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Parental care, offspring abandonment, and filial cannibalism

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Chapter 1: Costs, benefits, and forms of parental care in relation to offspring survival

Parental care is a fundamental life-history trait that is common among many animals (reviewed in Royle et al. 2012). Parental care has been broadly defined as "any parental trait that enhances the fitness of a parent's offspring, and that is likely to have originated and/or be currently maintained for this function" (Royle et al. 2012). Parental care typically involves a certain level of parental investment, which is referred to as any parental expenditure, including time, energy, or other resources, that benefits offspring fitness but reduces parental ability to invest in other components of their own fitness (Trivers 1972). Because parental care is expected to be beneficial to offspring and costly to parents, previous studies have focused on quantifying the costs and benefits of parental care and the effects of such costs and benefits on how much care is provided to the offspring (Klug & Bonsall 2010; Royle et al. 2012: Chapter 3; Klug & Bonsall 2014). Benefits of care typically include increased survival of the offspring beyond the baseline survival rate that is observed in the absence of care (Klug & Bonsall 2010; Royle et al. 2012: Chapter 3; Klug & Bonsall 2014). Likewise, common costs include decreased parental survival and future reproduction relative to the survival and future reproductive rates observed if parents were to provide no care for their offspring (Klug & Bonsall 2010; Royle et al. 2012: Chapter 3; Klug & Bonsall 2014). The evolution of a given parental care strategy is expected to depend on the various costs and benefits associated with the given strategy.

Though parental care is common among some species, it is complex in how it is manifested. There are several forms of parental care, including male (i.e., paternal), female (i.e., maternal), and bi-parental care. One of the most basic forms of parental care is provisioning of gametes and involves the female supplying energy and nutrients for the egg beyond the amount

required for survival. In some cases, this initial egg provisioning is referred to as initial egg investment (Klug & Bonsall 2010). Such provisioning can increase the egg's size, and therefore the offspring's size and nutrient reserve, thereby increasing the survival fitness of the offspring (Royle et al. 2012, pg. 2). Females may also supply antioxidants, hormones and antibodies to the eggs (Royle et al. 2012, pg. 2). Males can also contribute to the provisioning of gametes by protecting resources females use to produce eggs, being eaten by females after mating, providing them with nuptial gifts, or giving females nutrients or chemicals through ejaculate (Simmons & Parker 1989; Hilker & Meiners 2002). In some species that hatch eggs, the parent may deliberately choose the location of egg laying, which is known as oviposition-site selection and is mainly seen in birds, fish, and amphibians (Refsnider & Janzen 2010). Oviposition-site selection can ensure that the offspring are born in a suitable climate or are sufficiently hidden from any potential predators. Another parental care behavior, nest building and burrowing, is common among many vertebrate and invertebrate species that exhibit care and can increase the offspring's fitness by the parent hiding eggs and juveniles from predators and parasitoids, or by giving them increased protection against environmental factors such as extreme temperature, flooding and desiccation (Royle et al. 2012, pg. 3). The most basic examples of nest building and burrowing include the burial of eggs below the ground surface and the covering of eggs with substrate after spawning (Blumer 1982; Baur 1994).

Another care behavior, egg attendance, occurs when parents stay with their eggs at a constant location after egg laying, which is usually at the oviposition site (Crump 1995). Egg attendance increases offspring fitness by protecting the eggs from various environmental hazards (Royle et al. 2012, pg. 4). Egg attendance has a range of degrees of manifestation, one of which is egg guarding. Egg guarding involves parents actively defending their eggs against predators,

sometimes even approaching or attacking the predator (Royle et al. 2012, pg. 4). Egg attendance can also include incubation in many bird species. Egg brooding is a parental care behavior that involves the parent carrying its eggs around after laying them. Eggs can be carried internally or externally, and by the male or the female. This protects the eggs against predators as well as environmental hazards (Royle et al. 2012, pg. 5). This method also provides parents with a better opportunity to forage while still caring for their offspring and protecting them from the environment. Viviparity is a type of parental care mainly seen in marsupials, in which fertilized eggs are retained in the female reproductive tract. This can provide protection against predators and harsh environmental conditions to the offspring (reviewed in Clutton-Brock 1991).

Food provisioning is a type of parental care in which parents give their offspring a source of food after birth. This food source may be found in the natural environment, or may be previously digested food that the parent regurgitates and feeds to its offspring (Royle et al. 2012, pg. 6). The most extreme form of food provisioning is the process of the offspring eating its mother for nutrition, which is known as matriphagy (Evans et al. 1995; Suzuki et al. 2005). Parental care that is provided after the offspring's nutritional independence is considered a rare form of care. It is most common in longer-lived vertebrates (reviewed in Clutton-Brock 1991). Another extremely rare form of parental care is care of mature offspring, in which the presence of the female parent helps the mature male offspring in his competition with other males, which therefore increases the male's mating success (Surbeck et al. 2011). This overview of parental care behaviors is by no means an exhaustive list. There are many other ways that parents may increase the fitness and survival rate of their offspring, some of which have yet to be extensively researched or studied.

In animals that provide care behavior such as guarding, nest tending, and provisioning, filial cannibalism and/or offspring abandonment is often observed (Klug & Bonsall 2007). Parental care and filial cannibalism/abandonment are typically seen as contradictory processes, given that abandoning and eating offspring decrease offspring survival, and as such it is difficult to see how these behaviors might coexist in nature. However, if we consider the idea that filial cannibalism or offspring abandonment can be beneficial to some other offspring, then these behaviors can be seen as a form of parental care to those offspring that are not eaten or abandoned. There are certain conditions under which we might expect that filial cannibalism or offspring abandonment could be beneficial to offspring. For example, in many cases offspring survival is likely density-dependent (Shepherd & Cushing 1980; Bjørnstad et al. 1999; Einum & Nislow 2005; Vallon et al. 2016), meaning that only a certain number of the total offspring can survive and the mortality rate of offspring increases as offspring density increases. If there are too many offspring in a given clutch, the parents of these offspring are likely unable to effectively care for all of them, disease might spread more rapidly, there might be decreased oxygen availability for each individual egg, or the nest might be more likely to attract predators (Shepherd & Cushing 1980; Bjørnstad et al. 1999; Einum & Nislow 2005; Vallon et al. 2016).

An example of a species in which there are density effects on within-clutch egg mortality is the common goby (*Pomatoschistus microps*). In the common goby, pathogenic water molds spread more easily throughout high density clutches than throughout lower density clutches (Vallon et al. 2016). For this reason, many male parents will eat a certain amount of their offspring before this mold can spread, in order to be able to invest more in the fitness of the surviving offspring. Density effects on within-clutch egg mortality are also observed in other fish species in which the growth of larval fish depends on the abundance of food per larva (Shepherd

& Cushing 1980). If there are more larvae in a given clutch, then there may not be a sufficient amount of food for each fish in the clutch, causing them not to grow as large as they should. Smaller fish are more vulnerable to predators, so most of the offspring from the larger clutches will end up being eaten by predators (Shepherd & Cushing 1980). Among Atlantic salmon (*Salmo salar*) that reside around coral reefs, local density affects within-clutch egg mortality (Einum & Nislow 2005). A given area around a coral reef can only support a limited number of organisms. For this reason, once a given habitat fills up with salmon, other salmon are no longer able to enter and are forced to leave, running the large risk of being eaten by predators (Einum & Nislow 2005). Additionally, the mortality of juvenile cod (*Gadus morhua*) populations in Norwegian coastal waters is affected by density, with death occurring due to cannibalism, competition for habitat, and food limitation among individuals of the population when density is greater (Bjørnstad et al. 1999).

One type of aquatic bird, the cormorant (*Phalacrocorax carbo sinesis*), has been increasing in population size in Europe since the 1970s. The cormorant's offspring survival is affected by within-clutch egg density, because as more cormorants enter an environment, more die off as they succumb to harsh winters. The birds will compete for better quality winter habitats, forcing other birds to live in lower quality habitats where they will die from cold weather and lack of fish to eat (Frederiksen & Bregnballe 2000).

Ostertagia ostertagi, a parasitic nematode of cattle, is a unique example of density effects on offspring mortality. When a large number of the parasite was introduced into cattle, there was a nearly instantaneous death rate of the parasite. This is mainly due to the competition for limited resources among the individual parasites, as well as the triggering of an innate immune response

by the host cattle in order to fight the invasion of too many parasites at one time (Smith et al. 1987).

In mallards (*Anas platyrhynchos*), duckling mortality has been shown to increase as broods of young ducklings increase in density. These ducklings are the most vulnerable in their first two weeks of life, as having too many in a brood doesn't allow the parents to properly care for them in their vulnerable state, resulting in mortality of many individual offspring (Gunnarsson et al. 2006).

In cases such as these, it could be beneficial for the surviving offspring for a certain amount of their clutch to be eaten. The hypothesis that abandonment or filial cannibalism can be forms of parental care has not yet been formally tested, which is what I will do in my thesis (discussed in Chapter 2).

Chapter 2: Offspring abandonment and filial cannibalism as possible forms of parental care (a study)

Introduction

Parental care is a fundamental life-history trait that is found in many animals (reviewed in Royle et al. 2012). Parental care can be paternal, maternal, or bi-parental (reviewed in Royle et al. 2012), and can include behaviors such as egg cleaning (Knouft et al. 2003), egg guarding (Royle et al. 2012, pg. 4), egg provisioning (Simmons & Parker 1989; Hilker & Meiners 2002; Royle et al. 2012, pg. 2), and oviposition-site selection (Refsnider & Janzen 2010). Such forms of parental care commonly co-occur with other behaviors such as offspring abandonment (Lack 1954; Rettig 1978; Clark & Wilson 1981; Nuechterlein & Johnson 1981; Maple 2002) and filial cannibalism (i.e., the consumption of one's offspring; Rohwer 1978; Hoelzer 1995; Payne et al. 2002; Klemme et al. 2006; Klug & Bonsall 2007). Offspring abandonment and filial cannibalism have typically been viewed as evolutionary conundrums that are contradictory to parental care (e.g., Klug & Bonsall 2007). However, some authors have noted that offspring abandonment and filial cannibalism might occur in response to density-dependent egg mortality (i.e., a situation in which offspring mortality increases as offspring density increases; Lack 1954; Clark & Wilson 1981; Payne et al. 2002; Payne 2003; Klug & Bonsall 2007; Zuckerman et al. 2014). If egg survival is density dependent such that removing some offspring from a clutch improves the overall survival of remaining offspring, offspring abandonment and filial cannibalism might themselves be forms of parental care that benefit remaining offspring, where they can then be selected for, spread, and maintained in a population. In many cases, selection is expected to act at the level of the gene (see selfish gene hypothesis discussion in Dawkins 1976), and as such, we
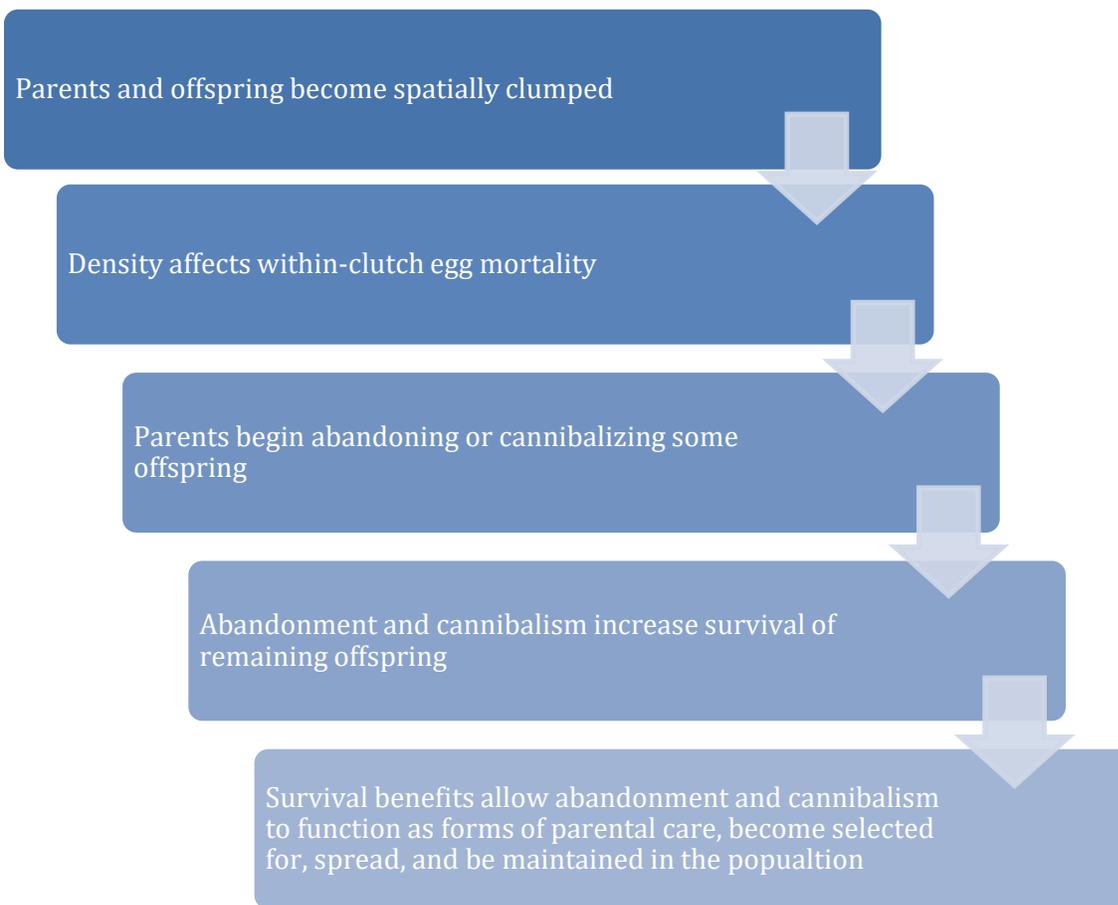
would expect behaviors that increase an individual's inclusive fitness to be selected for and evolve. To the best of our knowledge, the idea that offspring abandonment and filial cannibalism—two behaviors that at first glance seem detrimental to offspring fitness—might themselves actually be forms of parental care, even in the absence of other more conventional care behaviors, has not been explicitly considered previously. Below, we outline how abandonment and filial cannibalism might serve as forms of care, particularly during the early evolution of care, and we then develop a mathematical model of offspring abandonment and filial cannibalism to determine whether these behaviors can function as forms of parental care and be selected for evolutionarily.

Parental care behaviors such as provisioning, cleaning, and thermoregulation typically require offspring to be clumped spatially (McNally & Schneider 1996). Given this, we would often expect offspring density to increase early in the evolution of parental care. If offspring become clumped spatially early in the evolution of parental care—either because other forms of care require such clumping or for some other reason (e.g., because eggs are deposited in a territory, e.g., Baylis 1981)—we might then expect offspring mortality to be influenced by within-clutch density. For example, when offspring are present at high density, there is potentially increased disease transmission (Vallon et al. 2016), decreased oxygen availability (Payne et al. 2002), and/or decreased food availability (Shepherd & Cushing 1980; Frederiksen & Bregnballe 2000). Indeed, density-dependent offspring mortality has been found in a range of systems (Smith et al. 1987; Bjørnstad et al. 1999; Einum & Nislow 2005; Gunnarsson et al. 2006; Vallon et al. 2016).

Because increased offspring density often leads to increased offspring mortality, certain strategies typically viewed as unconventional, such as offspring abandonment and/or

cannibalism, might, as mentioned above, function as forms of parental care when offspring density within a clutch is high. In this study, we utilize mathematical modeling to test this hypothesis. We explore the fitness benefits associated with offspring abandonment and filial cannibalism when egg mortality is either affected by within-clutch egg density or not affected by within-clutch egg density. We expect that when egg mortality is affected by within-clutch density, abandonment and/or filial cannibalism can be selected for due to increases in overall offspring survival (see Figure 1); in contrast, we would expect abandonment and/or cannibalism to be associated with no benefits or relatively weak benefits when egg survival is not affected by within-clutch density.

Figure 1. An outline of how offspring abandonment and filial cannibalism could function as parental care early in the evolution of care.

Parents and offspring become spatially clumped

Density affects within-clutch egg mortality

Parents begin abandoning or cannibalizing some offspring

Abandonment and cannibalism increase survival of remaining offspring

Survival benefits allow abandonment and cannibalism to function as forms of parental care, become selected for, spread, and be maintained in the popualtion

Materials and Methods

Using an evolutionary ecology model following Klug & Bonsall (2010) (see also: Vincent & Brown 2005; Klug & Bonsall 2007; Otto & Day 2007; Klug & Bonsall 2014), a rare mutant that exhibits either offspring abandonment or filial cannibalism is introduced into a resident population in which no abandonment or cannibalism occurs (see Equations 1-22 in Appendix 1 for full model details). The resident population is assumed to be in equilibrium (Equations 3-4 in Appendix 1), and we can then ask whether the rare mutant that exhibits either offspring abandonment or filial cannibalism can invade the resident population. In other words, we can identify if abandonment and filial cannibalism can increase overall offspring survival (i.e., function as a form of parental care for remaining offspring) and therefore result in positive fitness that would allow the mutant strategy to invade and spread in the population.

Following Klug & Bonsall (2007, 2010), newborn individuals undergo egg and juvenile stages before maturing and reproducing as adults. It is assumed that the resident and the mutant individuals have the same baseline death, maturation, and reproductive rates (i.e., mutants and residents have the same basic life-history parameters; Appendix 1). The mutant strategy then differs from that of the resident in two ways: First, as mentioned in the introduction, we would expect offspring to become spatially associated with parents during the early evolution of parental care; as such, within-clutch density is expected to increase early in the evolution of parental care, and we therefore assume that mutant egg survival is affected by within-clutch density. Specifically, as within-clutch density increases (r_m in Equation 5 in Appendix 1), egg mortality increases for mutants (Equations 17-18 in Appendix 1). In our model, the spatial clumping of parents and offspring is implicit, and we are not modeling explicit spatial structure. Second, resident and mutant individuals also differ because mutants can either exhibit offspring

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abandonment (i.e., they remove some offspring from the clutch; Equation 15 in Appendix 1) or

filial cannibalism (i.e., they consume some of their own offspring; Equation 16 in Appendix 1),

and both abandonment and cannibalism increase egg mortality (Equations 15 and 16 in

Appendix 1). When parents consume offspring, they receive some energetic benefit such that

cannibalism increases adult mutant survival (Equation 21 in Appendix 1). Both abandonment

and cannibalism reduce clutch density and therefore reduce the magnitude of density effects on

egg mortality (Equations 19-20 in Appendix 1). The full model dynamics are presented in

Appendix 1.

For each of the two strategies—abandonment and cannibalism—we model and present

two different scenarios: one in which density effects on within-clutch egg mortality are present

and another in which these density effects are absent; in doing so, we are able to determine if the

effect of density on within-clutch egg mortality allows abandonment and/or cannibalism to result

in net positive fitness and function as forms of parental care to remaining offspring.

Results

*Can offspring abandonment function as a form of parental care?*

When mortality within a clutch increases as within-clutch egg density increases, offspring

abandonment can function as a form of parental care, and the fitness associated with

abandonment is positive over a range of levels of abandonment (Figure 2A, solid line). When

egg mortality does not depend on within-clutch egg density, the fitness of abandonment is

negative relative to the no abandonment scenario across the parameters considered (Figure 2A,

dashed line). Thus, the positive fitness that results from offspring abandonment in this scenario is

due to the presence of density effects on egg mortality within a clutch. The qualitative patterns were similar across a range of levels of density effects on egg mortality (Appendix 2).
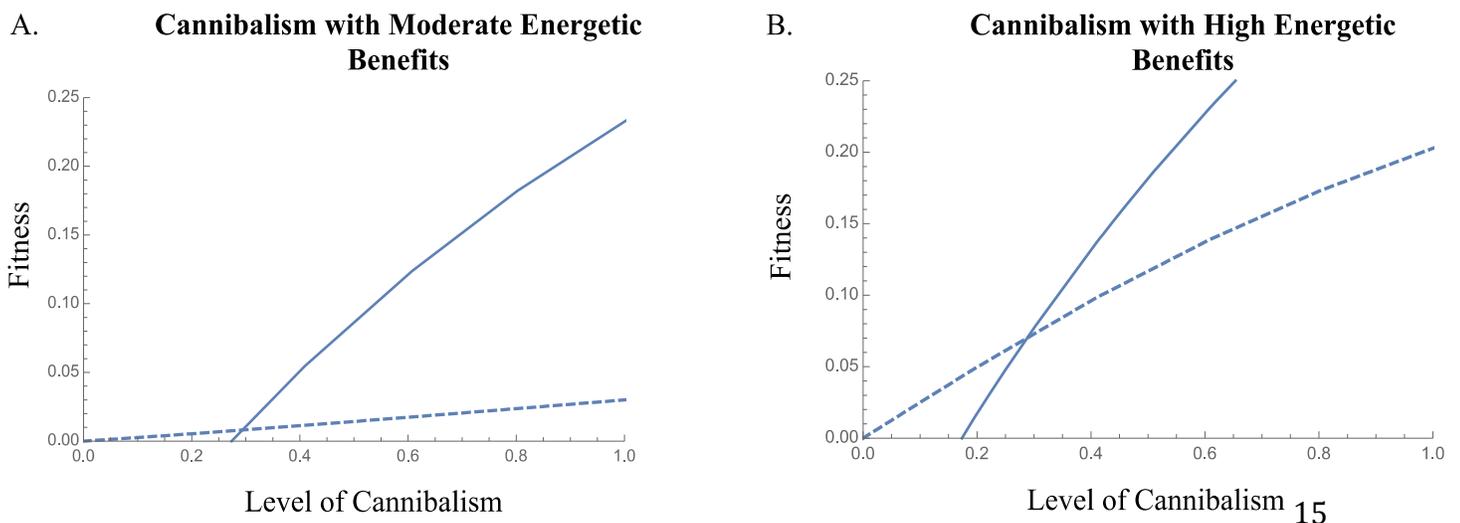
Can filial cannibalism function as a form of parental care?

Filial cannibalism that is associated with energetic benefits to parents and that reduces the effects of density on the within-clutch egg mortality can also function as a form of parental care (Figure 2B, solid line). Indeed, filial cannibalism that reduces density, thereby decreasing overall mortality within a clutch, is associated with relatively high fitness in comparison to the scenario in which there are no effects of density on within-clutch egg mortality (Figure 2B, dashed line). As such, the within-clutch effects of density on egg mortality allow filial cannibalism to function as a form of care. Another factor that influences the fitness of filial cannibalism is the level of the energetic benefits provided to the parent by eating their young. In Figure 2B, we assume relatively low energetic benefits. If, however, the energetic benefits of cannibalism are assumed to be moderate or relatively high, energetic benefits of eating offspring can allow filial cannibalism to be associated with positive fitness even when there are no effects of density on within-clutch egg mortality (Figure 3A-B, dashed lines). These qualitative patterns were similar across a range of levels of density effects on egg mortality (Appendix 2).

Figure 2. Within-clutch effects of density on egg mortality allow offspring abandonment and filial cannibalism to function as forms of parental care. When (A) egg mortality increases as within-clutch egg density increases, offspring abandonment can function as a form of parental care and is associated with positive fitness over a range of levels of abandonment (solid line). In contrast, if egg mortality does not increase as within-clutch egg density increases, then offspring abandonment will not function as a form of parental care, and fitness associated with offspring abandonment will always be negative (dashed line). When (B) filial cannibalism reduces the density effects of egg mortality within a clutch and provides some energetic benefits to the parent, cannibalism can function as a form of parental care and has positive fitness among ranges of levels of cannibalism (solid line). If, however, filial cannibalism does not reduce the density effects of egg mortality in a clutch, then filial cannibalism will not evolve as a form of parental care in the population (dashed line; note: the dashed line overlaps with the x-axis).

A. **Offspring Abandonment**

B. **Filial Cannibalism**
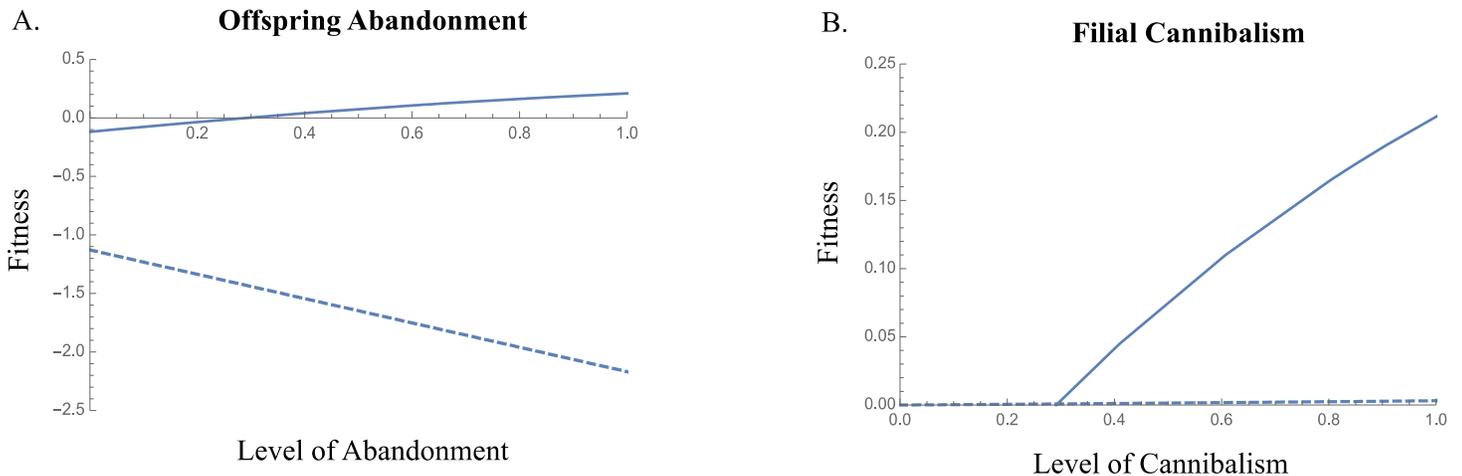
Figure 3. Level of energetic benefits provided to the parent by eating their young influences the fitness of filial cannibalism. When (A) cannibalism provides moderate energetic benefits to the parent, fitness associated with filial cannibalism starts to become positive even when there are no effects of density on within-clutch egg survival (dashed line). Additionally, when (B) cannibalism provides high energetic benefits to the parent, the fitness associated with filial cannibalism increases relative to that of moderate energetic benefits, even when there are no density effects on within-clutch egg survival (dashed line).

A. **Cannibalism with Moderate Energetic Benefits**

B. **Cannibalism with High Energetic Benefits**

Discussion

Our results illustrate that offspring abandonment and filial cannibalism can indeed function as forms of parental care, resulting in positive net fitness under certain circumstances (Table 1). Here, the positive net fitness of these strategies is a result of the benefits of abandonment and cannibalism (i.e., increased offspring survival of the remaining offspring and, in the case of cannibalism, energetic benefits to the parent) outweighing the costs of abandonment and cannibalism (namely, initial loss of a certain amount of the eggs within a clutch). This positive net fitness, however, is largely contingent on the presence of density effects on within-clutch egg mortality. As mentioned previously, density has been found to affect egg survival in a range of species (Smith et al. 1987; Bjørnstad et al. 1999; Einum & Nislow 2005; Gunnarsson et al. 2006; Vallon et al. 2016), and as such, abandonment or cannibalism might function as forms of parental care in such species. It is important to note that the quantitative fitness results might change if the resident and/or mutant parameters were to be changed in the mathematical model used. Nonetheless, our results illustrate that under some conditions abandonment and cannibalism can be forms of care. However, not all abandonment and cannibalism is beneficial. It can be challenging for these strategies to evolve initially because parents have to abandon or consume a non-trivial amount of offspring before abandonment or cannibalism become beneficial, which could explain why we don't see abandonment and cannibalism in all species.

In general, our results suggest that we would expect abandonment and filial cannibalism to be able to invade a resident population lacking these strategies when local, within-clutch density affects offspring mortality. Contrarily, though, when within-clutch density effects do not affect egg mortality, we would expect neither offspring abandonment nor filial cannibalism to evolve as forms of parental care. Offspring abandonment or filial cannibalism could, however,

evolve due to other selective pressures. For example, previous authors have suggested that energetic benefits (Rohwer 1978; Manica 2002), lack of oxygen (Payne et al. 2002), offspring development (Klug & Bonsall 2007), and resource or mate competition (Klug & Bonsall 2007) can independently favor filial cannibalism. Likewise, our findings are consistent with the hypothesis that offspring abandonment will be selected for in some cases (e.g., Lack 1954; Clark & Wilson 1981). Once again, this highlights that selection is acting at the level of the gene and traits that improve inclusive fitness can evolve even in if they reduce the fitness of some offspring (Dawkins 1976). However, to the best of our knowledge, the hypothesis that filial cannibalism and abandonment can actually function as forms of parental care—even in the absence of more traditional care behaviors such as guarding or provisioning—has not been explicitly considered prior to the work presented herein. Indeed, while offspring abandonment and filial cannibalism are typically seen as contradictory to parental care, our results illustrate that they might actually not be as contradictory as is commonly thought.

Table 1. Overview of the conditions under which offspring abandonment and filial cannibalism might evolve.

	Offspring Abandonment	Filial Cannibalism
No Density Effects	Fitness is negative, will not evolve as a form of care	Will not evolve as a form of care
Moderate Density Effects	Fitness is positive, will evolve as a form of care	Fitness is positive, will evolve as a form of care
Weak Density Effects	Fitness is positive, will evolve as a form of care	Fitness is positive, will evolve as a form of care
Strong Density Effects	Fitness is positive, will evolve as a form of care	Fitness is positive, will evolve as a form of care
Moderate-to-High Energetic Benefits with No Density Effects		Fitness is positive, will evolve as a form of care

Acknowledgements

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Appendix 1.

Model Dynamics

<u>Resident Parameters:</u>

Individuals pass through an egg (E), juvenile, and adult stage (A). In the population, eggs increase as adults reproduce and decrease as eggs mature and as they die, such that

$$\frac{dE}{dT} = r \cdot A(t) \cdot [1 - \frac{A(t)}{K}] - d_E \cdot E(t) - m_E \cdot E(t). \tag{1}$$

Here, r represents the rate of egg fertilization by individual adults in the population; as such, in this model, r can be thought of as a measure of within-clutch egg number. The term d_E represents egg death rate and m_E represents egg maturation rate. The population has a carrying capacity represented by K, and adult reproduction is restricted by density-dependence. Adults in the population increase as eggs mature and pass through the juvenile stage, and decrease as adults die, such that

$$\frac{dA}{dT} = m_E \cdot E(t - \tau) \cdot \sigma_J - d_A \cdot A(t). \tag{2}$$

Here, τ represents the length of the juvenile stage and σ_J represents the rate of survival through the juvenile stage.

The equilibrium densities in the resident population are:

$$E^* = \frac{d_A * A^*}{m_E \cdot \sigma_J}, \tag{3}$$

and

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

Mutant Dynamics and Fitness

The following equations provide the invasion dynamics of the rare mutant:

$$\frac{dE_m}{dt} = r_m \cdot A_m(t) \cdot \left[1 - \frac{A^*}{K}\right] - d_{E_m} \cdot E_m(t) - m_{E_m} \cdot E_m(t) \tag{5}$$

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

Here, the subscript *m* is used to show that these variables relate to the mutant strategy of abandoning or cannibalizing offspring, and A^* represents the equilibrial abundance of the resident adult population. Because the mutant is assumed to be rare, mutant reproduction is limited by competition with adult residents (Equation 5). For mutants, parents are assumed to be spatially associated with their young. Given this, r_m can be thought of as a measure of within-clutch density.

Unless otherwise noted, all resident parameters are equal to their corresponding baseline values, such that:

$$d_E = d_{E_0} \tag{7}$$

$$r = r_0 \tag{8}$$

$$\sigma_J = \sigma_{J_0} \tag{9}$$

$$d_A = d_{A_0} \tag{10}$$

Additionally, unless otherwise noted below, all mutant parameters are equal to their corresponding baseline values, such that:

$$d_{E_m} = d_{E_{m_0}} \tag{11}$$

$$r_m = r_{m_0} \tag{12}$$

$$\sigma_{J_m} = \sigma_{J_{m_0}} \tag{13}$$

$$d_{A_m} = d_{A_{m_0}} \tag{14}$$

In other words, except for where noted below, we assume no trade-offs on mutant or resident parameters.

Mutant Trade-offs Associated with Abandonment and Cannibalism

When mutant parents exhibit offspring abandonment or filial cannibalism, the baseline mutant egg death rate is equal to the baseline resident egg death rate plus the level of abandonment or cannibalism exhibited, such that:

$$d_{E_{m_K}} = d_{E_{m_0}} + K \tag{15}$$

where *K* is equal to the rate of egg abandonment, and

$$d_{E_{m_\beta}} = d_{E_{m_0}} + \beta \tag{16}$$

where β represents the rate of filial cannibalism. Thus, the rate of egg mortality initially increases as eggs are directly lost due to abandonment or cannibalism.

In scenarios in which there are density effects on within-clutch egg mortality, the mutant egg death rate then increases as mutant within-clutch density (r_m) increases:

$$d_{E_{m_{dd}}} = 1 - ((1 - d_{E_{m_K}}) * Exp[-((1 - d_{E_{m_K}}) + (r_{m_0} * z))]) \tag{17}$$

for the case of abandonment, and:

$$d_{E_{m_{dd}}} = 1 - ((1 - d_{E_{m_\beta}}) * Exp[-((1 - d_{E_{m_\beta}}) + (r_{m_0} * z))]) \tag{18}$$

for the case of filial cannibalism. Here, *z* represents the magnitude of density effects acting on egg mortality, and the magnitude of density effects on egg mortality increases as the value of *z* increases. Using this invasion analysis approach, the mutant strategy of either abandonment or cannibalism is assumed to be rare, so we would expect these density effects to be relatively small

during the early evolution of abandonment or cannibalism (see parameter values below for additional information of the magnitude of density effects considered).

When we consider the case in which there are no density effects on egg mortality, $d_{E_m} = d_{E_{m_0}}$, as mentioned in Equation 11 above.

When density affects within-clutch egg mortality, the rate of abandonment or cannibalism offsets the effects of density on egg mortality, such that:

$$d_{E_m} = d_{E_{m_{dd}}} * Exp\ [-K] \qquad (19)$$

for the case of offspring abandonment, and:

$$d_{E_m} = d_{E_{m_{dd}}} * Exp\ [-\beta] \qquad (20)$$

for the case of filial cannibalism.

When parents abandon their offspring, we assume that offspring are killed or removed from the vicinity of the parent and other offspring (e.g., they might be pushed out of a nest of removed from a territory). When parents exhibit filial cannibalism, we assume that there is an energetic benefit of eating eggs that leads to increased parental survival, such that:

$$d_{A_m} = d_{A_{m_0}} * Exp[0.01 * \beta] \qquad (21)$$

Here, 0.01 represents the relative level of energetic benefits provided to the parent through filial cannibalism. In this model, 0.01 is used to represent relatively low energetic benefits of cannibalism, but other values are modeled in Figures 2A-B to represent moderate and high energetic benefits of cannibalism.

Invasion Matrix for the Invading Strategies

The fitness level of the mutant can be calculated by taking the determinant of the following

matrix:

$$\lambda + d_{E_m} + m_{E_m} \qquad\qquad r_m[1 - \frac{A^*}{K_m}]$$

$$m_{E_m} * \mathrm{Exp}(-\lambda \cdot \tau) \cdot \sigma_{J_m} \qquad \lambda + d_{A_m} \qquad\qquad\qquad \textbf{(22)}$$

and solving the resulting equation for λ. Here, λ represents the measure of fitness of the mutant

strategy relative to the resident strategy (Klug & Bonsall 2010). When λ is positive, the mutant

strategy (abandonment or filial cannibalism) is associated with positive fitness and would be

expected to be able to invade the resident strategy of no abandonment/no cannibalism.

In all cases, the baseline parameters were as follows in our analyses:

$d_{E_0} = d_{E_{m_0}} = 0.3$, $d_{A_0} = d_{A_{m_0}} = 0.4$, $m_E = m_{E_m} = 0.4$, $K = K_m = 50$, $r = r_m = 25$, $\sigma_J = $

$\sigma_{J_m} = 0.01$, $\tau = \tau_m = 0.1$, and $z = 0.01$.

Note: for our simulations presented in the main text, we used the value 0.01 for z, but in

Appendix 2 we consider different values for z, including 0.1 to represent strong density effects

on within-clutch egg mortality and 0.001 to represent weak density effects on within-clutch egg

mortality.

Appendix 2. **A consideration of varying density effects on within-clutch egg mortality.** When egg mortality increases within a clutch as egg density increases, density effects on egg survival are present. We varied the effect of density on egg mortality (z in equations 17 and 18 in Appendix 1). When the density effects on within-clutch egg mortality are relatively strong (Fig. A1 and A3; see Appendix 1 for details of strong, moderate, and relatively weak density effects), the resulting fitness of offspring abandonment and filial cannibalism, respectively, is only slightly higher than that of scenarios depicting relatively weak density effects (Fig. A2 and A4). Among the scenarios that show strong (Fig. A1 and A3), weak (Fig. A2 and A4), and moderate (Fig. 1A-B, solid lines) density effects on within-clutch egg mortality, there does not appear to be a large difference in resulting fitness. Thus, the qualitative fitness patterns are similar among offspring abandonment and filial cannibalism at varying ranges of density effects on within-clutch egg mortality.

Figure A. Varying density effects on within-clutch egg mortality. When density effects on within-clutch egg mortality are relatively strong (A1 and A3), the resulting fitness of offspring abandonment or filial cannibalism is only slightly higher than that resulting from relatively weaker effects of density on within-clutch egg mortality (A2 and A4).

A1.
Offspring Abandonment with Strong Density Effects

A2.
Offspring Abandonment with Weak Density Effects

A3.
Filial Cannibalism with Strong Density Effects

A4.
Filial Cannibalism with Weak Density Effects