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I/We declare we have no competing interests

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HK and MBB both contributed to the conceptual framework, model development and analyses, and manuscript preparation.

**CO-EVOLUTION INFLUENCES THE EVOLUTION OF FILIAL CANNIBALISM, OFFSPRING
ABANDONMENT, AND PARENTAL CARE**

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ABSTRACT

Understanding evolutionary patterns of parental investment and care has been a longstanding focus in studies of evolutionary and behavioral ecology. Indeed, patterns of investment and care are highly diverse, and fully understanding such diversity has been challenging. Recently, several studies have highlighted the need to consider co-evolutionary dynamics in studies of parental care, as parental care is likely to co-occur and co-originate with a range of other traits. Two traits that commonly co-occur with parental care are offspring abandonment (the termination of parental investment prior to full independence in offspring) and filial cannibalism (the consumption of one’s offspring). Here, we use a mathematical framework to explore how co-occurrence and co-evolution among care, abandonment, and cannibalism can influence the life-history conditions under which care is expected to evolve. Our results suggest that in some cases the evolution of parental care can be inhibited by offspring abandonment and filial cannibalism. In other cases, abandonment and filial cannibalism that benefits parents can promote the evolution of parental care. It is particularly interesting that behaviors that seem so contrary to care—that is, eating or abandoning one’s young—can in some cases broaden the conditions under which care can evolve. In general, our findings highlight that considering co-occurrence and co-evolutionary dynamics between two or more traits is essential to understanding the evolution of trait diversity.

Background

Understanding diversity in life-history strategies is a long-standing focus of studies of evolutionary biology (1-6). Parental investment (any parental expenditure that benefits offspring fitness but reduces a parent's ability to invest in other aspects of fitness, (7)) is a fundamental life-history trait (1, 2, 8, 9). The magnitude of parental investment varies widely both within and across taxonomic groups (reviewed in: (1, 2, 9-11)). For example, in some species, one or both parents provide extensive care that can include provisioning, protection from predators, thermoregulation, and behavioral support of offspring in intra-specific interactions (reviewed in: (12, 13)). In other species, however, post-hatching or post-oviposition parental care is entirely absent (reviewed in: (9, 11)). In such cases, parental investment often consists solely of the provisioning of resources into eggs (2) and offspring are left to fend for themselves after fertilization or asexual reproduction. Why such variation in parental investment exists in nature remains a key unresolved question in evolutionary ecology (1, 2, 8, 9).

We currently know that variation in parental investment can be influenced by individual- and population-level factors. For example, in some cases, greater parental investment is expected when offspring mortality in the absence of care is high (i.e., when offspring need care the most (2, 14)) and when fertilization mode is internal (10). Likewise, parental investment can be influenced by ecological factors, such as breeding pool size (15) and predation (16, 17). Mating systems and sexual selection are also known to influence parental investment and care (reviewed in: (8, 18-22)). For instance, in some cases, sexual selection can lead to the evolution of paternal care (18).

In addition to focusing on individual-level traits and characteristics of populations, some studies have emphasized the need to consider how co-evolutionary dynamics can influence parental investment (e.g., (8, 19, 23-25). Multiple mating by females, for instance, can lead to paternity uncertainty, which has been hypothesized to lead to the evolution of reduced paternal investment (21) (see also more recent discussion of this hypothesis in: (8, 26, 27)). Likewise, when providing care is associated with greater mortality than competing for mates, co-evolutionary feedback can occur such that individuals of the non-caring sex will experience relatively low mortality, become relatively common in the population, and have difficulty finding a mate; this, in turn, can lead to selection for greater parental investment by both sexes (19).

Despite some attention on the influence of co-evolutionary dynamics on parental investment and care, we still know relatively little about which traits can facilitate or inhibit the evolution of increased parental investment (25). That is, we know little about whether certain traits are likely to co-occur and co-evolve with and influence the likelihood of parental care evolving. In particular, relatively few studies focus on generating *a priori* predictions of which traits can facilitate the evolution of increased parental investment; this means that in many cases researchers are forced to rely on *post hoc* explanations when varying patterns of parental investment are observed (see discussion of this issue in (8)).

To expand our understanding of how co-evolutionary dynamics influence the evolution of parental investment, we focus on the relationship between the evolution of parental care, a key form of parental investment, and two behaviors that initially seem contrary to care: offspring abandonment (the termination of parental investment prior to full independence in offspring) and

filial cannibalism (the consumption of one's offspring). We focus on these two behaviors as species across a range of taxa abandon their young prior to independence by aborting them (e.g., ((28)), removing them from a nest or territory, or simply terminating parental care (1, 2, 9). Likewise, filial cannibalism co-occurs with, or in some cases might precede the evolution of, care in a range of animals, including fish, birds, mammals, and insects (29). For instance, in a species in which parental care is thought to be relatively recently evolved, the flagfish (*Jordanella floridae*), males both cannibalize and care for their young, suggesting that cannibalism can potentially occur relatively early in the evolution of care (30).

Filial cannibalism and offspring abandonment are often viewed as evolutionary conundrums that are antagonistic to parental care (but see (31, 32)). However, as of yet, it is unknown whether the co-occurrence of care and abandonment or filial cannibalism might affect the likelihood of parental care evolving. Here, we use a mathematical framework to explore whether offspring abandonment and filial cannibalism affect the likelihood that parental care will be selected for. In doing so, we identify whether co-occurrence and co-evolutionary dynamics between care and abandonment or filial cannibalism can alter the conditions under which increased parental investment is expected to occur. We consider cases in which abandonment has no benefit to parents (i.e., it does not offset costs of care) and scenarios in which it benefits parents by offsetting care. Filial cannibalism is assumed to be associated with energetic benefits to parents (33, 34). Filial cannibalism has also been found to be selective with respect to the development rate of offspring, as preferentially consuming slower developing young can reduce the duration and costs of care (35). It is possible that abandonment might, in some cases, also depend on offspring development. As such, we additionally consider scenarios in which filial cannibalism

and offspring abandonment are selective such that parents preferentially consume or abandon slower developing young. In all scenarios, abandonment or cannibalism are assumed to co-originate with care.

MATERIALS AND METHODS

(a) Model overview

We develop an evolutionary ecology model that is based on our previous theoretical work (13, 29, 31, 32, 36, 37) in which a rare mutant (i.e., a mutant strategy that is rare relative to a resident strategy) 1) provides parental care that increases offspring egg survival, 2) provides parental care that increases offspring egg survival *and* exhibits offspring abandonment, or 3) provides parental care that increases offspring egg survival *and* exhibits filial cannibalism. The mutant is introduced into a resident population that exhibits no abandonment, cannibalism, or parental care and that is in ecological equilibrium. We then ask whether the rare mutant exhibiting parental care is more or less likely to invade the resident population of no care when offspring abandonment or filial cannibalism co-originate and co-occur with care. In doing so, we identify whether abandonment or cannibalism can inhibit or facilitate the conditions under which parental care can evolve.

In our model, we assume a stage-structured system in which individuals pass through egg and juvenile stages and then mature and reproduce as adults, as such a system is likely to be applicable to a range of animals. The mutant and resident individuals experience the same

baseline conditions (i.e., the same death, maturation, and reproductive rates prior to accounting for care, abandonment, or cannibalism). Parental care is then assumed to be associated with benefits to offspring (increased egg survival beyond the baseline survival rate in the absence of care) and costs to the parent providing it (decreased parental survival and future reproduction). In this study, we assume that abandonment of eggs and filial cannibalism both decrease egg survival as eggs are abandoned or consumed. In some cases, abandonment and cannibalism can be beneficial to remaining offspring, particularly when offspring survival depends on within-clutch density (discussed in (32)). In the current model, we focus on cases in which abandonment and cannibalism negatively impact young, as these are the conditions under which it is more difficult to make *a priori* predictions about whether abandonment or cannibalism could ever facilitate the evolution of care.

Filial cannibalism is assumed to be associated with an energetic benefit to parents, such that consuming eggs increases parental survival and future reproduction. For abandonment, we consider both scenarios in which abandonment is 1) beneficial to parents (e.g., due to decreased investment in abandoned young, reduced risk of predation, increased re-mating opportunities) and 2) not beneficial to parents, which would be realistic if, for instance care is shareable among offspring and abandoning some young does not reduce energetic investment, risk of predation, or costs associated with missed mating opportunities. We also consider scenarios in which filial cannibalism and offspring abandonment are selective with regard to the development rate of young (see also (29)). These costs and benefits of care, abandonment, and cannibalism are described in detail below.

(b) Model dynamics

To explore the evolutionary invasion potential of parental care, abandonment, and cannibalism, we first identify the dynamics of the resident individuals that provide no care and exhibit no cannibalism or abandonment (see discussion of invasion analysis methods in (38)). Resident individuals pass through an egg (E), juvenile, and adult stage (A). Eggs increase as adults reproduce and decrease as eggs mature and as eggs die:

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

where r represents the rate of egg fertilization by individual adults in the population, d_E represents egg death rate, and m_E represents egg maturation rate. The population has a carrying capacity of 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

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

where τ represents the length of the juvenile stage and σ_J represents the rate of survival through the juvenile stage. The resident will be in ecological equilibrium (38) when $\frac{dE}{dt} = \frac{dA}{dt} = 0$. The equilibria are thus:

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

and

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

After identifying the resident dynamics, we then identify the dynamics of mutant individuals (38). Prior to accounting for care and benefits of cannibalism or abandonment (discussed below), the egg-stage mutant dynamics for offspring abandonment and filial cannibalism follow:

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

The mutant strategy experiences the same general demography as the resident strategy. As with the resident strategy, mutant eggs increase in density as adults reproduce and decrease as eggs die or mature and leave the egg stage. Here, the subscript m denotes the mutant strategy of providing care and abandoning or cannibalizing offspring. The variable A^* represents the equilibrium abundance of the resident adult population. The mutant is assumed to be rare (i.e., $A_m(t)$ and $E_m(t)$ are assumed to be small), and as such, mutant reproduction is limited by competition with adult residents. That is, through competition for resources that limit reproduction, mutant and resident individuals are assumed to interact. In all analyses, we assume that $K_m = K$ (i.e., mutants and residents are assumed to experience the same carrying capacity). The variable β represents the rate of behavior—i.e. offspring abandonment or filial cannibalism—both of which decrease the number of surviving mutant eggs in this model, although they can also be associated with benefits to parents (discussed below). Specifically, the number of eggs abandoned or consumed at any point in time t will equal the rate of abandonment

or cannibalism multiplied by the number of eggs present. Likewise, the number of eggs abandoned or cannibalized at time t in the population will also depend on the number of adults present in the population that exhibit those behaviors. Importantly, the baseline egg-stage dynamics for abandonment and cannibalism (eqn. 5) are identical to one another with the exception of whether abandonment or cannibalism occurs. Both abandonment and cannibalism can be beneficial to parents in relation to offsetting costs of care. However, abandonment and cannibalism differ in that cannibalism is also associated with energetic benefits to parents. As such, cannibalism is assumed to be associated with greater benefits than abandonment (discussed below).

The adult-stage mutant dynamics for both abandonment and cannibalism follow:

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

As with the resident strategy, mutant adults increase in density as mutant eggs mature, survive, and pass through the juvenile stage and decrease in density as adults die. For mutants, parents are assumed to be spatially associated with their young, although the cause of this spatial association is not explicit in our model.

(c) Costs and Benefits of Parental Care, Offspring Abandonment, and Filial Cannibalism

Parents affect offspring survival by 1) investing energy and nutrients into eggs (referred to as initial egg allocation) and 2) providing post-oviposition parental care behavior (referred to as

parental care). Baseline egg death rate (d_{E_o} or $d_{E_{mo}}$) is our measure of initial egg allocation, and as such eggs have greater survival when there is relatively greater initial egg allocation, but this initial egg allocation is costly such that it reduces parental survival (d_A and d_{Am}) and future reproduction (r and r_m) (eqns. 7-8, 10-11). Likewise, parental care (c) reduces mutant egg death rate (eqn. 9 but is costly such that it reduces parental survival and reproduction (eqns. 10-11).

Survival and reproductive costs of egg allocation (residents):

$$d_A = 1 - [(1 - d_{Ao}) * \text{Exp}(- (1 - d_{E_o}))] \quad (7)$$

$$r = r_o * \text{Exp}[-(1 - d_{E_o})] \quad (8)$$

Benefits of parental care (mutants):

$$d_{Em} = d_{Emo} * \text{Exp}(- a * c) \quad (9)$$

where a is the magnitude of the benefit of parental care.

Survival and reproductive costs of egg allocation and parental care, which are offset by energetic benefits of cannibalism or abandonment, when applicable (to the mutant strategy) are:

$$d_{Am} = 1 - [(1 - d_{Amo}) * \text{Exp}(- ((1 - d_{Emo}) + (c - g * \beta)))] \quad (10)$$

$$r_m = r_{mo} * \text{Exp}[-((1 - d_{Emo}) + (c - g * \beta))] \quad (11)$$

Filial cannibalism, and in some cases offspring abandonment, offset the costs of parental care and lead to increased parental survival and reproduction relative to the no cannibalism scenario;

243 these benefits of cannibalism and abandonment are reflected in equations 10-11 above, where g
244 the magnitude of the benefit of cannibalism or abandonment.

245
246 As mentioned above, we consider scenarios in which abandonment is 1) beneficial to parents
247 (e.g., due to decreased investment in abandoned young), in which case g would be greater than
248 zero, and 2) not beneficial to parents (e.g., because care is shareable among offspring), in which
249 case g would be equal to zero. We assume that the benefits of cannibalizing young are greater
250 than the benefits of abandoning young in all analyses because cannibalistic parents can
251 potentially reduce costs of care and gain energetic benefits from eating offspring, whereas
252 abandoning parents can only potentially offset costs of care. Thus, in all cases, g is assumed to be
253 greater for filial cannibalism than for offspring abandonment, and this is how these two
254 behaviors fundamentally differ in our model. We additionally consider varying levels of benefits
255 of cannibalism and abandonment. Specifically, large benefits of cannibalism or abandonment are
256 likely to occur when parents consume offspring relatively early during development, as younger
257 eggs have greater time until hatching and would also be expected to have greater nutritional
258 content (e.g., due to decreases in lipid or protein content throughout egg development (39, 40)).
259 For scenarios in which we assume low and high benefits of abandonment, g is equal to 0.5 and
260 0.75, respectively; for scenarios in which we assume low, moderate, and high benefits of filial
261 cannibalism, g is equal to 1, 1.5, and 1.75, respectively, such that cannibalism always offsets
262 costs of care more than abandonment due to the energetic benefits of consuming eggs.

263
264 In addition to considering energetic benefits, we also consider whether filial cannibalism and
265 abandonment are in some cases selective. For example, parents might preferentially consume or

abandon young that are taking a relatively long time to develop (35). For the scenarios in which we assume that cannibalism or abandonment is selective, parents preferentially consume or abandon slower developing young. Filial cannibalism or abandonment is then assumed to result in the death of some offspring but decreases the time remaining offspring spend in the egg stage such that:

$$m_{Em} = 1 - m_{Emo} * \text{Exp}[-\beta * s] \quad (12)$$

where s is the magnitude of the selectivity of cannibalism or abandonment, and the maturation rate increases as the rate of filial cannibalism or abandonment and selectivity increase.

In the above scenarios, we assume non-linear trade-offs with care and cannibalism, as non-linear trade-offs are often thought to be biologically realistic (e.g. (11)). However, our qualitative patterns would be expected to be unchanged if we assumed linear trade-offs (14).

(d) Invasion dynamics and fitness

After defining the mutant and resident dynamics and trade-offs associated with care, cannibalism, and abandonment, we then performed a local stability analysis to determine the magnitude and sign of the dominant eigenvalue of the invasion matrix associated with the resident and mutant dynamics. The dominant eigenvalue is the reproductive factor or growth rate of the mutant when the mutant is rare and provides a measure of fitness of the mutant strategy (38). That is, the relative fitness of the mutant (i.e., the fitness of the mutant strategy relative to

that of the resident) is measured as the growth rate of that mutant strategy, which is the dominant eigenvalue from following matrices.

For offspring abandonment or filial cannibalism, the invasion matrix is as follows:

$$\begin{pmatrix} \lambda + d_{E_m} + m_{E_m} + \beta * A_m & -r_m \left[1 + \frac{A^*}{K_m} \right] + \beta * E_m \\ -m_{E_m} * \text{Exp}(-\lambda\tau) \sigma_{J_m} & \lambda + d_{A_m} \end{pmatrix}$$

(13).

The components of the above matrix are derived from the dynamics of the linearized mutant strategy around the trivial steady state and are determined by the partial derivative of the demographic dynamics of the mutant. The dominant eigenvalue of the above matrix can be determined by solving the resulting characteristic equation for λ . Specifically, as $\tau \rightarrow 0$, and assuming that A_m is relatively small (i.e., equal to 1 in our scenarios), taking the determinant of the above expression allows us to determine fitness (λ). When λ is greater than zero, the mutant strategy (parental care with offspring abandonment or filial cannibalism) is associated with positive fitness and would be expected to be able to invade the resident strategy of no care/no abandonment/no cannibalism. When fitness is negative, abandonment and cannibalism are not expected to be able to evolve.

Using the above approach, we calculated the fitness associated with parental care only, parental care with offspring abandonment, and parental care with filial cannibalism in relation to two key life-history parameters: baseline egg death rate and baseline adult death rate. We focus on these

two parameters, as they have previously been found to influence the likelihood of the evolution of care (e.g. (14)). Comparing the fitness associated with parental care only with the fitness of parental care with offspring abandonment and parental care with filial cannibalism allows us to determine if the co-occurrence of offspring abandonment and filial cannibalism with care can influence the likelihood that parental care will evolve from an ancestral state of no care.

All analyses were performed in Mathematica 8.0.1 or higher. The code and parameters used in all analyses is available at the following link: osf.io/n7qgf. Unless otherwise noted above or in a figure, $d_{Ao} = d_{Amo} = 0.7$, $d_{Eo} = d_{Emo} = 0.7$, $\sigma_J = \sigma_{Jm} = 0.01$, $m_{Eo} = m_{Emo} = 0.4$, $K = K_m = 50$, $r = r_m = 50$, $\beta = L = 0.5$, $c = 0.5$, $a = 6$, and $s = 6$.

Results

The life-history conditions over which parental care will evolve depend on whether parental care occurs alone or whether it co-occurs and co-originates with abandonment or filial cannibalism (Fig. 1-2). If care co-occurs with abandonment or filial cannibalism, the benefits of abandonment or cannibalism will additionally influence the life-history conditions over which care with abandonment or cannibalism will be favored (Fig. 1-2).

When parental care occurs alone, care is expected to result in fitness benefits when baseline egg death rate (our proxy for offspring need) and baseline adult death rate are moderate or high (Fig. 1A and 2A). If parents provide care but also abandon some of their offspring, care will not result in fitness benefits, regardless of baseline egg death rate (Fig. 1 B) or baseline adult death rate (Fig. 2 B) if abandonment does not result in benefits to parents. In this sense, abandonment that

334 is not beneficial to parents inhibits the evolution of parental care. Importantly, we assume no
335 density effects on egg survival, and density-dependent egg survival might alter these patterns
336 (discussed in (31, 32) and below).

337

338 Parental care that co-occurs with abandonment that offsets costs of care can result in positive
339 fitness at relatively high baseline egg (Fig. 1C) and adult death (Fig. 2C) rates when the benefits
340 of abandonment to parents are relatively high (Fig. 1-2 C dashed line). Importantly, though, even
341 when the benefits of abandonment in relation to offsetting costs of care are relatively high, care
342 and abandonment will be favored over a narrower range of egg and adult mortalities relative to
343 those of the care only scenario (Fig. 1A vs. 1C and 2A vs. 2C). Thus, in general, abandonment
344 that simply offsets costs of parental investment tends to inhibit the evolution of parental care.

345

346 Parental care that co-occurs with abandonment that does not offset costs of care but is selective
347 such that parents preferentially abandon slower developing young also inhibits the evolution of
348 care—that is, the egg and adult mortalities over which care and abandonment will be favored is
349 reduced when parents abandon young relative to the care-only scenario (Fig. 1A vs. 1D large-
350 dashed line and 2A vs. 2D large-dashed line). In contrast, parental care that co-occurs with
351 abandonment that is 1) selective and 2) associated with relatively high offsets to the costs of care
352 can marginally facilitate the evolution of care. Specifically, the egg and adult mortalities over
353 which care and abandonment will be favored is broader when parents abandon young relative to
354 the care-only scenario (Fig. 1A vs. 1D small-dashed line and 2A vs. 2D small-dashed line). Thus,
355 in cases in which there are substantial and multiple benefits, abandonment can facilitate the
356 evolution of parental care.

If parental care co-occurs and co-originates with filial cannibalism, parental care will be favored over a narrower range of baseline egg death rates relative to the care-only scenario when filial cannibalism results in relatively small energetic gain (Fig. 1A vs. 1 E solid line), and as such, in some cases filial cannibalism can inhibit the evolution of care. In contrast, filial cannibalism that results in relatively moderate or large energetic benefits can broaden the egg death rates over which care can evolve (Fig. 1A vs. 1 E dashed lines). Parental care that co-occurs with filial cannibalism that is energetically beneficial and selective such that parents preferentially consume slower developing young will be favored over a broader range of baseline egg death rates relative to the no-care scenario (Fig. 1A vs. 1F), regardless of the magnitude of the energetic benefits of cannibalism. Thus, filial cannibalism that 1) results in relatively large energetic benefits or 2) is beneficial to parents and is selective is expected to facilitate the evolution of care. Similarly, care that co-occurs with filial will be favored over a broader range of adult death rates relative to the no-care scenario when filial cannibalism is energetically beneficial to parents (Fig. 2A vs. 2E) and when it results in energetic benefits and is selective (Fig. 2A vs. 2F). Again, in this case, filial cannibalism is broadening the life-history conditions over which care can evolve.

As outlined above, the precise benefits of abandonment and cannibalism will influence whether these behaviors inhibit or facilitate the evolution of care, and the benefits of abandonment and cannibalism will depend on the timing of abandonment and cannibalism. Abandonment and cannibalism that happen relatively early in development are likely to be associated with greater benefits to parents. Thus, in general, we would expect abandonment and cannibalism to facilitate

the evolution of care when: 1) abandonment is selective and associated with relatively large offsets to the costs of care, which would be expected to occur when abandonment happens relatively early in development; 2) filial cannibalism is associated with relatively large energetic benefits, which would be expected to occur when cannibalism happens relatively early in development; and 3) filial cannibalism is energetically beneficial and selective such that parents consume slower developing young.

Discussion

Co-evolution of traits can influence the conditions under which parental care is expected to evolve. If parental care co-occurs and co-evolves with offspring abandonment, the loss of offspring due to abandonment can in some cases prevent the evolution of care (Fig 1-2 B & C). Similarly, in some cases, filial cannibalism that is only weakly energetically beneficial to parents can reduce the life-history conditions under which care can evolve (e.g., Fig. 1-2 E, solid line). In contrast, and perhaps more surprisingly given that filial cannibalism involves eating one's own offspring, if parental care co-occurs and co-evolves with filial cannibalism, in some cases, the presence of filial cannibalism can broaden the conditions under which care can evolve. Specifically, if 1) there are moderate or large energetic benefits of cannibalism or 2) cannibalism is energetically beneficial and also selective such that parents preferentially consume slower developing offspring, cannibalism can expand the range of egg and adult mortalities under which we would expect care to be able to evolve. Likewise, offspring abandonment of young prior to independence, which is typically assumed to be contradictory to care, can facilitate the evolution of care in some cases. When abandonment 1) strongly offsets costs of care and 2) is selective

such that parents preferentially abandon slower-developing young, abandonment can expand the egg and adult mortalities over which care will be favored.

Previous work (e.g., (11, 14)) suggests that parental care will be more likely to evolve when egg death rate in the absence of care is relatively high (i.e., when offspring need care the most). Our current findings suggest that this might not always be the case, and depending on how care co-evolves with behaviors such as filial cannibalism and offspring abandonment, we might expect to see the evolution of parental care even in situations in which offspring need is relatively low. Additionally, if parents provide care but also abandon some of their young, the net benefits of care can in some cases be relatively low, which might in turn prevent parental care from evolving even when offspring need is relatively great.

In general, these findings highlight that it is essential to consider co-evolutionary dynamics—and more specifically the traits that co-occur across evolutionary time scales—to understand, more fully, diversity in trait evolution (8, 18, 20, 24, 25, 41). For instance, if we had focused only on the evolution of parental care and explored when care is most likely to evolve (as in (14)), we would have missed the more complex dynamics that offspring abandonment and filial cannibalism can create, and we would have either over- or under-estimated the conditions under which we would expect care to evolve. Understanding diversity in care—and any behavior—requires that we give thought to the traits that are likely to co-occur and co-evolve together. This finding that co-evolution matters is consistent with work conducted in other contexts. For example, previous research has found that cooperation and choosiness are likely to co-evolve on an evolutionary scale (42), and other studies have found that the evolution of parental care can

co-evolve with traits such as mate preferences (18), competition (20, 24, 26), and care that is provided by the other parent (24).

In addition, our results highlight the importance of carefully considering costs and benefits of behaviors that potentially co-occur and co-evolve together. In our model, we assume that parental care, offspring abandonment, and filial cannibalism are associated with costs and benefits. As filial cannibalism is associated with energetic or nutritional gain, we assumed that the benefits of filial cannibalism are greater than those of offspring abandonment, and this is the fundamental difference between abandonment and cannibalism in our model. If filial cannibalism was associated with trivial energetic benefits, this would restrict the life-history parameters under which care with cannibalism could evolve. Likewise, if abandonment or cannibalism are in some cases associated with substantial costs (e.g., due to costs of removing young from the reproductive site or costs associated with disease transmission when parents eat offspring), then we would expect care with cannibalism or abandonment to be favored over a narrower range of life-history parameters. In general, the finding that the evolution of care can in some cases be inhibited or facilitated by abandonment or cannibalism is directly related to the benefits and potential costs of abandonment or cannibalism.

The qualitative results of our model could be altered if we considered much larger energetic benefits to parents of filial cannibalism or abandonment, which would be expected to increase the conditions under which care with cannibalism or abandonment could evolve. Similarly, in some cases cannibalism or abandonment might reduce the mortality of remaining offspring, particularly when offspring mortality is density dependent. In the modeling work presented

herein, we assume that offspring survival is density-independent; however, if within-clutch density affects offspring survival, then offspring abandonment or cannibalism could facilitate the evolution of parental care (see related discussion in (31, 32, 43)). Indeed, our recent work suggests that in some cases when egg survival is affected by within-clutch density, offspring abandonment and cannibalism can themselves function as forms of parental care and improve offspring survival (31, 32). Regardless of the specific benefits of abandonment and cannibalism, though, our general conclusion remains the same: co-evolutionary dynamics between filial cannibalism, offspring abandonment, and parental care are likely to influence the conditions under which care can evolve, and to understand fully the evolution of parental investment and care, we must consider the traits that are likely to co-occur with care.

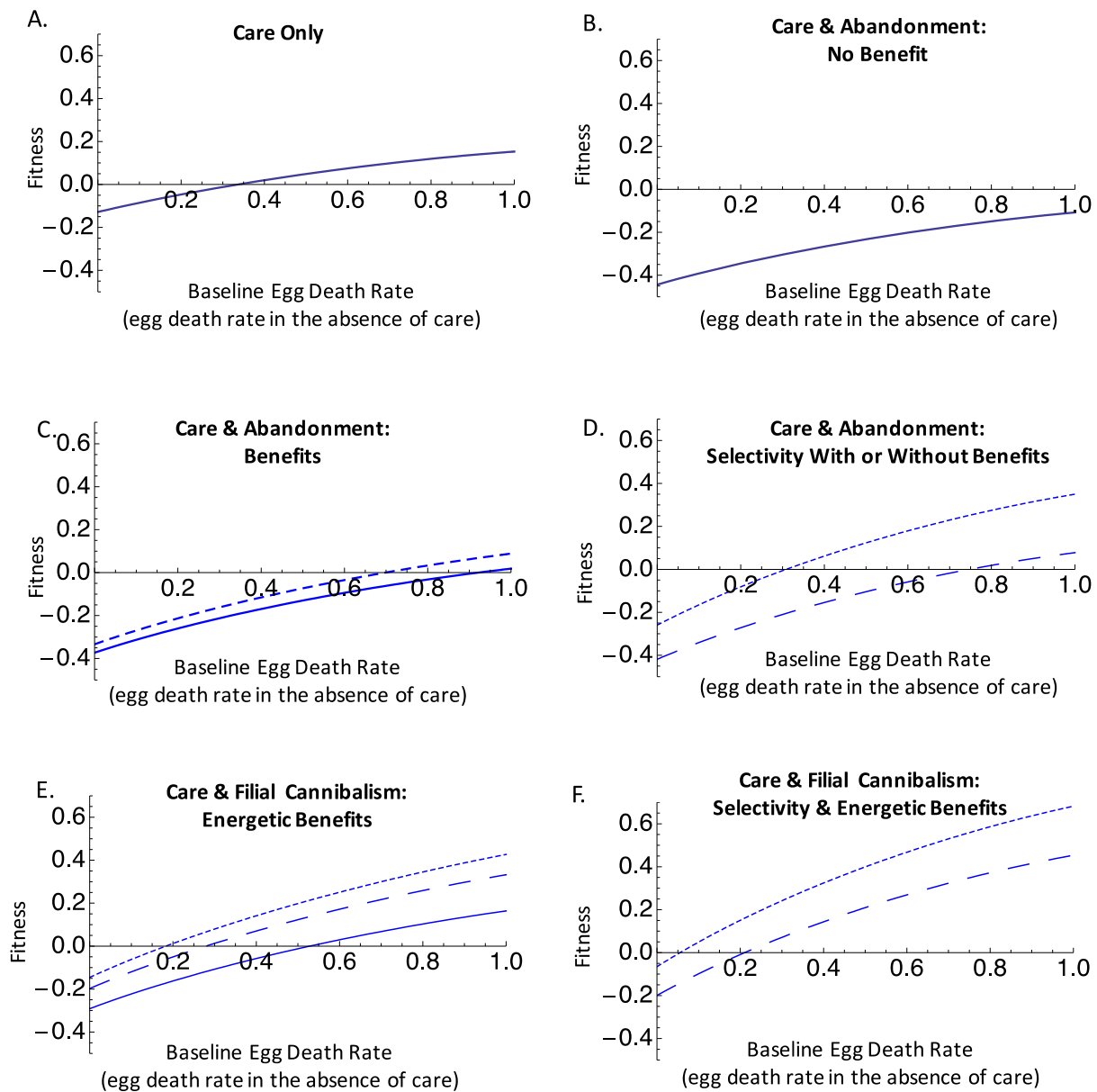
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Figures.

Figure 1. Co-evolutionary dynamics influence the egg death rates over which parental care will be favored. (A) Parental care in the absence of filial cannibalism or abandonment results in fitness benefits when baseline egg death rate is moderate to high. (B) Parental care that co-occurs with offspring abandonment that does not offset costs of care will not result in fitness benefits relative to the no-care/no-abandonment resident strategy. (C) Parental care that co-occurs with abandonment that offsets costs of care (dashed line = high benefit, solid line = low benefit) is favored at a narrower range of baseline egg death rates relative to the care-only scenario. (D) Parental care that co-occurs with abandonment that results in relatively high benefits to parents and is selective (small dashed line) is favored at a broader range of baseline egg death rates relative to the no-care scenario; in contrast, parental care that co-occurs with abandonment that does not offset costs of care but is selective (large dashed line) will be favored over a narrower range of baseline egg death rates relative to the care-only scenario. (E) Parental care that co-occurs with filial cannibalism that is associated with moderate or high energetic benefits (small dashed line = high benefit, large dashed line = moderate benefit) is favored at a broader range of baseline egg death rates relative to the care-only scenario; in contrast, parental care that co-occurs with filial cannibalism that is associated with low energetic benefits (solid line = low benefit) is favored at a narrower range of baseline egg death rates relative to the care-only scenario. (F) Parental care that co-occurs with filial cannibalism that results in relatively low (large dashed line) or moderate (small dashed line) energetic benefits and is selective is favored at a broader range of baseline egg death rates relative to the no-care scenario. Note: in all cases, fitness refers to the fitness of the mutant strategy (care with abandonment or filial cannibalism) relative to that of the no-care/no-abandonment/no-cannibalism resident strategy.

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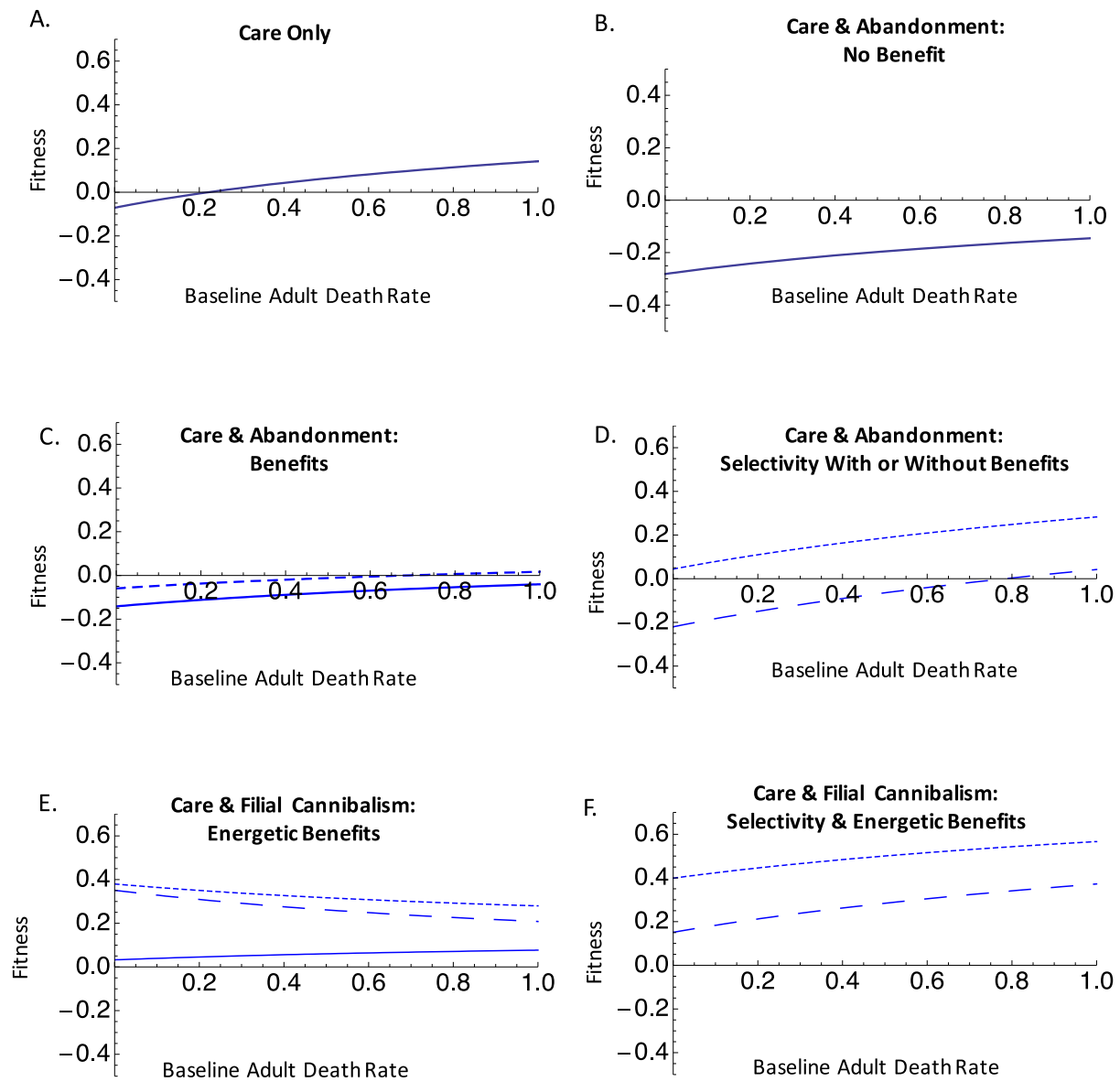


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Figure 2. Co-evolutionary dynamics influence the adult death rates over which parental care will be favored. (A) Parental care that occurs in the absence of filial cannibalism or abandonment results in fitness benefits when baseline adult death rate is moderate to high. (B) Parental care that co-occurs with offspring abandonment that does not offset costs of care will not result in fitness benefits. (C) Parental care that co-occurs with abandonment that offsets costs of care (dashed line = high benefit, solid line = low benefit) is either not favored or favored at a narrower range of adult death rates relative to the care-only scenario. (D) Parental care that co-occurs with abandonment that results in relatively high benefits to parents and is selective (small dashed line) is favored at a broader range of adult death rates relative to the no-care scenario; in contrast, parental care that co-occurs with abandonment that does not offset costs of care but is selective (large dashed line) will be favored over a narrower range of adult death rates relative to the care-only scenario. (E) Parental care that co-occurs with filial cannibalism that is associated with low, moderate, or high energetic benefits (small dashed line = high benefit, large dashed line = moderate benefit, solid line = small benefit) is favored at a broader range of adult death rates relative to the care-only scenario. (F) Parental care that co-occurs with filial cannibalism that results in relatively low (large dashed line) or moderate (small dashed line) energetic benefits and is selective is favored at a broader range of adult death rates relative to the no-care scenario. Note: in all cases, fitness refers to the fitness of the mutant strategy (care with abandonment or filial cannibalism) relative to that of the no-care/no-abandonment/no-cannibalism resident strategy.

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References

1. Roff DA. The evolution of life histories. New York, USA: Chapman & Hall; 1992.
2. Stearns SC. The evolution of life histories: Oxford University Press Oxford; 1992.
3. Jones OR, Scheuerlein A, Salguero-Gómez R, Camarda CG, Schaible R, Casper BB, et al. Diversity of ageing across the tree of life. *Nature*. 2014;505(7482):169.
4. Pontzer H, Brown MH, Raichlen DA, Dunsworth H, Hare B, Walker K, et al. Metabolic acceleration and the evolution of human brain size and life history. *Nature*. 2016;533(7603):390.
5. Dale J, Dey CJ, Delhey K, Kempenaers B, Valcu M. The effects of life history and sexual selection on male and female plumage colouration. *Nature*. 2015;527(7578):367.
6. Martin TE. Age-related mortality explains life history strategies of tropical and temperate songbirds. *Science*. 2015;349(6251):966-70.
7. Trivers R. Parental investment and sexual selection. 1972.
8. Alonzo SH. Social and coevolutionary feedbacks between mating and parental investment. *Trends in Ecology & Evolution*. 2010;25(2):99-108.
9. Royle NJ, Smiseth PT, Kölliker M. The evolution of parental care: Oxford University Press; 2012.
10. Mank JE, Promislow DEL, Avise JC. Phylogenetic perspectives in the evolution of aprental care in ray-finned fishes. *Evolution*. 2005;59(7):1570-8.
11. Clutton-Brock TH. The evolution of parental care: Princeton University Press; 1991.
12. Alonso-Alvarez C, Velando A. Benefits and costs of parental care. *The evolution of parental care*. 2012:40-61.
13. Klug H, Bonsall MB. What are the benefits of parental care? The importance of parental effects on developmental rate. *Ecology and evolution*. 2014;4(12):2330-51.
14. Klug H, Bonsall MB. Life history and the evolution of parental care. *Evolution*. 2010;64(3):823-35.
15. Brown JL, Morales V, Summers K. A key ecological trait drove the evolution of biparental care and monogamy in an amphibian. *The american naturalist*. 2010;175(4):436-46.
16. Huang WS, Lin SM, Dubey S, Pike DA. Predation drives interpopulation differences in parental care expression. *Journal of Animal Ecology*. 2013;82(2):429-37.
17. Pike DA, Clark RW, Manica A, Tseng H-Y, Hsu J-Y, Huang W-S. Surf and turf: predation by egg-eating snakes has led to the evolution of parental care in a terrestrial lizard. *Scientific reports*. 2016;6:22207.
18. Alonzo SH. Sexual selection favours male parental care, when females can choose. *Proceedings of the Royal Society B: Biological Sciences*. 2012;279(1734):1784-90.
19. Kokko H, Jennions MD. Parental investment, sexual selection and sex ratios. *Journal of evolutionary biology*. 2008;21(4):919-48.
20. Kokko H, Jennions MD. Sex differences in parental care. *The evolution of parental care*. 2012:101-16.
21. Klug H, Alonzo SH, Bonsall MB. Theoretical foundations of parental. *The Evolution of Parental Care*. 2012:21.
22. Gilbert JDJ, Manica A. The evolution of parental care in insects: A test of current hypotheses. *Evolution*. 2015;69(5):1255-70.
23. Székely T, Weissing F, Komdeur J. Adult sex ratio variation: implications for breeding system evolution. *Journal of evolutionary biology*. 2014;27(8):1500-12.

24. Fromhage L, Jennions MD. Coevolution of parental investment and sexually selected traits drives sex-role divergence. *Nature communications*. 2016;7:12517.
25. Royle NJ, Alonzo SH, Moore AJ. Co-evolution, conflict and complexity: what have we learned about the evolution of parental care behaviours? *Current opinion in behavioral sciences*. 2016;12:30-6.
26. Requena GS, Alonzo SH. Sperm competition games when males invest in paternal care. *Proc R Soc B*. 2017;284(1860):20171266.
27. Head ML, Hinde CA, Moore AJ, Royle NJ. Correlated evolution in parental care in females but not males in response to selection on paternity assurance behaviour. *Ecology letters*. 2014;17(7):803-10.
28. Hausfater G, Hrdy SB. *Infanticide: comparative and evolutionary perspectives*: Routledge; 2017.
29. Klug H, Bonsall MB. When to care for, abandon, or eat your offspring: the evolution of parental care and filial cannibalism. *The American Naturalist*. 2007;170(6):886-901.
30. Klug H, Chin A, St Mary CM. The net effects of guarding on egg survivorship in the flagfish, *Jordanella floridae*. *Animal Behaviour*. 2005;69(3):661-8.
31. Davenport M. Parental care, offspring abandonment, and filial cannibalism. 2018.
32. Davenport MB, Michael B; Klug, H. . Unconventional care: Offspring abandonment and filial cannibalism can function as forms of parental care. *Frontiers in Ecology & Evolution*. 2019;7:113.
33. Rohwer S. Parent cannibalism of offspring and egg raiding as a courtship strategy. *The American Naturalist*. 1978;112(984):429-40.
34. Manica A. Filial cannibalism in teleost fish. *Biological Reviews*. 2002;77(2):261-77.
35. Klug H, Lindström K. Hurry-up and hatch: selective filial cannibalism of slower developing eggs. *Biology letters*. 2008;4(2):160-2.
36. Bonsall MB, Klug H. The evolution of parental care in stochastic environments. *Journal of evolutionary biology*. 2011;24(3):645-55.
37. Bonsall MB, Klug H. Effects of among-offspring relatedness on the origins and evolution of parental care and filial cannibalism. *Journal of evolutionary biology*. 2011;24(6):1335-50.
38. Otto SP, Day T. *A biologist's guide to mathematical modeling in ecology and evolution*: Princeton University Press; 2007.
39. Figueiredo J, Penha-Lopes G, Anto J, Narciso L, Lin J. Potential fertility and egg development (volume, water, lipid, and fatty acid content) through embryogenesis of *Uca rapax* (Decapoda: Brachyura: Ocypodidae). *Journal of Crustacean Biology*. 2008;28(3):528-33.
40. Gardner C. Composition of eggs in relation to embryonic development and female size in giant crabs [*Pseudocarcinus gigas* (Lamarck)]. *Marine and Freshwater Research*. 2001;52(3):333-8.
41. Requena GS, Munguía-Steyer R, Machado G. Paternal care and sexual selection in arthropods. *Sexual selection: perspectives and models from the Neotropics Elsevier*. 2013:201-3.
42. McNamara JM, Barta Z, Fromhage L, Houston AI. The coevolution of choosiness and cooperation. *Nature*. 2008;451(7175):189.
43. Payne AG, Smith C, Campbell AC. A model of oxygen-mediated filial cannibalism in fishes. *Ecological Modelling*. 2004;174(3):253-66.

