to the parent providing it, and thus, I assumed that the reproductive rate of adults (i.e., their rate of producing fertilized eggs) decreases and that the death rate of adults increases as care increases (i.e., r decreases and d_A increases as d_E decreases). Furthermore, in all cases in which care is provided, a decrease in the maturation rate of the eggs was associated with an increase in the reproductive rates of adults: the less time that an individual has to spend caring for a clutch of eggs, the greater that individual's reproductive rate will be (i.e., as m_E decreased, r increased).

When I considered the case of a rare mutant practicing filial cannibalism, I assumed some energetic benefit of cannibalism, such that the death rate of adults decreased and the reproductive rate of adults increased as cannibalism increased (i.e., d_A decreases and r increases as the rate of cannibalism, β , increases). A further goal of these analyses was to determine if cannibalism could evolve in the absence of a substantial benefit of cannibalism. In these analyses, I assume no direct benefit of cannibalism (i.e., there is no effect of β on d_A or r).

I analyzed the model both assuming that egg survivorship was density-independent and for the case in which egg survivorship was density-dependent. For the cases in which egg survivorship was assumed to be density-dependent, the death rate of eggs follows an increasing function in E , and I considered two functions:

$$d_E \cdot E^2, \text{ and} \tag{6-5}$$

$$d_E \cdot (1 + \omega \cdot E)^{-1}, \tag{6-6}$$

where ω is the strength of density-dependence (following Bellows 1981). I considered these two particular density-dependent functions because they are very general forms of density

dependence that are common in nature (Bellows 1981). The first function (eqn. 6-5) assumes that egg mortality increases exponentially as egg density increases; the second equation (eqn. 6-6) assumes that egg mortality increases with increasing egg density, but the increase is not exponential and the precise nature of this relationship is determined by ω . Specifically, a relatively large ω represents more intense density-dependence (i.e., a relatively great increase in mortality as density increases) and a relatively small ω represents relatively weak density-dependence (i.e., a relatively small increase in mortality as density increases).

Invasion Dynamics and Fitness

Under the density-independent egg survivorship scenario and the assumptions given above, the dynamics of the rare mutant are given by the following equations and by incorporating relevant trade-offs (Table 6-1):

$$\frac{dE_m}{dt} = r_m \cdot A_m(t) \cdot \left[1 - \frac{A_m(t)}{K_m} \right] - d_{E_m} \cdot E_m(t) - m_{E_m} \cdot E_m(t) - \beta \cdot E_m(t) \cdot A_m(t) \quad (6-7)$$

$$\frac{dA_m}{dt} = m_{E_m} \cdot E_m(t - \tau) \cdot \sigma_{J_m} - d_{A_m} \cdot A_m(t), \quad (6-8)$$

where β is the mutant's rate of cannibalism (β equals an average rate of cannibalism, which could represent some combination of whole- and partial-clutch cannibalism; $\beta = 0$ if the mutant does not cannibalize). Specifically, the rate of cannibalism is a function of the number of rare mutants in the population (A_m) and then number of eggs the mutant has (E_m). If the mutant does not cannibalize, $\beta = 0$. The mutant is assumed to be rare in the population, and thus, density-dependence operating on adult mutant reproduction occurs through competition with the resident.

To evaluate the life-history characteristics and trade-offs affecting the invasion of a rare, novel strategy, I calculated the fitness of individuals exhibiting the mutant strategy relative to the fitness of individuals exhibiting the resident strategy. The stage-structured nature of the model

and the time delay representing the juvenile stage makes it impossible to compute relative fitness from the differential equations above (eqns. 6-7 and 6-8). Instead, the lifetime fitness of the mutant can then be found from the determinant of the matrix describing the mutant's invasion dynamics:

$$\begin{pmatrix} \lambda + d_{Em} + m_{Em} + \beta & -r_m \cdot \left[1 - \frac{A^*}{K_m} \right] \\ -m_{Em} \exp(-\lambda \cdot \tau) \cdot \sigma_{Jm} & \lambda + d_{Am} \end{pmatrix}. \quad (6-9)$$

Hence, while some life-history parameters (e.g., fertilization rate of eggs, r) will be correlated with lifetime fitness under some scenarios, the real measure of fitness in this model is the eigenvalues of the invasion matrix. The eigenvalues represent the fitness (and hence the invasibility) of the mutant strategy relative to the resident strategy when both evolutionary factors (e.g., trade-offs between current and future reproduction) and ecological factors (e.g., resident population density, the intensity of competition amongst adults) are considered. To evaluate the invasion and replacement dynamics of a rare mutant that provides parental care and/or practices filial cannibalism, I used the fitness function of the mutant to calculate the evolutionary stable state(s) (i.e., when the rate of change in fitness is zero). I then performed mutual invasion analyses by evaluating when the fitness function is greater than zero (using a Newton-Raphson algorithm with the resident dynamics (A^*) set at equilibrium) for different values of a life-history trait (see Table 6-1 and Online Appendix in Klug and Bonsall 2007). I evaluated and present pairwise invasion boundaries for different values of maturation rate of eggs. Comparing the invasion potential with regard to maturation rate of eggs is ideal because: 1) it allows me to represent a wide range of life-history strategies, including faster and slower reproducers, and 2) preliminary results suggest that lifetime fitness is highly sensitive to maturation rate. Specifically, I illustrate the conditions for which 1) the mutant would invade and out-compete the resident, 2) the boundaries for which the resident would invade and out-compete

the mutant, 3) the putative coexistence range, in which the strategies have the potential to coexist, 4) a region of non-persistence, where neither strategy will persist (i.e., a region of extinction), and 5) a region in which neither strategy will persist or initial conditions of the model determine the strategy that invades. Local stability analyses were performed and are described in the Online Appendix of Klug and Bonsall (2007), and numerical simulations were performed to confirm that strategy coexistence occurs when the dynamics are stable and that regions of parameter space exist (labeled NP/IC and NP in Figures 6-2 through 6-6) where either neither strategy persists or the outcome is based on initial conditions. I evaluated the invasion potential of the rare mutant for several biologically relevant scenarios by changing the value(s) of a single life-history parameter of interest for the mutant and/or resident populations.

Biologically Relevant Comparisons

In addition to the fixed trade-offs reflecting varying life-history strategies (Table 6-1), I explicitly considered the effects of varying selective regimes (e.g., differential mating success associated with a particular strategy, effects of care or cannibalism on population resources and hence carrying capacity) on the invasion dynamics. To do this, I used pairwise comparisons in which I altered the magnitude of one (or more) parameter(s) to reflect a biological scenario of interest.

First, I evaluated the importance of offspring survival benefits of care on the invasion patterns of varying strategies. Empirically, parental care has been shown to reduce the death rate of offspring (discussed in Clutton-Brock 1991), and thus I compared the invasion patterns of the caring mutant for a range of cases in which care was effective (i.e., $d_{Em} < d_E$) to those in which it was ineffective (i.e., $d_{Em} = d_E$).

Second, sexual selection has been hypothesized to be a major force in the evolution and fixation of parental care (Andersson 1994; Baylis 1981). In some systems mate choice for a partner who will provide care is thought to affect the reproductive rate of the non-limiting sex (e.g., the number of eggs a caring parent receives per reproductive bout or over the course of the breeding season is correlated with parental care: *Jordanella flordiae*, St. Mary et al. 2001; *Pomatoschistus minutus*, Pampoulie et al. 2004). Likewise, filial cannibalism has been shown to increase the attractiveness of a caring parent's nest in some cases (e.g., Sikkel 1994) and might be preferred during mate choice if there are benefits of cannibalism to remaining offspring (e.g., through density-dependent egg survivorship). With regard to the model, if care or filial cannibalism is a trait that is preferred by one sex, we would expect the mutant exhibiting care or cannibalism to receive more fertilizations per time period (e.g., a breeding season or lifetime) than a resident who does not exhibit care. In this sense, r_m (i.e., egg fertilization rate in eqn. 6-7) of a mutant who exhibits a preferred trait would be expected to be greater on average than that of a resident who does not exhibit the preferred trait. To incorporate this aspect of sexual selection, I compared invasion patterns for cases in which caring and/or cannibalism increased the reproductive rate of the caring mutant relative to the resident (i.e., $r_m > r$) to those in which the magnitude of the reproductive rate did not differ between the mutant and resident (i.e., $r_m = r$).

Likewise, it is possible that filial cannibalism creates reproductive conflict between parents. In this case one would expect non-cannibalistic individuals to be favored during mate choice (Kraak 1996; Lindström 2000). To assess the importance of mate preference for a non-cannibalistic partner, I compared cases in which the mutant has a reduced reproductive rate relative to the resident (i.e., $r_m < r$), with the case in which the mutant and resident have equal reproductive rates (i.e., $r_m = r$).

Parental care, no care, and filial cannibalism might affect population-level resources, and hence the competitive regime that individuals experience, in different ways. For example, providing care might necessitate greater per capita resources (e.g., increased energetic need and nesting resources per individual) than not providing care (i.e., $K > K_m$ for a caring mutant invading a resident without care). Similarly, the ability to cannibalize while providing care might represent a more efficient use of resources by individuals. Such an individual-level change in resource use would be reflected in the carrying capacity of a population of individuals exhibiting a particular strategy. Specifically, if a strategy allows individuals to use resources more efficiently (i.e., increase their productivity), we would expect an increase in the carrying capacity of a population of individuals exhibiting that strategy (relative to individuals who do not exhibit the strategy of interest, i.e., $K < K_m$ for a mutant who can cannibalize and care invading a resident who can only care). In this sense, the population-level carrying capacity K associated with a strategy is a proxy for the effect that strategy has on individual-level resource use. To begin to evaluate the importance of such resource-related effects of varying strategies, I compare cases in which carrying capacity varies between the mutant and the resident population. Likewise, for cases in which the mutant and residents have equal carrying capacities, I compared patterns for a range of carrying capacities to determine if a relatively productive ecosystem (i.e., system with a large carrying capacity) or unproductive ecosystem (i.e., system with a relatively small carrying capacity) favors the invasion of a particular strategy.

Finally, to evaluate further patterns of cannibalism evolution, I compared the fitness boundaries for cases in which parents were allowed to selectively cannibalize eggs with reduced future survivorship (i.e., $d_{Em} < d_E$ and $\sigma_{Jm} > \sigma_J$) with those of parents that could not selectively cannibalize (i.e., $d_{Em} = d_E$ and $\sigma_{Jm} = \sigma_J$).

Results

All of the strategies considered (i.e., parental care, no care/total offspring abandonment, filial cannibalism) evolved over a range of parameter space in all analyses. While the evolution of parental care and/or filial cannibalism were favored by benefits to adults and/or offspring (discussed below), such benefits were not essential for the invasion of a particular strategy, highlighting the plausibility of a range of non-mutually exclusive alternative hypotheses (Table 6-2). In all cases considered, the coexistence dynamics were stable (Online Appendix of Klug and Bonsall 2007). While incorporating non-linear trade-off functions (Table 6-1) into the model altered the results quantitatively, there were no qualitative effects of these functions (i.e., the patterns were the same), and thus, I only present results in which linear trade-offs were used.

Invasion of Parental Care

Effects of egg maturation rate, egg death rate, adult reproductive rate, and carrying capacity: A mutant with parental care invaded or coexisted with a resident population lacking care over a wide range of life-history parameters (Figure 6-2 A), particularly when care was effective at decreasing the death rate of eggs (i.e., when $d_{Em} < d_E$), when it increased survivorship through the juvenile stage (i.e., when $\sigma_{Jm} > \sigma_J$), and when caring increased maturation rate of the eggs (i.e., when $m_{Em} > m_E$, Figure 6-2 A) relative to the non-caring strategy. Similarly, the range over which care invaded or coexisted with no care increased when parental care was associated with an increased rate of egg fertilization (e.g., if it was a preferred trait, such that $rm > r$; Figure 6-2 A versus 6-2 B) and when care was associated with a decreased carrying capacity relative to the resident population (Figure 6-2 A versus 6-2 C). The evolution of parental care was relatively insensitive to changes in carrying capacity for cases in which the resident and mutant had equal carrying capacities.

Effect of cannibalism on the evolution of care: To evaluate whether the ability to practice filial cannibalism affects the evolution of parental care, I compared the case in which a mutant with only parental care was allowed to invade a resident population with no parental care and no cannibalism, with the scenario in which the mutant could care and cannibalize (Figure 6-2 A versus 6-2 D). Indeed, filial cannibalism facilitated the evolution of care (Figure 6-2 D). When the caring mutant was allowed to cannibalize (Figure 6-2 D), parental care (and filial cannibalism) evolved over a wider range of parameter space and coexisted more often with no care than when the mutant was not allowed to cannibalize (Figure 6-2 A).

Invasion of Filial Cannibalism (With and Without Parental Care)

Effects of Egg Maturation Rate, Reproductive Rate, and Selective Cannibalism:

Parental care with filial cannibalism was more likely to invade and/or coexist with a state of only care when practicing filial cannibalism increased the maturation rate of eggs over what would be achieved by only providing care (i.e., when $m_{Em} > m_E$, Figure 6-3 A), and when filial cannibalism allowed a parent to improve the quality of care provided for remaining offspring (i.e., cannibalism decreases d_{Em} relative to d_E). Care and cannibalism invaded and coexisted more often when filial cannibalism increased the reproductive rate of the caring parent(s) (e.g., care and/or cannibalism are preferred, such that $rm > r$, Figure 6-3 A versus B), but invaded less often if it decreased the reproductive rate of adults (e.g., non-cannibalism is preferred, such that $rm < r$; Figure 6-3 A versus C). Similarly, care with cannibalism evolved more often when parents could selectively cannibalize their offspring. Specifically, if parents cannibalized offspring with a higher egg death rate and a lower juvenile survival rate (Figure 6-3 D), cannibalism invaded more often than in cases in which parents were not capable of selectively cannibalizing (Figure 6-3 A). These patterns were consistent when we considered parental care

and filial cannibalism evolving from a state of care or a state of no care. Likewise, filial cannibalism (without care) invaded and/or coexisted with no care/no cannibalism over a greater range of parameter space if filial cannibalism improved offspring survival (i.e., $d_{Em} < d_E$, or $\sigma_{Jm} > \sigma_J$), increased the maturation rate of eggs ($m_{Em} > m_E$), or when parents were able to practice selective filial cannibalism of offspring that had reduced survival during the egg and/or juvenile stage.

Effects of Density-Dependent Egg Survivorship

When egg survivorship was density-dependent, parental care and/or filial cannibalism evolved and co-existed over a wide range of parameter space. However, in the absence of any other benefits of filial cannibalism, density-dependent egg survivorship alone did not facilitate the evolution of cannibalism. In fact, allowing a mutant that provides care to cannibalize decreased the range over which care and cannibalism evolved, in comparison to the case in which the mutant could not cannibalize (Figure 6-4 A versus B). However, when the mutant provided care and cannibalized, parental care and cannibalism invaded over a greater range of parameter space as the strength of density-dependence (i.e., ω) increased (Figure 6-4 B versus C). In other words, the evolution of filial cannibalism was not facilitated by density-dependent egg survivorship *per se*, but relatively intense density-dependence (i.e., a relatively large increase in egg mortality with increasing egg density) allowed cannibalism to evolve more often in comparison to weaker density-dependence (i.e., a relatively small increase in egg mortality with increasing egg density; as ω , in eqn. 6, increased, the range over which care with cannibalism and no care could invade and/or coexist increased). These patterns were the same for both density-dependent functions considered.

Effects of Energetic Benefits of Consuming Offspring

Energetic benefits of filial cannibalism (i.e., benefits associated with d_{Am} and r_m) increased the range over which care and cannibalism could invade and coexist with no care (Figure 6-5 A versus B). However, in this scenario (i.e., considering care and cannibalism invading from a state of no care or cannibalism) it is possible that cannibalism could be thought of as simply hitchhiking in with care. Thus, I considered the case in which cannibalism and care invaded a resident who already provides care. While energetic benefits of cannibalism to adult reproduction and survival increased the range of invasion and coexistence (Figure 6-5 C), filial cannibalism (which in this case is equivalent to simply killing offspring, or abandoning offspring that have no chance of surviving alone, during the course of care) was still able to invade in the absence of benefits to adults (Figure 6-5 D) over the range of parameters considered.

Effects of Carrying Capacity

For cases in which cannibalism alters the efficiency with which individuals use resources (and hence, population carrying capacity), filial cannibalism with parental care was more likely to evolve from a state of only care if cannibalism increased the resource-use efficiency of a population of individuals exhibiting that strategy (i.e., the carrying capacity). In other words, filial cannibalism was more likely to invade if it somehow increased the productivity of the system (Figure 6-6 A versus B). In contrast, for the case of filial cannibalism with parental care evolving from a state of no care, cannibalism and care were more likely to evolve if they were associated with a decrease in the population carrying capacity (i.e., if care with cannibalism decreased the productivity of the system and the efficiency with which individuals use resources, Figure 6-6 C versus D). Likewise, for the case of filial cannibalism (without parental care)

invading a resident state of no care/no cannibalism, filial cannibalism invaded and coexisted over a greater range of parameter space if it increased carrying capacity (i.e., resource-use efficiency).

If carrying capacities were equal for the resident providing parental care and the mutant providing care and practicing filial cannibalism (i.e., the efficiency of resource use was equivalent for individuals exhibiting mutant and resident strategies), cannibalism invaded and/or coexisted more often when carrying capacity was relatively low (i.e., in relatively unproductive systems, Figure 6-6 A versus E). This trend (i.e., more invasion and coexistence of the mutant at lower carrying capacities) was consistent for the case in which filial cannibalism (with no parental care) invaded a resident with no care/no cannibalism. However, when I considered the case in which cannibalism with care invaded a state of no care (and assumed the carrying capacities were equal for populations exhibiting the resident and mutant strategies), cannibalism and care were more likely to invade or coexist with no care/no cannibalism when carrying capacity was relatively large (i.e., when the system was relatively more productive, Figure 6 C versus F).

Discussion

I have shown that parental care, filial cannibalism, and no care/total offspring abandonment can evolve over a wide range of life-history parameters. My results suggest that the ability to abandon or consume offspring during the course of parental care can actually facilitate the evolution of parental care, and that offspring abandonment/no care, parental care, and filial cannibalism often have the potential to coexist. Even in the absence of direct benefits of filial cannibalism, such as energetic gain or increased survival of remaining offspring, filial cannibalism invaded (and coexisted with) non-cannibalistic strategies in multiple contexts (i.e., with or without care, across varying resident strategies, over a range of life-history parameters). In the absence of such benefits, cannibalism is simply equivalent to killing (or abandoning

offspring that will subsequently die) during the course of care. My results suggest that the evolutionary dynamics of filial cannibalism are likely comparable to those of simple offspring abandonment (which provides no immediate benefits, such as energetic gain, to parents). However, my results suggest that the evolution and fixation of filial cannibalism is favored by a variety of evolutionary and ecological factors. While no single benefit of consuming eggs was essential for the invasion of filial cannibalism to occur, several potential benefits facilitate the evolution of filial cannibalism.

In particular, my model highlights the plausibility of several non-mutually exclusive alternative hypotheses favoring the evolution filial cannibalism (Table 6-2). The ability to selectively cannibalize eggs facilitated the evolution of cannibalism in all contexts. The ability to cannibalize offspring selectively allows parents to alter the phenotypes of the offspring they produce after fertilization and on a relatively fine time scale, which might be particularly beneficial in a variable environment (although I didn't explicitly consider environmental variability in this model). Selective cannibalism of clutches of lower reproductive value has been demonstrated in relation to uncertainty of paternity (i.e., possible cuckolding events) in some fishes (*Lepomis macrochirus*, Neff 2003; *Telmatherina sarasinorum*, Gray et al. 2007; *Gasterosteus aculeatus*, Frommen et al. 2007), and the elimination of low quality offspring has been focused on in other contexts (e.g., allowing lower quality offspring to be eliminated by siblicide, Stearns 1987; spontaneous and selective abortion in humans, sex ratio adjustment in red deer; Stearns 1987; Kozłowski and Stearns 1989). However, selective filial cannibalism of viable offspring in relation to other aspects of offspring quality has received little empirical attention (but see Chapters 4 and 5). In particular, I hypothesize that in some contexts filial

cannibalism of offspring with (1) reduced expected future survival, or (2) slower maturation rates during the period in which care is being provided can be an adaptive strategy.

Alternatively, it is possible that filial cannibalism itself increases the development rate of eggs. If filial cannibalism increases the maturation rate of eggs relative to those of non-cannibalistic parents, filial cannibalism evolves over a greater range of parameter space (Figure 6-3 A). Indeed, for cases in which parent-offspring conflict exists over the optimal duration of parental care, filial cannibalism might be a way in which parents speed-up the developmental rate of their eggs, thereby allowing them to reduce per offspring costs of care or re-enter the mating pool faster. According to this hypothesis, caring parents potentially benefit by providing care for a shorter duration of time if filial cannibalism creates an environment in which offspring are eager to escape the egg stage (e.g., because of increased risk of death; see also work on non-parent predators increasing egg development rate, e.g., Warkentin 2000). To my knowledge, this idea of filial cannibalism speeding-up egg development has not previously been considered, and as mentioned previously, is likely to be relevant for cases in which parents and offspring differ in the optimal amount of care they provide/receive.

Incorporating an energetic benefit of cannibalism facilitated the invasion of filial cannibalism. This finding is consistent with previous theoretical and empirical work suggesting that energetic need affects filial cannibalism (e.g., Rohwer 1978; Sargent 1992; Kraak 1996; reviewed by Manica 2002). However, some empirical work suggests that the effects of energetic need on filial cannibalism are not always straightforward-- in some species cannibalism increases as parental energetic need increases (e.g., Thomas and Manica 2003), whereas in other species an opposite pattern is observed (e.g., Klug et al. 2006). Moreover, in other systems, there appear to be no effects of parental condition on filial cannibalism under some conditions (e.g., Lindström

and Sargent 1997), and in other species the relationship between energetic need and cannibalism differs in varying contexts (Klug and Lindström, unpublished data). Furthermore, some have suggested that the energetic benefits of cannibalism are not sufficient to explain the prevalence of filial cannibalism (Smith 1992). In my model, filial cannibalism invaded over a range of parameter space even when we removed benefits of cannibalism, suggesting that substantial energetic benefit of cannibalism is not necessarily essential for the evolution of cannibalism. That said, there is little doubt that filial cannibalism provides a caring parent with energy and/or nutrients and such benefits are likely critical for adult survival and successful nest defense in systems where parents are unable to feed during the course of providing parental care (Manica 2002, 2004). Indeed, energetic benefits certainly favor the evolution of filial cannibalism (Figure 6-5; previous work by Rohwer 1978; Sargent 1992; reviewed in Manica 2002).

Likewise, increasing the strength of density-dependent egg survivorship increased the parameter space over which filial cannibalism evolved. However, density-dependent egg survivorship alone did not facilitate the evolution of filial cannibalism. Indeed, it seems unlikely that density-dependent egg survivorship *per se* would lead to the evolution of filial cannibalism in the absence of other trade-offs associated with egg number. If animals can track their environment, they would simply be expected to adjust the number of eggs they produce according to expected egg survivorship (i.e., they should lay at densities that maximize survival). Further work is needed to evaluate the importance of density-dependent egg survivorship when other trade-offs are associated with the number of offspring produced or when the environment is variable. Spatial and temporal variation in the environment has been hypothesized to influence patterns of cannibalism observed in nature (e.g., Payne et al. 2004) and non-cannibalistic brood

reduction (e.g., Forbes and Mock 1998), but additional work is needed to understand more fully the importance of such stochasticity at varying scales.

Sexual selection via mate choice and/or sexual conflict also affected the invasion and fixation of filial cannibalism and/or parental care. My model suggests that the evolution and fixation of parental care from a state of no care can be facilitated by differential reproductive success if parental care or filial cannibalism increases the reproductive rate of individuals exhibiting care or cannibalism (e.g., if parental care or cannibalism is preferred during mate choice). This finding is consistent with some previous work. For example, Pampoulie et al. (2004) and Lindström et al. (2006) recently demonstrated mating preferences for parental care, suggesting a potentially larger role for sexual selection in the evolution of care than previously thought. Additionally, filial cannibalism is possibly favored by sexual selection if cannibalism directly benefits a choosing mate or when it makes a caring parent more attractive in some other way (Sikkel 1994; Lindström 2000). Likewise, if a mating preference exists for non-cannibals, the parameter space over which filial cannibalism evolves decreases. Interestingly, the role of sexual conflict has received relatively little theoretical or empirical attention previously (but see Kraak and van den Berghe 1992; Kraak 1996; Lindström 2000). In fishes, where filial cannibalism is typically practiced by caring fathers, the focus of almost all work has been on costs and benefits of cannibalism to caring males. One must also wonder if benefits to non-cannibalistic females exist, and if such benefits are absent, why do females tolerate filial cannibalism? Additionally, sexual conflict is also likely to exist when both parents practice filial cannibalism, but this idea has received no attention. More empirical work is needed to better understand costs and benefits of filial cannibalism to a parent who's mate practice filial cannibalism.

Finally, population-level resource competition likely plays a role in the evolution of both parental care and filial cannibalism. When care and/or cannibalism affected the efficiency with which individuals exhibiting a given strategy use resources, parental care was more likely to evolve if caring was associated with a reduction in the carrying capacity (e.g., when caring decreased the efficiency with which individuals use resources), whereas, filial cannibalism was more likely to invade if it increased carrying capacity (e.g., if cannibalism increased the resource-use efficiency of individuals). Additionally, the evolution of filial cannibalism (with or without parental care) was affected by the population carrying capacity, even for the case in which the carrying capacity of the mutant and residents were equal. It is unclear how parental care and filial cannibalism potentially alter population-level dynamics and resulting carrying capacities in nature, but this idea warrants further attention. For example, it is possible that the ability to cannibalize increases resource availability to caring parents, thereby freeing-up other resources and increasing the productivity of a system. Regardless, understanding the ecological dynamics of a system (i.e., intensity of resource competition and population growth parameters such as carrying capacity) is likely to be critical for understanding the evolution of parental care and filial cannibalism across animal taxa. While previous work has sometimes incorporated population-level growth dynamics in parental care theory (e.g., McNamara et al. 2000), this is not a common approach.

In summary, my results suggest that parental care and filial cannibalism can evolve over a range of life-history patterns and ecological conditions, and that multiple strategies often have the potential to coexist. Coexistence, while not well-studied (but see Webb et al. 1999), is prevalent in nature (e.g., maternal- or paternal-only care in many taxa, reviewed in Clutton-Brock 1991; care and no-care with total offspring abandonment following egg fertilization:

Jordanella floridae, Hale pers. comm., the white stickleback *Gasterosteidae* spp., Blouw 1996; care and care followed by abandonment, *Hypoptychus dybowskii*, Narimatsu and Munehara 2001). Likewise, there are many cases in which caring parents never or rarely consume or abandon their offspring. Even in fishes, where care with filial cannibalism has been well-documented, there are still many species exhibiting parental care in which filial cannibalism is absent (e.g., *Micropterus dolomieu*, Gillooly and Baylis 1999). For species exhibiting filial cannibalism, there is a great deal of variation in the patterns of cannibalism observed among species and within and between individuals (e.g., how many eggs are consumed, who practices cannibalism and when; Petersen and Marchetti 1989; Okuda and Yanagisawa 1996; Lindström and Sargent 1997; Lissåker et al. 2002; Klug et al. 2005; Klug and St. Mary 2005).

Understanding such within- and between-species variation in filial cannibalism and parental care will require more detailed theoretical and empirical work that simultaneously considers multiple factors (such as variation in offspring quality, energetic needs of parents, mating preferences and sexual conflict, general resource competition). Additionally, it will also be important to assess the importance of environmental heterogeneity in the evolution of filial cannibalism. From this study, my approach and results provides a novel basis for further developing this theme of whether to care for or consume one's own offspring.

Table 6-1. Trade-off functions. The following trade-off functions were used to reflect the unique life histories of individuals who provide parental care and/or practice filial cannibalism. The death rate of eggs is assumed to be a function of the parental care provided (i.e., as d_e decreases, care is presumed to increase), and thus egg death rate is the proxy for care.

Parameter	Trade-offs	Strategy			
		No parental care & no filial cannibalism	Parental care only	Filial cannibalism only	Parental care & filial cannibalism only
Reproductive rate; r and r_m	<p>1) Reproductive rate decreases as caring increases (i.e., r or r_m decreases as d_e or d_{em} decreases).</p> <p>2) Reproductive rate increases as maturation rate of eggs increases (for a carer only) (i.e., r or r_m increases as m_E or m_{Em} increases).</p> <p>3) Reproductive rate increases as cannibalism increases (i.e., r_m increases as β increases).</p>	<p>Linear & Non-linear: $r = r_0$</p>	<p>Linear: $r_m = r_{m_0} \cdot (1 + d_{Em} + m_{Em})$</p> <p>Non-linear: $r_m = r_{m_0} \cdot \frac{(d_{Em} + m_{Em})}{(1 + d_{Em} + m_{Em})}$</p>	<p>Linear: $r_m = r_{m_0} \cdot (1 + \beta)$</p> <p>Non-linear: $r_m = r_{m_0} \cdot \frac{\beta}{(1 + \beta)}$</p>	<p>Linear: $r_m = r_{m_0} \cdot (1 + d_{Em} + m_{Em} + \beta)$</p> <p>Non-linear: $r_m = r_{m_0} \cdot \frac{(d_{Em} + m_{Em} + \beta)}{(1 + d_{Em} + m_{Em} + \beta)}$</p>
Juvenile survival rate; σ_j and σ_{jm}	<p>1) Juvenile survival rate increases as care increases (i.e., σ_j or σ_{jm} increases as d_E or d_{Em} decreases).</p>	<p>Linear & Non-linear: $\sigma_J = \sigma_{J_0}$</p>	<p>Linear: $\sigma_{Jm} = \sigma_{Jm_0} \cdot (1 - d_{Em})$</p> <p>Non-linear: $\sigma_{Jm} = \sigma_{Jm_0} \cdot \frac{(1 + d_{Em})}{d_{Em}}$</p>	<p>Linear & Non-linear: $\sigma_{Jm} = \sigma_{Jm_0}$</p>	<p>Linear: $\sigma_{Jm} = \sigma_{Jm_0} \cdot (1 - d_{Em})$</p> <p>Non-linear: $\sigma_{Jm} = \sigma_{Jm_0} \cdot \frac{(1 + d_{Em})}{d_{Em}}$</p>
Adult death rate; d_A and d_{Am}	<p>1) Adult death rate increases as caring increases (i.e., d_A or d_{Am} increases as d_E or d_{Em} decreases).</p> <p>2) Adult death rate decreases as cannibalism increases (i.e., d_A or d_{Am} decreases as β increases).</p>	<p>Linear & Non-linear: $d_A = d_{A_0}$</p>	<p>Linear: $d_{Am} = d_{Am_0} \cdot (1 - d_{Em})$</p> <p>Non-linear: $d_{Am} = d_{Am_0} \cdot \frac{(1 + d_{Em})}{d_{Em}}$</p>	<p>Linear: $d_{Am} = d_{Am_0} \cdot (1 - \beta)$</p> <p>Non-linear: $d_{Am} = d_{Am_0} \cdot \frac{(1 + \beta)}{\beta}$</p>	<p>Linear: $d_{Am} = d_{Am_0} \cdot (1 - d_{Em} - \beta)$</p> <p>Non-linear: $d_{Am} = d_{Am_0} \cdot \frac{(1 + d_{Em} + \beta)}{d_{Em} \cdot \beta}$</p>

Table 6-2. Alternative hypotheses regarding the evolutionary significance of filial cannibalism (FC). Here, I present several, non-mutually exclusive hypotheses and briefly describe the findings of our model and those of some previous work in relation to these hypotheses.

Hypothesis	Description	Model findings	Related previous findings
1. Selective Filial Cannibalism	Offspring with particular characteristics (e.g., reduced survival, decreased maturation rate) are preferentially consumed.	Evolution of FC facilitated by selective cannibalism of offspring with lower maturation rates, lower egg survival, and/or lower juvenile survival.	FC affected by certainty of paternity in some systems (Neff 2003; Frommen et al. 2007; Gray et al. 2007) but not in others (Svensson et al. 1998); effect of other aspects of offspring quality on FC largely unknown.
2. Filial cannibalism speeds-up egg development	By increasing costs associated with remaining in the egg stage, filial cannibalism increases maturation rate of eggs (i.e. FC decreases the time it takes for eggs to develop).	Evolution of FC more likely if cannibalism increases egg maturation rate.	Not previously examined; potentially relevant for systems in which parent-offspring conflict exists over the optimal amount of care provided/received.
3. Energy-Based Filial Cannibalism	FC provides energy that offsets costs of care and is re-invested into current and/or future reproduction.	Energetic benefit of eggs facilitated evolution of FC.	Substantial energetic benefit of FC and/or effect of energetic need on FC found in several systems (reviewed in Manica 2002).
4. Density-Dependent-Egg-Survivorship-Mediated Filial Cannibalism	Density-dependent egg survival mediates FC: by consuming some young, parents increase survival of remaining offspring.	Density-dependent egg survival alone did not facilitate the evolution of FC; more intense density-dependence facilitated evolution of FC in comparison to weaker density-dependence.	FC is affected by density-dependent egg survivorship in two species (Payne et al. 2002, 2004; Klug et al. 2006)
5. Mate Choice-Mediated Filial Cannibalism	FC is preferred in mate choice, thereby increasing relative reproductive rate.	If FC increases relative reproductive rate of cannibals, FC evolves more often.	FC increases nest attractiveness (and consequently eggs received) in some cases (Sikkel 1994).
6. Sexual Conflict-Mediated Filial Cannibalism	FC is a non-preferred trait and decreases relative reproductive rate.	If FC decreases reproductive rate, FC evolves less often.	Sexual conflict can inhibit FC in some cases (Lindström 2002); sexual conflict regarding FC not well-studied empirically (but see Kraak 1996).
7. Filial Cannibalism Driven by Resource Competition	FC is driven by population-level resource competition among adults.	Evolution of FC sensitive to population-level carrying capacity.	Mate availability (Kondoh and Okuda 2002) and other resource competition (Creighton 2005) affects FC in some cases; effects of general resource availability on FC not well-known.

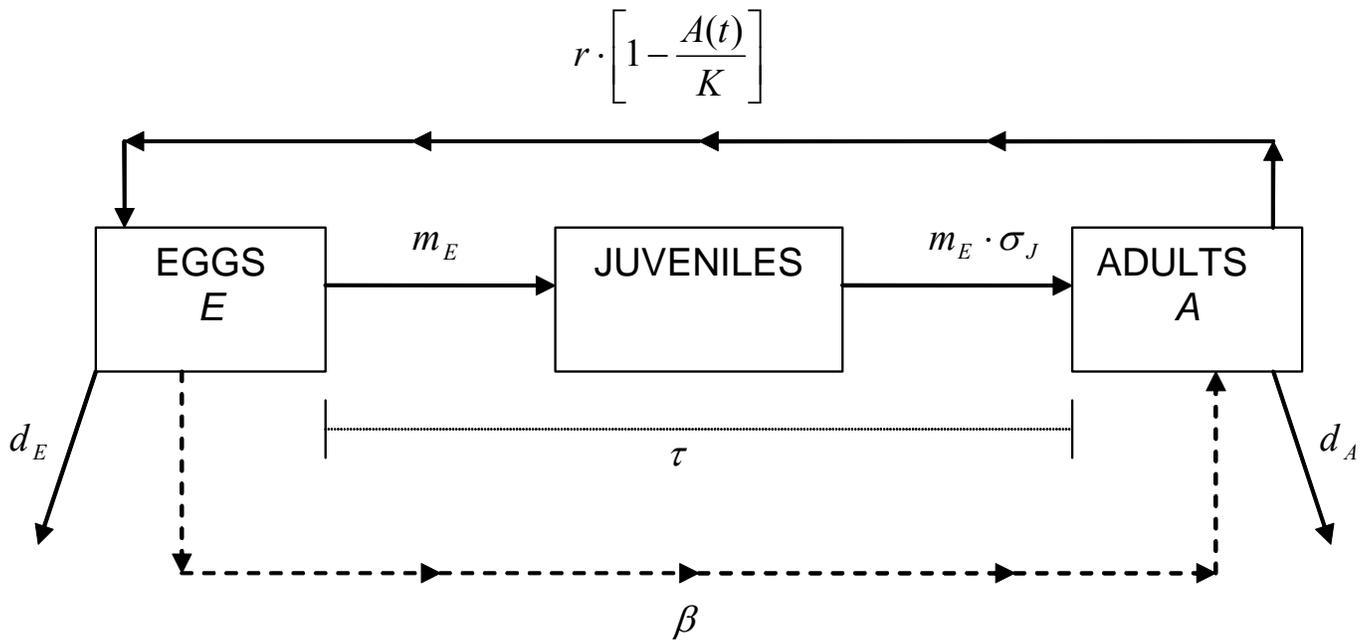


Figure 6-1. The model: individuals develop through an egg and juvenile stage and reproduce as adults. Eggs either die (at rate d_E), are consumed by their parent(s) (at rate β), or mature into juveniles (at rate m_E). Individuals survive and pass through the juvenile stage (at rate $m_E \cdot \sigma_J$), where τ represents the time spent in the juvenile stage. As adults, individuals either die (at rate d_A) or reproduce (at rate $r \cdot \left[1 - \frac{A(t)}{K}\right]$, where K represents the population carrying capacity). Boxes represent life-history stages; solid arrows represent death, reproduction, and maturation; the dashed line represents consumption of eggs by adults.

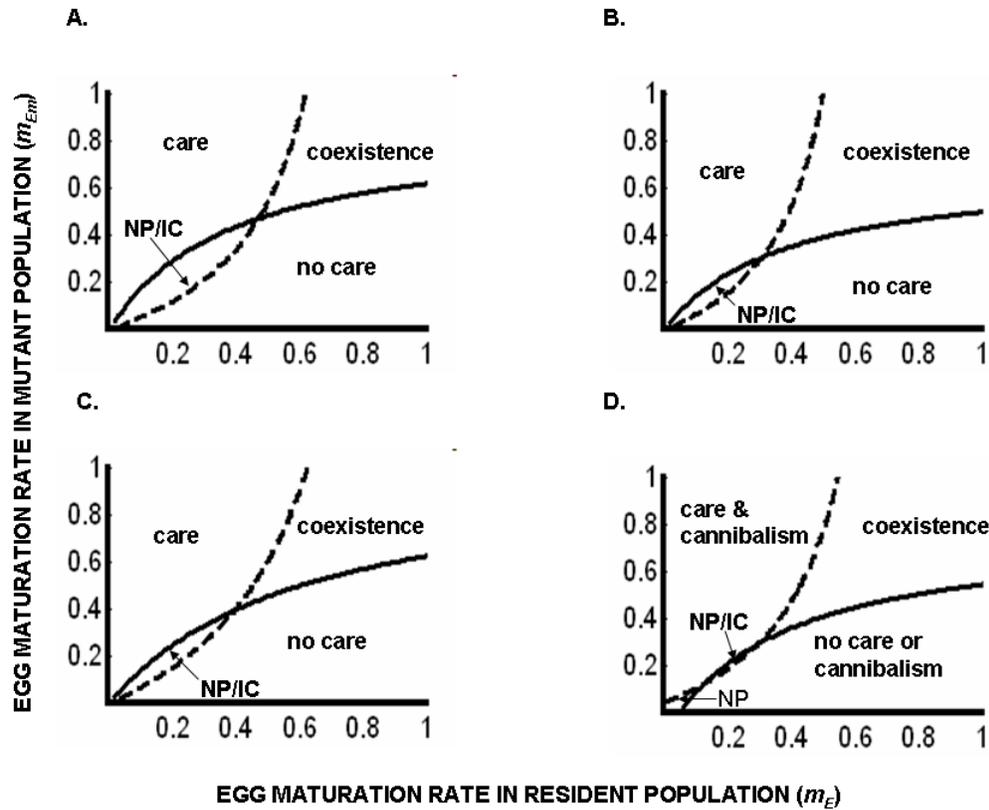


Figure 6-2. Invasion of parental care. Parental care invades and/or coexists with no care more often when parental care: (A) increases the maturation rate of eggs, (B) increases parental reproductive rate ($r = 1.0$, $r_m = 1.2$), (C) is associated with a decreased carrying capacity ($K = 20$, $K_m = 15$), and (D) when the caring mutant is able to cannibalize (i.e., $\beta = 0.01$ for the mutant, $\beta = 0$ for the residents). Lines represent invasion boundaries for the mutant (solid line) and the resident (dotted line). Invasion boundaries are shown for the maturation rate of the eggs. The mutant invades the resident in the regions labeled 'care' (A-C) or 'care & cannibalism' (D), the resident invades the mutant in the region labeled 'no care' (A-C) or 'no care or cannibalism' (D), and both strategies coexist in the region labeled 'coexistence'. Neither strategy will persist (i.e., they go extinct) in the region labeled 'NP'. The region labeled 'NP/IC' is a region in which neither strategy will persist, or where the outcome is dependent upon initial conditions of the model. Unless noted above, $r = r_m = 1.0$, $d_E = d_{Em} = 0.9$, $d_A = d_{Am} = 0.5$, $\sigma_J = \sigma_{Jm} = 0.5$, $K = K_m = 20$, $\beta = 0$, $\tau = 0.1$.

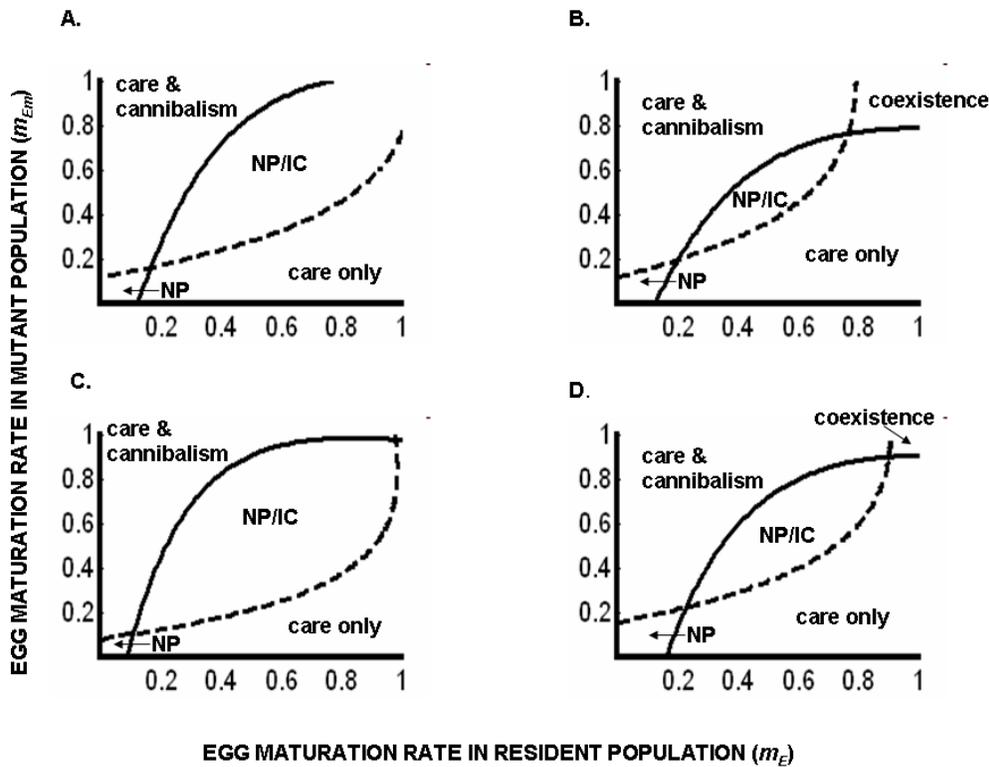


Figure 6-3. Invasion of filial cannibalism. A mutant that provides parental care and practices filial cannibalism invades and coexists with a resident that only provides care (A) more often when cannibalism increases the maturation rate of eggs, (B) more often when cannibalism increases the parent's reproductive rate ($r = 0.5, r_m = 0.6$), (C) less often when cannibalism decreases the parent's reproductive rate ($r = 0.6, r_m = 0.5$), and (D) more often when parents are able to selectively cannibalize offspring with reduced future survival ($d_e = 0.2, \sigma_j = 0.9, d_{em} = 0.1, \sigma_{jm} = 0.95$). Lines represent invasion boundaries for the mutant (solid line) and the resident (dotted line). Invasion boundaries are shown for the maturation rate of the eggs, m_E and m_{Em} , and unless otherwise noted, $r = r_m = 0.5, d_E = d_{Em} = 0.2, d_A = d_{Am} = 0.5, \sigma_J = \sigma_{Jm} = 0.9, K = K_m = 20, \beta = 0.015, \tau = 0.1$. The mutant invades the resident in the region labeled 'care & cannibalism', the resident invades the mutant in the region labeled 'care only', and both strategies coexist in the region labeled 'coexistence'. Neither strategy will persist in the region labeled 'NP'. The region labeled 'NP/IC' is a region in which neither strategy will persist, or where the outcome is dependent upon initial conditions of the model.

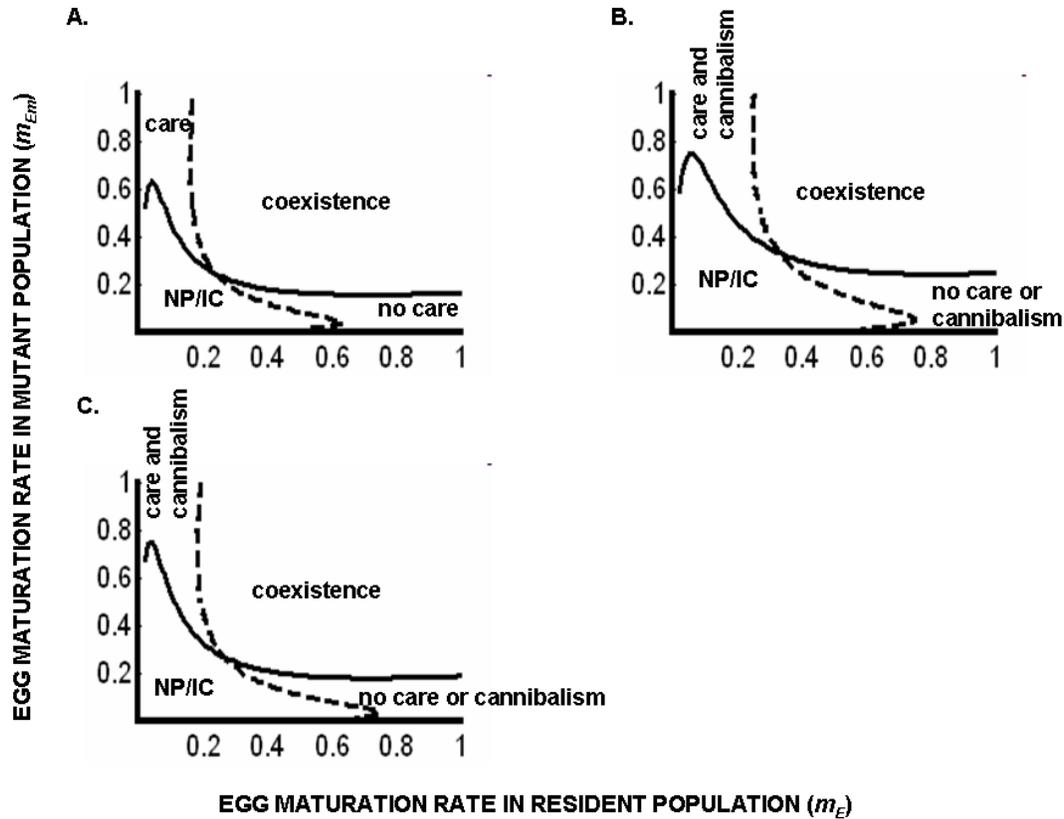


Figure 6-4. Effect of density-dependent egg survivorship on the evolution of parental care and filial cannibalism. Parental care and no care invade and/or coexist over a large range of parameter space when (A) the rare mutant does not cannibalize ($\beta = 0$). The range over which parental care invades decreases when (B) the rare mutant cannibalizes ($\beta = 0.01$). However, increasing the strength of density-dependence (ω , eqn. 6) increases the range over which care and cannibalism invades-- care with cannibalism invades more often when (C) the strength of the density-dependence is greater ($\omega = 0.9$), in comparison to B) the case in which it is relatively weak ($\omega = 0.6$). Lines represent invasion boundaries for the mutant (solid line) and the resident (dotted line). Invasions boundaries are shown for the maturation rate of the eggs, m_E and m_{Em} , and unless otherwise noted, $r = r_m = 3$, $d_E = 0.9$, $d_{Em} = 0.3$, $d_A = d_{Am} = 0.5$, $\sigma_J = \sigma_{Jm} = 0.5$, $K = K_m = 20$, $\beta = 0.01$, $\tau = 1$, $\omega = 0.6$. The mutant invades the resident in the region labeled 'care' (A) or 'care and cannibalism' (B-C), the resident invades the mutant in the region labeled 'no care' (A) or 'no care or cannibalism' (B-C), and both strategies coexist in the region labeled 'coexistence'. The region labeled 'NP/IC' is a region in which neither strategy will persist, or where the outcome is dependent upon initial conditions of the model.

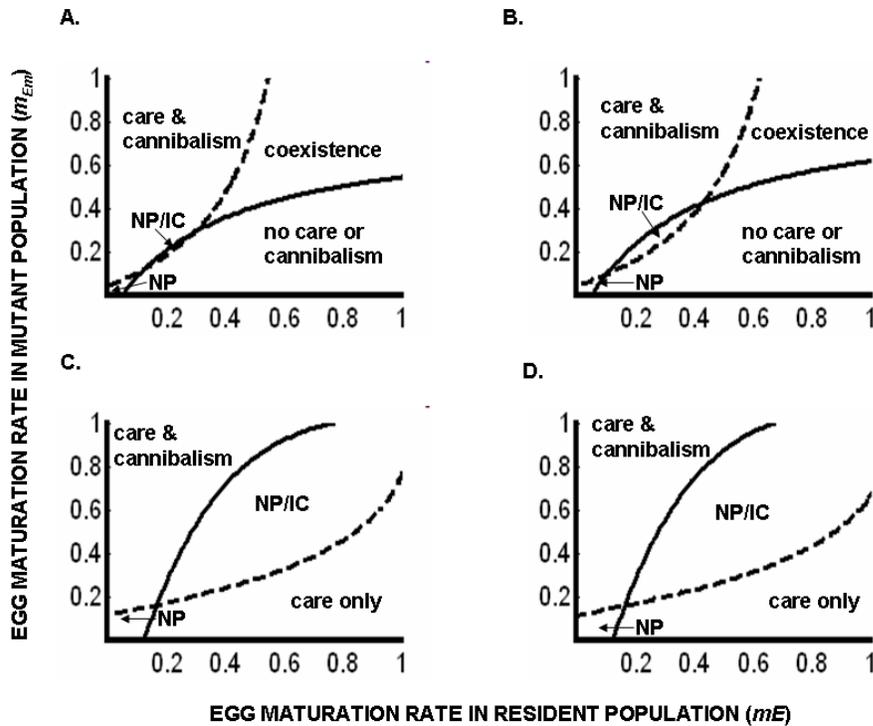


Figure 6-5. Effect of energetic benefits on the evolution of filial cannibalism. Parental care with filial cannibalism is more likely to invade and coexist with no care if filial cannibalism is (A) beneficial to a parent's survival and reproduction versus (B) the case where there are no benefits of cannibalism. Likewise, care with cannibalism is more likely to invade a state of only care when (C) adult survival and reproductive benefits of egg eating exist versus (D) the case where such benefits are absent. Lines represent invasion boundaries for the mutant (solid line) and the resident (dotted line). Invasion boundaries are shown for the maturation rate of the eggs, m_E and m_{Em} . Unless otherwise noted, $r = r_m = 1.0$, $d_E = d_{Em} = 0.9$, $d_A = d_{Am} = 0.5$, $\sigma_J = \sigma_{Jm} = 0.5$, $K = K_m = 20$, $\beta = 0.01$, $\tau = 0.1$ for A and B, and $r = r_m = 0.5$, $d_E = d_{Em} = 0.2$, $d_A = d_{Am} = 0.5$, $\sigma_J = \sigma_{Jm} = 0.9$, $K = K_m = 20$, $\beta = 0.015$, $\tau = 0.1$ for C and D. The mutant invades the resident in the region labeled 'care & cannibalism', the resident invades the mutant in the region labeled 'no care or cannibalism' (A-B) or 'care only' (C-D), and both strategies coexist in the region labeled 'coexistence'. Neither strategy will persist in the region labeled 'NP'. The region labeled 'NP/IC' is a region in which neither strategy will persist, or where the outcome is dependent upon initial conditions of the model.

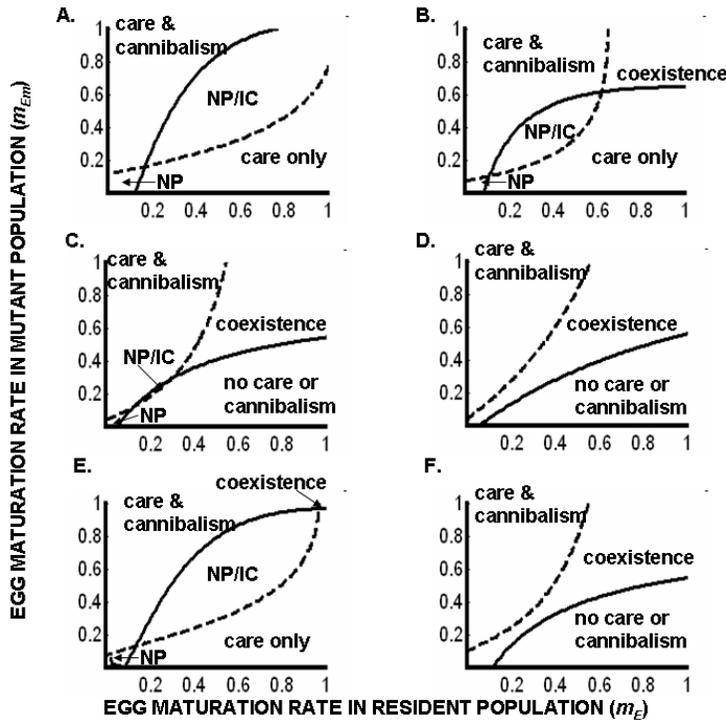


Figure 6-6. Effect of carrying capacity on the evolution of filial cannibalism. Parental care with filial cannibalism invades and coexists with care over a range of parameter space when (A) cannibalism does not affect carrying capacity ($K = K_m = 20$). However, cannibalism invades over a greater range of parameter space when (B) cannibalism increases carrying capacity ($K = 10, K_m = 20$). Likewise, care with cannibalism invades no care over a range of parameter space when (C) care and cannibalism do not affect carrying capacity ($K = K_m = 20$), but it invades or coexists more often when (D) care and cannibalism decrease carrying capacity ($K = 20, K_m = 10$). For cases in which the resident and mutant have equal carrying capacities, parental care and cannibalism are more likely to invade when (E) carrying capacity is relatively small ($K = K_m = 10$) versus the case in which it is relatively large (A). In contrast, care with cannibalism is more likely to invade no care/no cannibalism when (F) carrying capacity is relatively large ($K = K_m = 50$) versus (C) the case in which it is relatively small. Lines represent invasion boundaries for the mutant (solid line) and the resident (dotted line). Invasions boundaries are shown for the maturation rate of the eggs, m_E and m_{Em} . Unless otherwise noted, $r = r_m = 0.5, d_E = d_{Em} = 0.2, d_A = d_{Am} = 0.5, \sigma_J = \sigma_{Jm} = 0.9, \beta = 0.01, \tau = 0.1$ for A, B and E, and $r = r_m = 1.0, d_E = d_{Em} = 0.9, d_A = d_{Am} = 0.5, \sigma_J = \sigma_{Jm} = 0.5, \beta = 0.01, \tau = 0.1$ for C, D, and F. The mutant invades the resident in the region labeled 'care & cannibalism', the resident invades the mutant in the region labeled 'care only' (A-B, E) or 'no care or cannibalism' (C-D, F), and both strategies coexist in the region labeled 'coexistence'. Neither strategy will persist in the region labeled 'NP'. The region labeled 'NP/IC' is a region in which neither strategy will persist, or where the outcome is dependent upon initial conditions of the model.

CHAPTER 7 GENERAL CONCLUSIONS AND SYNTHESIS

Introduction

Parental care typically increases offspring survival and/or quality, thereby increasing parental fitness. Thus, it is surprising that filial cannibalism, the consumption of one's own offspring, is prevalent in fishes exhibiting paternal care. Indeed, it's difficult to imagine many situations in which regularly consuming one's own young is an adaptive strategy. Because parental males often consume more eggs than die naturally (Manica 2002; Klug et al. 2006 and Chapter 6), filial cannibalism does not solely serve to clean the nest of dead eggs. Currently, filial cannibalism is thought to represent an adaptive trade-off (Manica 2002).

Prior to my dissertation work, there were two general hypotheses explaining the adaptive significance of filial cannibalism: the energy-based hypothesis (Rohwer 1978; Sargent 1992) and the oxygen-mediated hypothesis (Payne et al. 2004, 2004). The energy-based hypothesis suggests that filial cannibalism is an adaptive strategy in which males gain energy or nutrients from eggs that are then reinvested into current or future reproduction, thereby increasing net reproductive success (Rohwer 1978). According to this hypothesis, filial cannibalism is expected to increase when food availability is low and/or when the caring parent's condition is poor. There has been mixed support for the energy-based hypothesis (Belles-Isles & Fitzgerald 1991; Smith 1992; Lindström and Sargent 1997), and at best, it can only explain filial cannibalism in some systems (e.g., Manica 2004). The oxygen-mediated hypothesis of filial cannibalism (Payne et al. 2002) suggests that filial cannibalism is an adaptive strategy in which partial clutch cannibalism improves the survival of remaining eggs by increasing oxygen availability to remaining eggs. Specifically, Payne et al. (2002) suggested that caring males potentially improve overall clutch

survivorship by consuming some of their eggs. The oxygen-mediated hypothesis has received support in one species (Payne et al. 2002), but has not been generally evaluated.

In addition to energy and oxygen availability, some studies suggest that mate choice or sexual conflict (Sikkel 1994; Kraak 1996; Lindström 2000), egg age (Salfert and Moodie 1985; Sikkel 1994), and certainty of paternity (Neff 2003; Gray et al. 2007; Frommen et al. 2007) affects the occurrence of filial cannibalism (but see Svensson et al. 1997 and Svensson and Kvarnemo 2007, who find that certainty of paternity does not affect filial cannibalism in the sand goby). There has been relatively little theoretical or empirical examination of such factors, and thus the general importance of mate choice, sexual conflict, egg age, and certainty of paternity remains unknown (e.g., Takeyama et al. 2007).

Because of (1) the lack of support for any particular hypothesis (i.e., the energy-based or oxygen-mediated hypothesis) and (2) a general lack of alternative hypotheses, the evolutionary significance of filial cannibalism in fishes remains unclear. In Chapter 1, I argued that an enhanced understanding of the evolutionary significance of filial cannibalism necessitates three approaches: 1) a re-evaluation of current theory by explicitly focusing on fitness consequences of filial cannibalism; 2) the development and examination of alternative hypotheses of filial cannibalism; and 3) the development and evaluation of a synthetic model of filial cannibalism that simultaneously considers the potential importance of a range of factors. In Chapters 2 and 3, I evaluated predictions of the energy-based and the oxygen-mediated hypotheses in two species, the flagfish (*Jordanella floridae*) and the sand goby (*Pomatoschistus minutus*). In Chapters 4 and 5, I developed the novel hypothesis of selective filial cannibalism, and I evaluated this hypothesis in the flagfish and the sand goby. In Chapter 6, I developed a model of filial cannibalism. Using this model, I evaluated the plausibility of a range of alternative hypotheses of

filial cannibalism, and I concluded that a variety of factors can favor the evolution of filial cannibalism.

In this final discussion, I will synthesize the findings of Chapters 2-5, and discuss my findings in terms of previous and novel hypotheses.

Are the Current Energy-Based and Oxygen-Mediated Hypotheses Sufficient?

Until 2002, the energy-based hypothesis was the only adaptive hypothesis of filial cannibalism and it remains the most widely accepted hypothesis of filial cannibalism (reviewed in Manica 2002). However, as mentioned before, evidence regarding this hypothesis has been mixed (Belles-Isles & Fitzgerald 1991; Smith 1992; Lindström and Sargent 1997).

In Chapter 2, I described an experiment in which I experimentally manipulated 1) the ability of parental males to cannibalize eggs (i.e., males either had full access to eggs, or filial cannibalism was prevented by a nest cover) and 2) diet (i.e., high quality versus low quality diet) to evaluate the effect of filial cannibalism and diet on components of reproductive success in male flagfish. According to the energy-based hypothesis, energy gained from eggs should be translated into increased future reproduction, and I therefore predicted that males that were able to practice filial cannibalism would receive more eggs and spawn more frequently during the 90 days of the experiment. Contrary to these predictions, I found that filial cannibalism did not increase the total number of eggs males received or the frequency of spawning. Indeed, filial cannibalism was always associated with a decrease in the total number of eggs received, suggesting that energy or nutrients attained from eggs is not directly translated into future reproduction in the flagfish. Furthermore, the energy-based hypothesis suggests that filial cannibalism should increase when food availability is low. In contrast to this prediction, I found that filial cannibalism decreased when food availability was low. Specifically, males on the low

quality diet consumed fewer of their eggs than males on the high quality diet. Thus, I found no support for the energy-based hypothesis in the flagfish.

Similarly, I examined the relationship between parental male condition and filial cannibalism in the sand goby (Chapter 3). The energy-based hypothesis predicts that males will consume more eggs when parental condition is relatively poor. However, I found that males in poorer condition consumed a smaller proportion (and fewer) of their eggs than males that were in better condition. This finding is directly in contrast to predictions of the energy-based hypothesis. Thus, I found no support for the energy-based hypothesis of filial cannibalism in either the flagfish or the sand goby. Because of my findings (Chapters 2 and 3) and those of other studies (Belles-Isles and Fitzgerald 1991; Smith 1992; Lindström and Sargent 1997), I conclude that the energy-based hypothesis is not sufficient to explain the prevalence of filial cannibalism. While eggs certainly provide some energy or/and nutrients, energetic benefits of cannibalism cannot explain filial cannibalism in an adaptive context.

Likewise, I did not find support for the oxygen-mediated hypothesis of filial cannibalism (Chapter 3). Specifically, the oxygen-mediated hypothesis of filial cannibalism predicts that 1) filial cannibalism of some eggs in a nest increases oxygen to the remaining eggs, thereby increasing total egg survival, 2) cannibalism will increase as oxygen decreases, and 3) cannibalism will decrease as egg density increases. In the sand goby, I found that filial cannibalism increased as oxygen decreased and as egg density increased. While both findings are consistent with the oxygen-mediated hypothesis, it is possible that males increased cannibalism at lower oxygen levels because the costs of providing care in low oxygen environments are greater than the costs in high oxygen environments. I therefore directly evaluated the effect of oxygen level and egg density by exposing eggs to two levels of simulated filial cannibalism (i.e.,

simulated cannibalism or no simulated cannibalism) and two levels of oxygen availability (i.e., high versus low oxygen). Eggs were reared in the absence of males and I quantified egg survival. Indeed, I found that egg survival was density-dependent, but this density-dependence was not mediated by oxygen. Specifically, there was no effect of oxygen on egg survival in this experiment. Thus, I propose a more general hypothesis of filial cannibalism mediated by density-dependent egg survival. I suggest that density-dependent egg survival might be due to a range of factors (e.g., waste accumulation in the nest or disease transmission), and that the factors affecting egg survival likely vary across species and environmental conditions.

In summary, current hypotheses of filial cannibalism (i.e., the energy-based and oxygen-mediated hypotheses) are inadequate for generally explaining the adaptive significance of filial cannibalism in fish species. While energetic need and oxygen might be important in some contexts and in some species, neither energy nor oxygen alone can explain the prevalence of filial cannibalism in fishes. Thus, my dissertation work aimed at re-evaluating current hypotheses (Chapters 2 and 3) further supports the need for 1) the development of alternative hypotheses and 2) increased theoretical examination of the importance of a range of factors in the evolution of filial cannibalism.

An Alternative Hypothesis: Selective Filial Cannibalism

Parental care is costly and leads to reduced future reproduction (reviewed in Smith and Wootton 1995). Therefore, males should not waste energy caring for low quality eggs if the cost to the male (i.e., reduced future reproduction) outweighs the current benefit in offspring produced. Specifically, I hypothesize that males should preferentially cannibalize offspring of reduced quality (i.e., offspring that have reduced expected future survival or reproductive success) when there is some energetic benefit of consuming eggs or when offspring survival is density-dependent. The elimination of lower quality offspring has been demonstrated in relation

to selective embryo abortion in humans and plants (Forbes 1997; Diamond 1987; Burd 1998; Karkkainen et al. 1999), brood reduction (Mock and Forbes 1995; Forbes and Mock 1998), and parents allowing or encouraging siblicide of low quality offspring (Stearns 1987), but this idea has not been considered in relation to filial cannibalism. Indeed, the elimination of low quality offspring is thought to play a central role in explaining the evolutionary significance of offspring abandonment and brood reduction (e.g. Stearns 1987, 1992; Forbes and Mock 1998), and thus I hypothesize that the ability to cannibalize offspring selectively might be an important factor in explaining the adaptive significance of filial cannibalism.

I evaluated the hypothesis of selective filial cannibalism in the sand goby (Chapter 4) and the flagfish (Chapter 5). In the sand goby, I examined within-clutch patterns of cannibalism when males received eggs from either one or two females. I focused on the relationship between filial cannibalism and egg size, which has been correlated with post-hatching survival in a range of fishes (reviewed in Kamler 2005). In the single-female scenario, I found that males exhibited no preferences with regard to egg size. In the multiple-female scenario, males preferentially consumed the larger eggs of the second female, but they exhibited no size preferences for the eggs of the first female they spawned with. To evaluate further patterns of egg survival and hatching, I reared subsets of eggs in the absence of males. For the clutches reared in the absence of males, there was no relationship between egg size and survival, but larger eggs took longer to hatch than smaller eggs. Thus, the findings that 1) larger eggs take longer to hatch and 2) males preferentially consume larger eggs of the second female whose eggs are already younger than those of the first female. This pattern suggests that males preferentially consume eggs in a manner that reduces the amount of time they spend caring for the current clutch of eggs (Chapter 4). Specifically, my results (e.g., Figure 4-1) suggest that males might be able to reduce the

duration of time spent caring by several days if they preferentially consume the largest eggs. In Chapter 4, I hypothesize that reducing the duration of time spent caring for a given brood might allow a male to re-enter the mating pool sooner. Specifically, if a male sand goby can reduce the per-clutch time he spends providing parental care, it is possible that he can gain an additional brood cycle, which might in turn increase his net reproductive success. This hypothesis is supported further by the finding that whole clutch cannibalism tends to decrease as the breeding season progresses (Chapter 3). Later in the breeding season, females become scarce and a male's expected future reproduction decreases. Thus, I would expect benefits associated with decreasing the duration of parental care to decrease later in the breeding season.

In the flagfish, I examined the relationship between filial cannibalism and mean egg energetic content and female size (Chapter 5). Whole clutch cannibalism increased as mean egg energetic content increased. In contrast, I found a negative relationship between partial clutch cannibalism and mean energetic content of eggs and maternal size. Egg energetic content and maternal size have been correlated with post-hatching survival in fishes (reviewed in Kamler 2005), and thus, it appears that when males practice whole clutch cannibalism, they preferentially consume their higher quality offspring, which provide a relatively high energetic benefit. However, when males practice partial clutch cannibalism, they preferentially cannibalize offspring that are likely to have lower future survival (Chapter 5). This finding is consistent with other work suggesting that filial cannibalism increases when a brood has relatively low expected reproductive value. For example, whole clutch cannibalism increases when the initial number of eggs present is relatively small (reviewed in Manica 2002) and when males have been cuckolded (e.g., Frommen et al. 2007).

My experiments on selective filial cannibalism in the sand goby and flagfish (Chapters 4 and 5) highlight the potential importance of the hypothesis of selective filial cannibalism. I have demonstrated that males preferentially consume eggs based on aspects of phenotype in some cases. As mentioned previously, selective elimination of low quality offspring is hypothesized to play a large role in the evolution of selective abortion, brood reduction, and offspring abandonment. I therefore hypothesize that selective cannibalism might play a large role in explaining the evolutionary significance of filial cannibalism, but additional theoretical and empirical work in other species is needed to evaluate the relative importance of selective filial cannibalism.

The Plausibility of Multiple Hypotheses

In Chapters 2, 3, 4, and 5, I demonstrated that food availability, paternal condition, density-dependent egg survival, egg size, egg energetic content, and maternal size affects filial cannibalism in the flagfish and/or sand goby. To begin to evaluate the relative importance of these (and other) factors in understanding the evolutionary significance of filial cannibalism, I developed and analyzed a general model of filial cannibalism (Chapter 6). The results of this model suggest that no single benefit of filial cannibalism is essential for the evolution of filial cannibalism. Indeed, my model suggests that the evolutionary dynamics of filial cannibalism appear to be similar to those of other forms of offspring abandonment (Chapter 6). Specifically, the ability to terminate parental care through filial cannibalism, infanticide, brood reduction, or abandonment can represent an adaptive strategy under some conditions (i.e., under certain environmental conditions, for organisms with particular life history characteristics) even when obvious benefits (i.e., energetic gain or benefits to remaining offspring) are absent. That said, benefits associated with energetic gain, offspring survival, and mate preferences certainly exist in

some species under some contexts (e.g., Manica 2004, Payne et al. 2002, Sikkel 1994) and can directly facilitate the evolution of filial cannibalism.

Indeed, I found that the evolution of filial cannibalism was facilitated when (1) parents could selectively cannibalize lower quality offspring or offspring with slower egg development rates (Hypothesis 1, Table 6-2), (2) filial cannibalism increased egg maturation rate (Hypothesis 2, Table 6-2), (3) energetic benefits of eggs existed (Hypothesis 3, Table 6-2), (4) cannibalism increased a parent's reproductive rate (e.g., through mate attractiveness; Hypothesis 5, Table 6-3). Density-dependent egg survivorship alone did not favor the evolution of cannibalism (Hypothesis 4, Table 6-2). However, when egg survival was density-dependent, filial cannibalism invaded more often when the density-dependence was relatively more intense. Additionally, sexual conflict potentially inhibits the evolution of filial cannibalism in some cases (Hypothesis 6, Table 6-2). I also hypothesize that population-level resource competition can play a large role in the evolution of filial cannibalism (Hypothesis 7, Table 6-2). Indeed, in my model, the evolution of filial cannibalism was highly sensitive to population carrying capacity, and filial cannibalism was more likely to evolve when it allowed individuals to utilize resources more efficiently.

In summary, my modeling work (Chapter 6) highlights the plausibility of several non-mutually exclusive alternative hypotheses. Additionally, I argue that attempting to explain the evolutionary significance of filial cannibalism with any single benefit (e.g., energetic need) is futile, and future work should consider the importance of a range of factors.

Future Directions

More research is needed to understand the evolutionary significance of filial cannibalism. Below, I discuss six avenues of future research.

Determining the Relative Importance of Varying Factors

Future work should focus on determining the relative importance of energetic and nutritional benefits of eggs, density-dependent egg survival, mate choice, sexual conflict, and egg quality and size in the evolution of filial cannibalism. Specifically, it will be important to assess the role of such factors in a range of organisms with diverse life histories and under varying conditions. Doing so will help characterize the selection pressures that shape patterns of filial cannibalism. Such an approach will also determine whether particular factors are more likely to affect filial cannibalism than others. Additionally, it will continue to be important to identify additional factors that affect filial cannibalism.

Role of Environmental Variation

Filial cannibalism raises a question that has been dealt with rarely: why do organisms produce more offspring than can survive to maturity? This question has received some attention in regard to selective embryo abortion (e.g., Burd 1988; Forbes and Mock 1998), but it has not been dealt with in relation to filial cannibalism. Some have hypothesized that the over-production of offspring can be favored when (1) the cost of producing additional offspring is relatively small and (2) there is a relatively large benefit associated with the ability to screen and weed out weaker offspring post-fertilization (Mock and Parker 1997; Forbes and Mock 1998). I hypothesize that benefits of screening and weeding out particular offspring post-fertilization are likely greatest when the environment is variable. Specifically, if the environment is static, parents would be expected to accurately gauge and produce some optimal number of offspring of an optimal quality. However, when the environment is highly variable, it presumably becomes more difficult for parents to gauge the optimal number and optimal quality of offspring. The role of environmental variation has not been explored directly in studies of filial cannibalism, but warrants additional research. Specifically, I hypothesize that environmental variability plays a

large role in the evolution of filial cannibalism, and that when the environment is highly variable, filial cannibalism is more likely to be selected for.

The Non-Cannibalistic Parent

As mentioned in Chapter 6, almost all of the focus of filial cannibalism has been on the cannibalistic parent (but see Lindström 2000). Thus, the question remains: what role does a non-cannibalistic parent play in the evolution of filial cannibalism? Lindström (2000) suggested that a non-caring parent might benefit from filial cannibalism if cannibalism by the caring parent increases the probability that the caring parent will successfully rear the clutch. However, the benefits of filial cannibalism to a non-cannibalistic parent remain unknown. Indeed, more empirical work that explicitly quantifies the costs and benefits of filial cannibalism to both parents is needed.

Identification of Additional Species Practicing Filial Cannibalism

For many years, filial cannibalism in fishes was dismissed as a rare behavior with little or no adaptive significance. Since beginning my dissertation work, I've had numerous people mention that their study organisms (e.g., bears, wasps, skinks) exhibit filial cannibalism, but because it was a relatively rare occurrence they didn't give it much thought. This view makes it less likely that researchers will document and investigate filial cannibalism. In the future, it will be particularly important to document filial cannibalism in other taxa. Only then can a truly synthetic framework of filial cannibalism be developed.

A Comparative Framework of Filial Cannibalism

Once filial cannibalism is better documented, it will be important to consider filial cannibalism from a comparative perspective. Using a comparative approach to better understand filial cannibalism is an obvious next step. However, I would argue this approach is currently impossible, in large part because filial cannibalism is not formally documented in many animals.

In particular, a comparative framework of filial cannibalism would facilitate better understanding of the general life-history characteristics that are likely to be associated with filial cannibalism.

Why Don't All Parents Exhibit Filial Cannibalism?

My dissertation research suggests that filial cannibalism represents an adaptive strategy in many contexts and in animals with varying life histories (Chapter 6). If this is the case, why isn't filial cannibalism more common in animals? In fact, I would argue that filial cannibalism is prevalent in animals and that it likely occurs at some level in the majority of animals. However, as discussed previously, filial cannibalism likely isn't documented in species in which it is difficult to detect or relatively infrequent. For animals that never or infrequently exhibit filial cannibalism, it will be important to quantify the costs of filial cannibalism. Indeed, costs of cannibalism in relation to disease transmission have been well-established in several species (Rudolf and Antonovics 2007), and disease transmission as a possible cost of filial cannibalism warrants further attention.

APPENDIX
ISOLATION AND CHARACTERIZATION OF MICROSATELLITE DNA MARKERS FOR
THE FLAGFISH *JORDANELLA FLORIDAE*

The flagfish, *Jordanella floridae*, is a freshwater fish found throughout Florida. Flagfish have been the focus of studies of behavior and evolution (Bonnievier et al. 2003; Klug et al. 2005; Klug and St. Mary 2005), population- and community-level ecology (Jordan and McCreary 1996; Barber and Babbitt 2003; Ruetz et al. 2005), toxicology (Holdway and Sprague 1979; Rowe et al. 1983; Reinert et al. 2002), and conservation biology (McCormick and Leino 1999). Despite such wide-spread interest in the flagfish, published microsatellite DNA markers are not yet available for this species. Such markers will be useful for paternity assays, estimating heritability, and characterizing genetic population diversity in the flagfish. Here, I describe the identification and characterization of 6 polymorphic microsatellite markers isolated from a population of flagfish found in the Otter Creek/Waccasassa River drainage in northwest-central Florida.

I isolated DNA from anal fin clippings using the DNeasy Blood and Tissue Kit (Qiagen). A genomic DNA library from one individual was enriched for CA/GT microsatellite repeats using the protocol described in *Tools for Developing Molecular Markers* (ICBR 2001; modified from Kandpal et al. 1994). I then digested the genomic DNA with *Sau3AI* enzyme and then fractionated the digested DNA using Chroma Spin columns (BD Biosciences) to capture fragments in the size range of 400 bp and larger. The resulting DNA fragments were ligated to *Sau3AI* linkers using T₄ DNA ligase. I used fractionation using Chroma Spin columns to remove excess *Sau3AI* linkers, and the fragments were polymerase chain reaction (PCR) amplified using the *Sau*-Linker-A as the primer. I then denatured the entire PCR library (by heating to 98°C) and hybridized the library to a biotinylated repeat probe (5'-(CA)₁₅TATAAGATA-biotin) at 45°C. The hybridized DNA was recovered using VECTREX Avidin D (Vector Laboratories), and the

resulting DNA was again PCR-amplified using the *Sau*-Linker-A as the primer. The enriched microsatellite libraries were cloned using a TOPO TA kit (Invitrogen) and transformed into *Escherichia coli* cells (One Shot TOPO cells, Invitrogen). I screened the clones using a biotin-labeled (CA)₁₅ probe (Lifecodes) and the chemiluminescent substrate Lumi-Phos 480 (Lifecodes). Clones from positive colonies were grown overnight at 37°C, purified using a Miniprep Kit (Qiagen), and then sequenced using an ABI 377 sequencer (Applied Biosystems).

I designed primers for 23 clones identified to be of sufficient length using OLIGO 6.0 (Molecular Biology Insights). For the 10 clones that PCR-amplified consistently, I ordered and optimized fluorescently-labeled primers (FAM upper primer; Biotech). PCR amplifications were performed in an Eppendorf MasterCycler EP gradient thermocycler. Each 25 µL reaction contained 1 x PCR buffer (Sigma), 800 µM dNTPs, 3.0 mM MgCl₂, 0.26 µM of each primer, 1 U *Taq* polymerase (Sigma), and at least 50 ng template DNA. PCR conditions were as follows: 94°C denaturation for 4 min followed by 30 cycles of 30 s at 94°C, 30 s at the locus specific annealing temperature T_a (Table A-1), and 30 s extension at 72°C, followed by 5 min at 72°C. Samples were run on an ABI 377 Automated DNA Sequencer (Applied Biosystems) and analyzed using GENESCAN and GENOTYPER (Applied Biosystems).

Of the clones that amplified consistently, six were polymorphic (Table A-1) and free of extraneous bands after optimization. I determined microsatellite variability for 37 to 135 individual flagfish (see Table A-1 for locus-specific sample sizes). I calculated observed and expected heterozygosities using POPGENE 1.31 (Yeh *et al.* 1999). I performed tests for deviations from Hardy-Weinberg expectations and linkage disequilibrium using GENEPOP 1.2 (Raymond *et al.* 1995). Expected heterozygosities ranged from 0.69 - 0.84 (Table A-1). Three of the loci (JFJ4, JF511, and JFJ25; Table A-1) showed significant deviations from Hardy-

Weinberg expectations after sequential Bonferroni correction (Rice 1989), suggesting the possibility of null alleles, non-random mating, or the Wahlund effect. None of the loci showed significant linkage disequilibrium after sequential Bonferroni correction. The microsatellite markers described herein will likely prove useful in studies characterizing population genetic diversity, assessing paternity, and quantifying heritability.

Table A-1. Characteristics of flagfish microsatellite loci; shown here are the locus name, primer sequences, repeat motif, optimum annealing temperature (T_a °C), size range, number of alleles (N_A), the number of individuals tested (N), observed heterozygosity (H_O), and expected heterozygosity (H_E). ** indicates statistically significant deviation from Hardy-Weinberg expectations after sequential Bonferroni correction.

Locus	Primer sequences (5'-3')	Repeat motif	T_a	Size range (bp)	N_A	N	H_O	H_E
JFJ25	GGAGGTCTCGAGGTGTTC AACCCTAAAACATCCTAAA	(TG) ₂₂	58	296-329	24	114	0.66	0.83**
JFI3	GGAAAACACTGGAACCTCG ATCATGCATGTGCCTCTAGC	(TG) ₁₉	58	228-252	14	103	0.81	0.84
JFJ4	GATAGAGGTGAGAAGGTGCAA CTGGCTGCGTGCCTGA	(CA) ₁₈	61	275-299	10	135	0.60	0.72**
JF511	CTCTGTTTGTGCGGTTTGTGTA AGAGGCCAAACATGCTACC	(GT) ₂₁	64.9	316-339	15	109	0.58	0.74**
JF5121	AAGGGTCACGGTTAGGCT AAATCTAACTCCCAATCCAA	(GT) ₂₈	60.1	278-288	4	44	0.59	0.69
JF515	GCCATGCGTCGTGAGTCAGA GGAGGGAGGACATTGGG	(CA) ₂₂	65.7	152-180	8	37	0.62	0.75

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BIOGRAPHICAL SKETCH

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