

Research



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Life history and the evolutionary loss of parental care

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Parental care has been gained and lost evolutionarily multiple times. While many studies have focused on the origin of care, few have explored the evolutionary loss of care. Understanding the loss of parental care is important as the conditions that favour its loss will not necessarily be the opposite of those that favour the evolution of care. Evolutionary hysteresis (the case in which evolution depends on the history of a system) could create a situation in which it is relatively challenging to lose care once it has evolved. Here, using a mathematical approach, we explore the evolutionary loss of parental care in relation to basic life-history conditions. Our results suggest that parental care is most likely to be lost when egg and adult death rates are low, eggs mature quickly, and the level of care provided is high. We also predict evolutionary hysteresis with respect to egg maturation rate: as egg maturation rate decreases, it becomes increasingly more costly to lose care than to gain it. This suggests that once care is present, it will be particularly challenging for it to be lost if eggs develop slowly.

1. Introduction

Parental care is a behaviour that is widespread in animals which has major ecological and evolutionary significance (reviewed in [1,2]). Parental care occurs post-fertilization, or after the production of daughter cells if reproduction is asexual, and increases parental fitness and offspring lifetime reproductive success [1–4]. Parental care is incredibly diverse, and in nature we see everything from simple guarding of eggs within a breeding territory in a fish [5] to suicidal maternal matrophagy in spiders [6]. A large body of research has focused on identifying the conditions that favour the evolutionary origin of parental care [7–11], the evolutionary and ecological drivers of different forms and types of parental care [12–17], and the ecological and evolutionary consequences of parental care [18–21]. These studies have revealed that parental care can co-evolve with and influence the evolution of other aspects of phenotype. For instance, parental care can influence sex roles and traits associated with mate acquisition [19], and care can co-evolve with behaviours such as filial cannibalism and offspring abandonment [22].

With regard to the origin of parental care, this trait has evolved independently in a range of animals. For example, a series of novel evolutionary events led to the independent evolution of matrotrophy in bryozoans [23]. In frogs, parental care has evolved independently and is correlated with breeding pool size [24]. Likewise, in ray-finned fishes, paternal care and maternal care have evolved at least 22 times and seven times, respectively, and the origin of parental care in ray-finned fishes is associated with fertilization mode [12]. Theoretical work suggests that parental care is most likely to originate when offspring need care the most (i.e. when survival in the absence of care is relatively low) [8,10]. Once care is present in a species, studies often aim to identify the factors that influence the level of care provided. For example, species that live in higher elevations provide more parental care to their offspring than species

at lower elevations [25]. In glass frogs (*Hyalinobatrachium fleischmani*), parental care is adjusted in response to fluctuating weather and hydration levels [26].

While a robust body of empirical and theoretical research has focused on the evolutionary origin of parental care, limited research has focused on the evolutionary loss of parental care. The few empirical studies on this topic have revealed that parental care has been lost across evolutionary time in multiple species. For instance, in amphibians egg attendance by parents is lost at a similar rate as it is gained evolutionarily [27], and paternal care has been lost multiple times in ray-finned fishes [12]. As expected, more complex and specialized forms of care (e.g. viviparity) are less likely to be lost than simpler forms of care (e.g. egg attendance) [27]. In three-spine sticklebacks (*Gasterosteus aculeatus*), most populations exhibit paternal care, but some populations of the white form of three-spine sticklebacks lack care, suggesting that care has been lost in some populations [28,29]. In general, though, there is limited empirical focus on the loss of care, and to the best of our knowledge no theoretical work has explicitly focused on identifying the factors that favour the evolutionary loss of parental care.

Conceptually, understanding the factors that favour the evolutionary loss of care is important, as the conditions that give rise to the loss of care are not necessarily expected to be simply the opposite of those that give rise to the origin of care. Evolutionary hysteresis refers to a situation in which the evolution of a system depends on the history of that system [30], and evolutionary hysteresis can create evolutionary tipping points in which it can become more difficult, or in some cases relatively easy, to lose a trait or strategy across evolutionary time [30–32]. Evolutionary hysteresis has previously been found to be important in non-parental-care contexts. For example, hysteresis can create irreversible biological change that is associated with evolutionary tipping points that increase the likelihood of extinction [30,32], and evolutionary hysteresis can make it challenging for obligate mutualisms to be lost once established in a system even as the costs of such mutualisms increase [31]. Given that evolutionary hysteresis has been documented in these other contexts—and given that the demographic factors associated with the loss of care will differ from those associated with the origin of care—it is possible that evolutionary hysteresis could make it relatively difficult (or perhaps relatively easy) for care to be lost once it arises in a system. Regarding the demographic differences during the origin versus loss of care, during a care → no-care transition we would expect realized egg death rate to increase and the number of surviving eggs to decrease in the population, whereas realized egg death rate would decrease and the number of surviving eggs would increase during a no-care → care transition. Likewise, all else equal, owing to the costs of care, adult mortality will decrease and the number of adults in the population would be expected to increase during a care → no-care transition, whereas the opposite pattern would be expected during a no-care → care transition. As such, the population-level dynamics (e.g. adult and egg densities, reproductive output, and population growth rate) experienced during a care → no-care transition will differ from those of a no-care → care transition, and these differences in population-level dynamics could potentially create differences in the invasion potential and fitness associated with the loss versus the gain of care. Whether such differences could create a situation in which it is more (or less) costly

to lose care than it is to gain it remains unknown. Further, a no-care mutation would be rare when it initially arises in a population; it is possible that the rarity of a novel mutation could also affect the fitness associated with the loss versus gain of care. As such, given the potential for evolutionary hysteresis, there is no *a priori* reason to assume that the conditions favouring the loss of care will simply be the reverse of those favouring the origin of care, and in general, explicitly considering the evolutionary loss of behaviours is an important yet understudied focus of evolutionary ecology research.

In the present study, we used a mathematical framework to explore the basic life-history conditions—that is, the stage-specific rates of maturation and mortality—that are most likely to favour the evolutionary loss of parental care of eggs. We modelled a system in which parental care of eggs is present as the ancestral state and identified the life-history conditions under which a state of no-care could invade. We then quantified the relationship between the fitness associated with the loss of parental care and (i) egg, juvenile and adult mortality rates, (ii) egg maturation rate, (iii) the duration of the juvenile stage, and (iv) the level of parental care provided. In doing so, we provide a set of *a priori* predictions of when care is most likely to be lost in relation to basic life history. We considered that evolutionary hysteresis might be associated with the loss of care. If the conditions that promote the loss of care are not simply the opposite of those that favour the origin of care, this would suggest that evolutionary hysteresis is creating a situation in which it becomes either more difficult or easier for care to be lost once it has originated. If the conditions that give rise to the loss of care are qualitatively and quantitatively opposite of those that give rise to the origin of care, this would suggest a lack of hysteresis. Surprisingly few studies have examined evolutionary hysteresis (but see [30]), and remarkably little empirical or theoretical research focuses on the evolutionary loss of behaviours. To the best of our knowledge, our study will be one of the first to examine whether evolutionary hysteresis is associated with the loss of a behaviour across evolutionary time.

2. Material and methods

(a) Model overview

To explore the conditions that are most likely to give rise to the evolutionary loss of parental care of eggs, we used a mathematical approach in which a mutant that does not exhibit parental care attempts to invade a resident population in which resident individuals provide parental care to their eggs. Following standard evolutionary invasion analysis methods (e.g. [33], electronic supplementary material), we assume that the resident strategy is in equilibrium and the alternative mutant strategy invades from rare. As with our previous work [4,10,11], we assume individuals pass through egg, juvenile and adult stages. We assume the mutant and resident experience the same population conditions and life-history parameters (i.e. both residents and mutants experience the same maturation and survival rates before any costs and benefits of care are accounted for and both the resident and mutant experience the same carrying capacity). In the present model, the life-history variables are represented as fixed parameter values. While some life-history variables trade-off with parental care (e.g. adult and egg death rates are influenced by the level of

parental care provided), the life-history parameters do not co-evolve with parental care in the current model. For simplicity, we focus only on post-fertilization parental care of eggs. Parental care is assumed to be beneficial in that it increases offspring egg survival but is costly in that it decreases parental survival and future reproduction (see also [4] for a discussion of costs and benefits of post-fertilization parental care). For a range of life-history parameters, we then explored the conditions under which the strategy of no parental care could invade the resident strategy of parental care and in doing so identify the basic life-history parameters under which the loss of care is expected to be favoured.

Post-fertilization parental care necessitates an association between parents and offspring. We assume that such a relationship exists for the resident individuals that provide care but do not specify how the relationship between parent and offspring arises. An association could exist if parents recognize their offspring or are in close physical proximity to young (e.g. [34,35]). The model dynamics described below are consistent with either of these scenarios. Further, in the current model, we do not consider the dynamics of two sexes, and as a result, individuals are assumed to be asexual. This is potentially the most challenging scenario for parental care to be lost since parent-offspring conflict and sexual conflict will be absent. Finally, we do not consider the gradual loss of care. Exploring the gradual loss of care would require the parameters of the model to vary temporally and sequential invasions across time, both of which are beyond the scope of the current framework. Given this, our model provides a baseline, foundational framework to investigate the evolutionary loss of parental care.

Below, we outline the model dynamics, which are an extension of those used in our previous work (e.g. [4,10,36,37]). Further details of the modelling framework are provided in the electronic supplemental material.

(b) Resident strategy dynamics

As mentioned above, resident individuals provide egg care to offspring, and the dynamics of care are incorporated into the model as trade-offs (described below). Resident individuals pass through an egg (E), juvenile and adult (A) stage. In the population, eggs increase as adults reproduce and decrease as eggs mature and as eggs die such that:

$$\frac{dE}{dt} = r \cdot A(t) \cdot \left[1 - \frac{A(t)}{K}\right] - d_E \cdot E(t) - m_E \cdot E(t), \quad (2.1)$$

where r represents the rate of egg fertilization by individual adults in the population, d_E represents the egg death rate, and m_E represents the egg maturation rate. The population has a carrying capacity of K , and adult reproduction is limited by density dependence (i.e. adult reproduction is limited by a logistic function). Adults in the population increase as eggs mature, survive, and pass through the juvenile stage and decrease as adults die, such that:

$$\frac{dA}{dt} = m_E \cdot E(t - \tau) \cdot \sigma_J - d_A \cdot A(t), \quad (2.2)$$

where τ is a time delay that represents the duration of the juvenile stage, σ_J is the juvenile survival rate and d_A is the death rate of adults. As mentioned above, resident individuals provide parental care of eggs to their offspring. This care is associated with costs and benefits that influence egg and adult survival and reproductive rate; these costs and benefits are described in detail below.

The equilibrium densities of eggs and adults are found when $dE/dt = dA/dt = 0$ and are equal to:

$$E^* = \frac{d_A \cdot A^*}{m_E \cdot \sigma_J} \quad (2.3)$$

and

$$A^* = K \cdot \left[1 - \frac{(d_A/\sigma_J) \cdot (1 + (d_E/m_E))}{r}\right]. \quad (2.4)$$

(c) Mutant dynamics and invasion

As mentioned above, the mutant strategy is one of no parental care. The mutant follows similar dynamics to the resident (equations (2.1) and (2.2)), given by the following equations:

$$\frac{dE_m}{dt} = r_m \cdot A_m(t) \cdot \left[1 - \frac{A^*}{K_m}\right] - d_{Em} \cdot E_m(t) - m_{Em} \cdot E_m(t) \quad (2.5)$$

and

$$\frac{dA_m}{dt} = m_{Em} \cdot E_m(t - \tau) \cdot \sigma_{Jm} - d_{Am} \cdot A_m(t), \quad (2.6)$$

where A^* is the equilibrium abundance of the resident adult population. As the mutant is assumed to be rare in the population, mutant reproduction is limited by between-strategy competition with the resident (equation (2.5)) [10,33]. The other parameters are as previously described for the resident, and the subscript m indicates the mutant strategy that exhibits no parental care. In all cases, K is assumed to be equal to K_m .

The fitness of the mutant strategy of no care can be calculated by taking the determinant of the following matrix:

$$\begin{pmatrix} \lambda + d_{Em} + m_{Em} & -r_m \left[1 + \frac{A^*}{K_m}\right] \\ -m_{Em} \exp(-\lambda \cdot \tau) \cdot \sigma_{Jm} & \lambda + d_{Am} \end{pmatrix}. \quad (2.7)$$

This then yields a quadratic characteristic equation from which the fitness (λ) of the mutant strategy (relative to the resident strategy) can be determined (see also the electronic supplementary material) [10,38]. When fitness is positive (i.e. when λ is greater than zero), we would expect the strategy of no parental care to be able to invade the resident strategy of parental care of eggs. When fitness is negative (i.e. when λ is less than zero), we would expect parental care to persist in the population (i.e. the no-care strategy will be selected against). Full details of invasion criteria and stability analyses are provided in the electronic supplementary material.

(d) Trade-offs associated with egg allocation and parental care

Parents affect offspring survival by investing energy and nutrients into eggs (referred to here as initial egg allocation) and by providing post-fertilization or post-oviposition parental care to offspring (referred to here as parental care) (see also [10]). Initial egg investment and parental care are costly to parents and incorporated into the dynamics through trade-offs (table 1). In our model, we assumed that both residents and mutants invest resources into eggs, and this investment is costly. Specifically, baseline egg death rate (d_{E0} and d_{Em0}) is our measure of initial egg investment; we assume that a lower egg death rate is reflective of greater parental investment into eggs. This initial egg investment is costly, such that as baseline egg death rate decreases, parental death rate (d_A and d_{Am}) increases and parental reproductive rate (r and r_m) decreases (table 1). For the resident who provides parental care, the level of care provided to offspring is estimated by a fixed value c (table 1). Parental

Table 1. Costs and benefits of parental care and initial investment in eggs. (Here, we describe the life-history trade-offs associated with parental care (c) and initial investment in eggs ($1 - d_{E0}$). In all analyses, $a = 6$.)

parameter	strategy	
	parental care (resident)	no parental care of eggs (mutant)
egg death rate (d_E)	egg death rate $\uparrow$ as care $\downarrow$: $d_E = d_{E0} \cdot \exp(-a \cdot c)$	$d_{Em} = d_{Em0}$
reproductive rate (r)	adult reproductive rate $\downarrow$ as initial egg investment $\uparrow$ and as care $\uparrow$: $\uparrow$: $r = r_0 \cdot (\exp[-((1 - d_{E0}) + c)])$	adult reproductive rate $\downarrow$ as initial egg investment $\uparrow$: $r_m = (r_{m0} \cdot (\exp[-(1 - d_{Em0})]))$
adult death rate (d_A)	adult death rate $\uparrow$ as initial egg investment $\uparrow$ and as care $\uparrow$: $d_A = (1 - (1 - d_{A0}) \cdot (\exp[-((1 - d_{E0}) + c)]))$	adult reproductive rate $\uparrow$ as initial egg investment $\uparrow$: $d_{Am} = (1 - (1 - d_{Am0}) \cdot (\exp[-(1 - d_{Em0})]))$

care is beneficial to offspring such that it is associated with an increase in offspring survival when provided to eggs (i.e. as c increases, d_E decreases). Providing care is costly, and as the level of care increases, the adult death rate increases and reproductive rate decreases (i.e. as c increases, d_A increases and r decreases; table 1). In all cases, we assumed nonlinear trade-offs since they are most biologically realistic [2,17] and have been employed in previous models of parental care [4,10].

The trade-offs described in table 1 provide some insight into the conditions under which the loss of parental care will lead to positive fitness. However, invasion analysis (equation (2.7) and electronic supplementary material) is needed to determine when a no-care strategy will evolve when a resident strategy of parental care is present given the stage-structured life-history conditions and ecological dynamics. To identify the life-history parameters that are most likely to result in the loss of parental care, we determined the fitness associated with the loss of care in relation to baseline egg death rate (i.e. egg death rate prior to accounting for the trade-offs associated with care), egg maturation rate, juvenile survival, the duration of the juvenile stage and baseline adult death rate (i.e. the adult death rate prior to accounting for the trade-offs associated with initial egg investment and parental care). Prior to accounting for the trade-offs associated with parental care (described below; table 1), all baseline parameter values (given in figure legends) were identical for the mutant and resident strategies. Importantly, it is the qualitative relationship between a life-history parameter and fitness that is important; if the specific parameter values are changed, the numerical value of fitness would be expected to change, but the qualitative patterns will remain the same. As we considered that evolutionary hysteresis might occur, we compared the life-history conditions that favour the loss versus the origin of care. If/when hysteresis was noted, we describe those results in the main text. In cases in which hysteresis was not observed, we provide results for the loss versus the origin of care in the electronic supplemental material.

3. Results

(a) Low egg death rates and high egg maturation rates favour the evolutionary loss of parental care

The evolutionary loss of parental care of eggs is most strongly selected for when baseline egg death rates (i.e. egg death rates in the absence of care) are relatively low (figure 1a), suggesting that care is most likely to be lost when eggs survive relatively well on their own. In particular, the fitness associated with the evolutionary loss of care will be greatest when baseline egg death rate is low and the amount of care provided is relatively high (figure 1b). The loss of care at low baseline egg death rates

and high levels of care occurs because: (i) offspring will need care the least when they survive well in the absence of care, and (ii) high levels of care are most costly for parents. The loss of parental care will be most strongly selected for when eggs develop relatively fast (i.e. at high values of egg maturation rate; figure 1c), particularly when the level of care provided is relatively high (figure 1d). Care is unlikely to be lost evolutionarily when eggs mature slowly (figure 1c). This pattern occurs as individuals who spend more time in the egg stage are more likely to die as eggs than individuals who have fast maturation rates and pass through the egg stage quickly. As a result, care is likely to be least important for individuals that have high egg maturation rates, particularly if they are receiving high levels of care that increase the likelihood of surviving through the egg stage.

(b) Juvenile stage survival and duration have minimal effects on the loss of parental care

Juvenile survival does not affect the fitness associated with the loss of egg-only parental care (figure 2a). Regardless of whether the level of care is low, moderate or high, the fitness associated with the loss of care is invariant across juvenile survival rates (figure 2a). This pattern probably occurs because juvenile survival is unaffected by care in the present model. The duration of the juvenile stage has limited effects on the fitness associated with the loss of care. When care level is relatively high, the fitness associated with losing care is marginally greater when the duration of the juvenile stage is relatively short (dotted line, figure 2b). When the level of care is moderate or low, the fitness associated with the loss of care will be greater when the duration of the juvenile stage is longer (bold and dashed lines, figure 2b). However, these effects of juvenile stage duration on the fitness associated with the loss of care are minimal. The fitness associated with the loss of care will be more strongly influenced by other variables (figure 2a,b), suggesting that life-history traits such as egg mortality and maturation rates, as well as the amount of care provided to eggs, will more strongly influence the loss of care.

(c) Low adult death rates favour the evolutionary loss of parental care

The loss of parental care is most strongly selected for when baseline adult death rates are relatively low (figure 3a). In

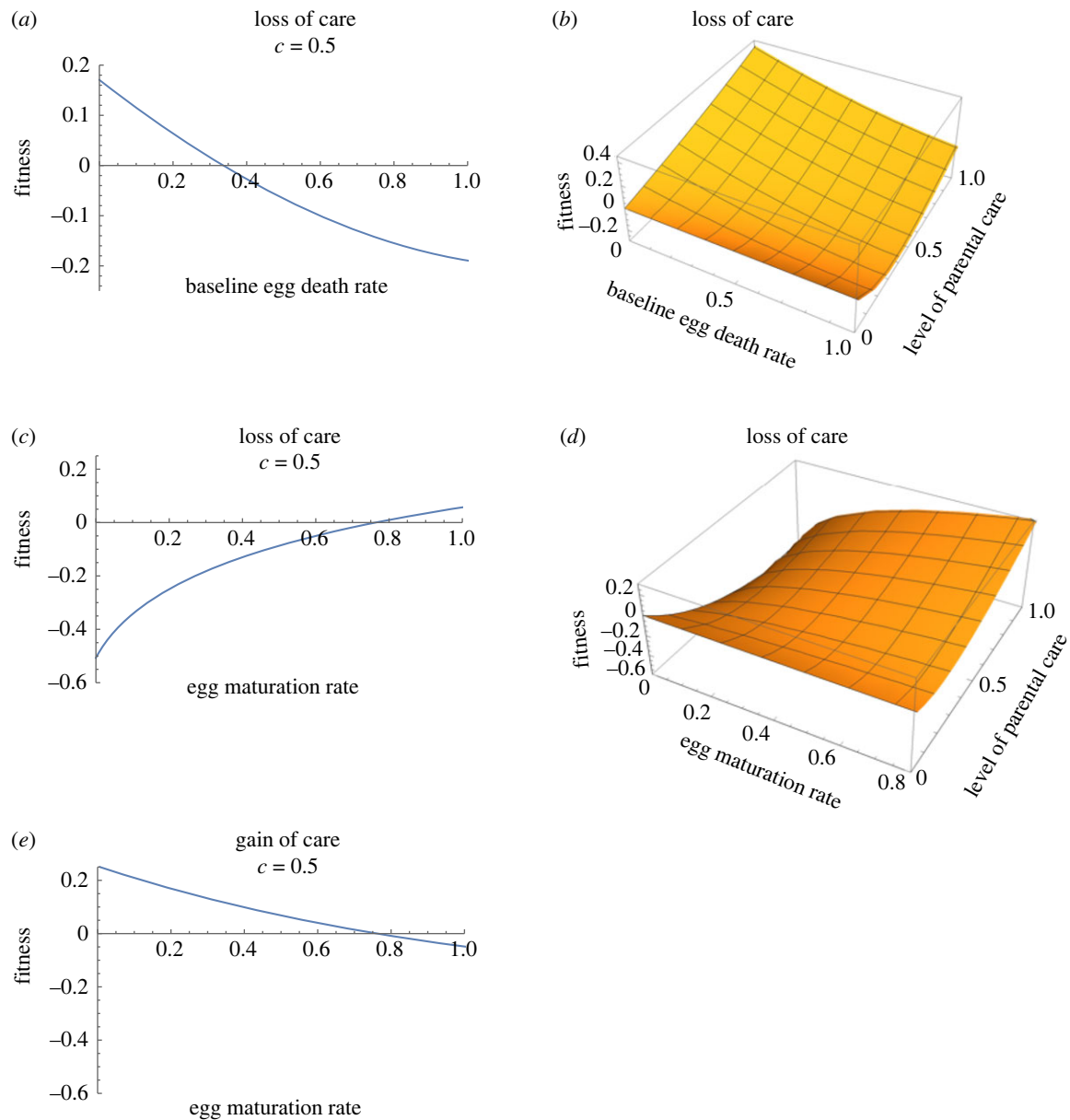


Figure 1. The evolutionary loss of parental care in relation to egg death rate and the evolutionary loss versus gain of parental care in relation to egg maturation rate. The fitness associated with the evolutionary loss of parental care will be greatest when baseline egg death rate (i.e. egg death rate in the absence of care) is relatively low (a), particularly when the level of care provided to eggs is relatively high (b). The fitness associated with the evolutionary loss of parental care will be greatest when egg maturation rate is relatively high (c), particularly when the level of care provided to eggs is relatively high (d). The fitness associated with the evolutionary gain of parental care will be greatest when egg maturation rate is relatively low (e), whereas the fitness associated with the evolutionary loss of parental care will be greatest when egg maturation rate is relatively high (c). As egg maturation rates decrease, the fitness associated with losing care (c) decreases at a steeper rate relative to the benefit of gaining care (e), suggesting that there is evolutionary hysteresis with respect to egg maturation rate and the loss of care. Unless otherwise noted or indicated in the figure: $m_E = m_{Em} = 0.4$, $d_{E0} = d_{Em0} = 0.7$, $d_{A0} = d_{Am0} = 0.7$, $r_o = r_{mo} = 50$, $\sigma_{Jo} = \sigma_{Jmo} = 0.01$, $K = K_m = 50$, $c = 0.5$, $\tau = 0.1$. (Online version in colour.)

particular, when the level of care provided is relatively high and adult mortality is low, the loss of parental care will be selected for (figure 3b). This pattern probably occurs as individuals who have low adult death rates have high potential for future reproduction; when individuals have high future reproductive potential, the fitness benefit associated with investing heavily into current offspring is reduced.

(d) The loss of parental care is most strongly selected for at relatively high levels of care

The evolutionary loss of parental care will be most strongly favoured when the level of care is high regardless of whether (i) baseline egg death rate is low or high (bold and dotted

lines, figure 4a), (ii) baseline adult death rate is low or high (bold and dotted lines, figure 4b), or (iii) egg maturation rate is low or high (bold or dotted line, figure 4c). When the level of care is high, parents incur substantial costs of care relative to the gain in fitness associated with increased egg survival; under such conditions, care is relatively easy to lose.

(e) Comparison between conditions favouring the origin versus the loss of care

The life-history parameter values that favour the loss of care were qualitatively opposite to the values that favour the gain of care for all parameters (figure 1c–e; electronic

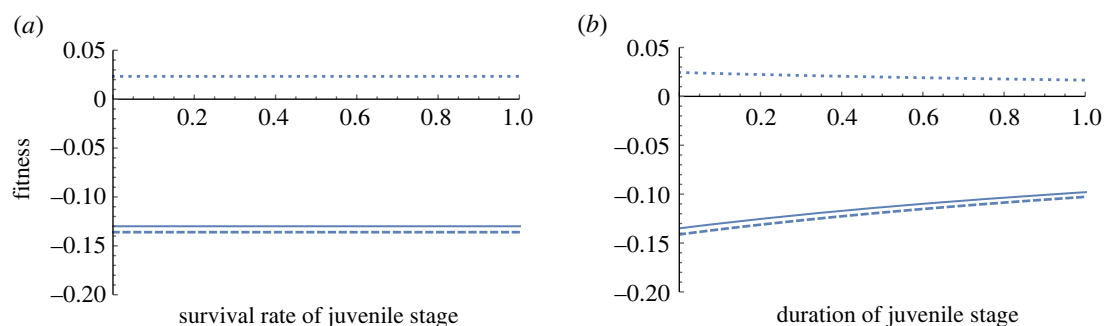


Figure 2. The evolutionary loss of parental care of eggs in relation to juvenile stage survival rate and duration. (a) The fitness associated with the evolutionary loss of parental care is not affected by the survival rate of the juvenile stage when the level of parental care to eggs is relatively high ($c = 0.9$, dotted line), moderate ($c = 0.5$, bold line), or low ($c = 0.2$, dashed line). (b) The fitness associated with the evolutionary loss of parental care is marginally greater at relatively small values of the duration of the juvenile stage when the level of parental care to eggs is relatively high ($c = 0.9$, dotted line), whereas the fitness associated with the evolutionary loss of parental care is marginally greater at relatively large values of the duration of the juvenile stage when the level of parental care to eggs is moderate ($c = 0.5$, bold line) or low ($c = 0.2$, dashed line). Unless otherwise noted or indicated in the figure: $m_E = m_{Em} = 0.4$, $d_{E0} = d_{Em0} = 0.7$, $d_{A0} = d_{Am0} = 0.7$, $r_0 = r_{m0} = 50$, $\sigma_{J0} = \sigma_{Jm0} = 0.01$, $K = K_m = 50$, $\tau = 0.1$. (Online version in colour.)

supplementary material, figures A2–A6). In general, the fitness values associated with the evolutionary loss of care versus the evolutionary gain of care were symmetrical for all parameters except egg maturation rate (figure 1c–e; electronic supplementary material, figures A2–A6). With regard to egg maturation rate, the loss of parental care was, as mentioned above, favoured at relatively high egg maturation rates, whereas the gain of care was favoured at relatively low egg maturation rates [10] (figure 1c,e). However, the slope of the relationship between egg maturation rate and the fitness of losing care is much greater than the slope of the relationship between egg maturation rate and the fitness of gaining care, particularly at low-to-moderate egg maturation rates (figure 1c,e). This suggests that it is relatively more costly to lose care than it is to gain care at low-to-moderate egg maturation rates. In other words, at low-to-moderate egg maturation rates, the fitness cost of losing care is much greater than the fitness cost of providing care (figure 1c,e). We would therefore expect it to be relatively difficult to lose care once it has evolved when individuals spend a relatively long time in the egg stage.

4. Discussion

Here, we have identified the basic life-history parameters that are most likely to favour the evolutionary loss of parental care of eggs. Our results suggest that parental care of eggs is most likely to be lost evolutionarily when (i) eggs survive relatively well in the absence of care, (ii) adult mortality is relatively low, (iii) egg maturation rate is relatively high (i.e. when individuals spend little time in the egg stage), and (iv) when the level of parental care is high. Juvenile survival rate and the duration of the juvenile stage has no-to-minimal impact on the fitness associated with the loss of parental care. Qualitatively, with respect to these life-history parameters, parental care is expected to be lost under conditions opposite to those under which care will be gained, as care is expected to originate when eggs survive poorly in the absence of care, when adult mortality is relatively high, and when egg maturation rate is relatively low (i.e. when eggs develop slowly) [10].

We did not find evidence of evolutionary hysteresis in relation to egg and adult death rates or juvenile mortality or juvenile stage duration. With respect to these life-history

parameters, care is lost both quantitatively and qualitatively under the opposite conditions under which it is gained (electronic supplementary material). While such a result might be intuitive in hindsight, there was no reason to *a priori* expect a lack of evolutionary hysteresis. We did find evolutionary hysteresis with respect to egg maturation rate. As egg maturation rate decreases (i.e. as eggs begin to develop more slowly such that individuals spend more time in the egg stage), it becomes increasingly costly to lose care than to gain it. This suggests that once care is present in a system, it will be relatively challenging for it to be lost if egg maturation rates are low-to-moderate. This result indicates that egg maturation rate might be a key life-history trait that strongly influences the evolutionary dynamics associated with parental care. It is biologically intuitive that egg maturation rate has strong effects on the evolution of care. Individuals who pass through the egg stage quickly are less likely to die as eggs. Given this, if individuals remain in the egg stage longer, parental care is associated with strong fitness benefits because it makes that stage relatively safe [4,39].

The finding of evolutionary hysteresis with respect to egg maturation rate suggests that the fitness benefits of gaining care are not always symmetrical to the fitness benefits of losing care, indicating that even in the absence of coevolution between traits, it might be relatively difficult for care to be lost in some cases (i.e. when eggs mature slowly). These results additionally highlight the importance of considering the evolutionary invasion of behavioural strategies; if we had simply focused on the fitness of parental care without considering invasion dynamics, the evolutionary hysteresis associated with egg maturation rate would have been missed. Evolutionary hysteresis has been found to occur in other contexts and can influence evolutionary tipping points and the likelihood of adaptation and extinction [30,32]. Given this previous work and our finding that evolutionary hysteresis can be associated with the evolutionary dynamics of parental care—albeit to a relatively small extent—it is possible that evolutionary hysteresis might influence the evolution of behavioural strategies in general. The consideration of evolutionary hysteresis in relation to behavioural evolution is a topic that warrants further consideration.

Care is most likely to be lost evolutionarily when eggs survive relatively well without care and when adult death rate is relatively low, which is consistent with classic life-history

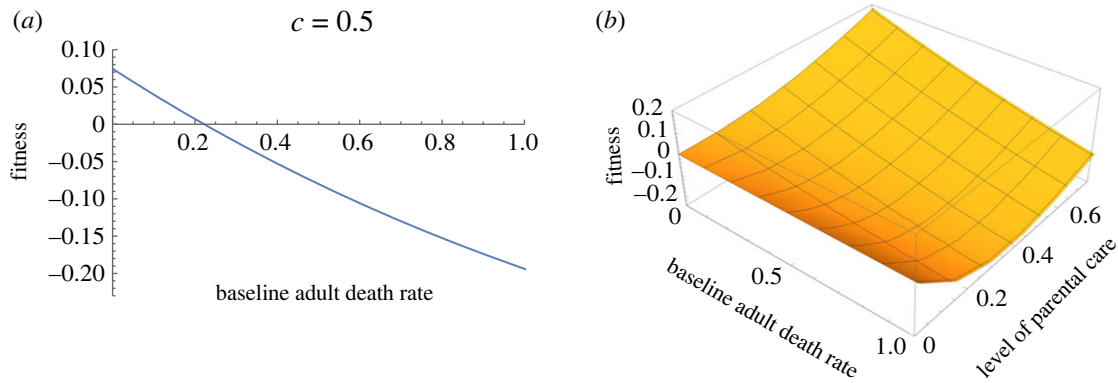


Figure 3. The evolutionary loss of parental care of eggs in relation to adult death rate. The fitness associated with the evolutionary loss of parental care will be greatest when baseline adult death rate (i.e. adult death rate in the absence of care) is relatively low (a), particularly when the level of care provided to eggs is relatively high (b). Unless otherwise noted or indicated in the figure: $m_E = m_{Em} = 0.4$, $d_{E0} = d_{Em0} = 0.7$, $d_{A0} = d_{Am0} = 0.7$, $r_o = r_{mo} = 50$, $\sigma_{Jo} = \sigma_{Jmo} = 0.01$, $K = K_m = 50$, $c = 0.5$, $\tau = 0.1$. (Online version in colour.)

theory which suggests parents will invest less in offspring that have high survival and when parental potential for future reproduction is relatively high [40,41]. In addition, within a species, adult and offspring survival are known to have strong impacts on parental care levels [42]. For example, in smallmouth bass (*Micropterus dolomieu*), adult survival and offspring survival strongly affect optimal parental care decisions [43]. In particular, parents are expected to be least likely to abandon their young when adult survival and offspring survival are low [43]. In this study on smallmouth bass, juvenile survival had little effect on parental care behaviour [43], which is additionally consistent with our finding that juvenile survival will not influence the evolutionary loss of care. Our general finding that care can be lost across a range of life-history parameters is consistent with empirical patterns. For example, care has been lost multiple times in fishes and amphibians with diverse life histories [12,27]. In a study focused on the evolution of parental care across amphibian species, Furness & Capellini [27] found that relatively simple forms of parental care, including egg-only attendance, are lost frequently. Indeed, egg attendance in amphibians is lost approximately as frequently as it is gained evolutionarily [27]. In general, though, relatively few studies focus on the evolutionary loss of care. Additional empirical research on the evolutionary loss of parental care is a worthwhile avenue for future research, particularly since the evolutionary loss of care is likely to influence the evolution of other traits. For instance, using experimental evolution, Rebar *et al.* [44] demonstrated that siblings compete when parental care is provided but evolve to cooperate when parental care is not provided. As such, the loss of care across evolutionary time is likely to influence other offspring behaviours.

While parental care is frequently lost in some animal groups [27], it is ubiquitous in other groups such as mammals [2]. Parent-offspring conflict and coevolution among parent and offspring traits are common once care originates in a system (reviewed in [45]) and likely to make the evolutionary loss of care difficult in many species. Specifically, if parents begin to provide more care to offspring, offspring survival is expected to become dependent on parental care. Our results suggest that as offspring become dependent on care—that is, as egg death rate in the absence of care increases—parental care is unlikely to be lost evolutionarily (figure 1). As offspring become dependent on care, we

might also expect egg maturation rate to decrease as the egg stage becomes relatively safe (safe-harbour hypothesis: [4,39]), which would make it even more difficult for care to be lost. Alternatively, in some cases, slow egg maturation rates might precede and favour the subsequent origin of parental care. For example, larger eggs have longer egg-stage durations and an increased likelihood of egg mortality than smaller eggs; this, in turn, could create selection for parental care, which reduces egg mortality [46]. In frogs, large egg size is positively associated with parental care [46], and comparative analyses revealed that large egg size tends to precede the origin of parental care [46]. In fishes, larger eggs are associated with longer developmental times across species, and parental care and developmental time can co-evolve (reviewed in [47]). In some cases, male fanning in fishes has been found to increase egg maturation rate and decrease the time spent in the egg stage (reviewed in [47]), further highlighting that parental care and egg maturation are highly inter-related.

Importantly, while our results suggest that parental care will be more challenging to lose when eggs mature slowly and when egg mortality in the absence of care is high, we did not consider coevolution between egg maturation rate or mortality and parental care in the present study. Instead, we considered fixed values of life-history parameters, which were then in some cases influenced by the costs and benefits of care (table 1), but the life-history parameter values did not evolve through time in response to the loss of care in our model. As such, we did not consider coevolutionary dynamics. As outlined above, coevolution between parental care and life-history parameters—and in particular, egg maturation rate—is expected based on previous theoretical and empirical research [39,46,47]. Given the likely coevolution between parental care and stage-specific rates of mortality and maturation in nature, it will be important for future theoretical work to identify any such coevolution that is expected to occur during the evolutionary loss of care. Similarly, and as mentioned previously, in the present model, we also did not consider the gradual loss of care (i.e. the resident always exhibits care and the mutant always lacks care in our model). From a biological perspective, it is unclear whether care is lost gradually or rapidly across evolutionary time. No empirical studies, to the best of our knowledge, have explored whether care is lost gradually versus rapidly, and we suggest that exploring whether

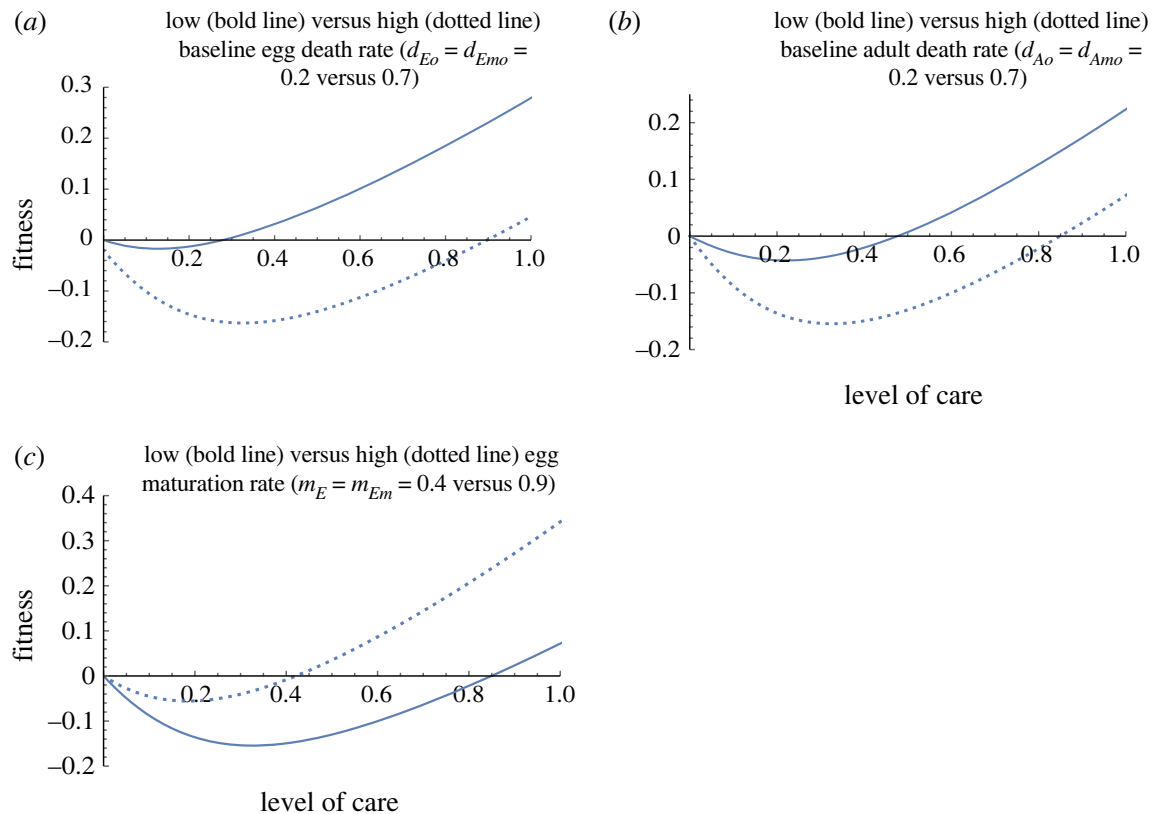


Figure 4. The evolutionary loss of parental care of eggs in relation to the level of care provided. (a) The fitness associated with the evolutionary loss of parental care will be greatest when the level of parental care provided to eggs is relatively high at both low (bold line, $d_{Eo} = d_{Emo} = 0.2$) and high (dotted line, $d_{Eo} = d_{Emo} = 0.7$) baseline egg death rates (i.e. egg death rates in the absence of care). (b) The fitness associated with the evolutionary loss of parental care will be greatest when the level of parental care provided to eggs is relatively high at both low (bold line, $d_{Ao} = d_{Amo} = 0.2$) and high (dotted line, $d_{Ao} = d_{Amo} = 0.7$) baseline adult death rates (i.e. adult death rates in the absence of care). (c) The fitness associated with the evolutionary loss of parental care will be greatest when the level of parental care provided to eggs is relatively high at both low (bold line, $m_E = m_{Em} = 0.4$) and high (dotted line, $m_E = m_{Em} = 0.9$) egg maturation rates. Unless otherwise noted or indicated in the figure: $m_E = m_{Em} = 0.4$, $d_{Eo} = d_{Emo} = 0.7$, $d_{Ao} = d_{Amo} = 0.7$, $r_o = r_{mo} = 50$, $\sigma_{Jo} = \sigma_{Jmo} = 0.01$, $K = K_m = 50$, $c = 0.5$, $\tau = 0.1$. (Online version in colour.)

care has been lost gradually versus rapidly is an important avenue of future empirical research. Given that it is currently unclear whether care has been lost gradually versus rapidly in nature, comparative studies will probably have data on whether care is present versus not in a species (rather than data on a particular level of care, which is challenging to consistently quantify across species). This, in turn, might make the predictions of our model particularly relevant for future comparative analyses. Regardless, it will be important to consider the gradual loss of care in future theoretical studies to determine whether the conditions that favour the gradual loss of care are similar to or differ from the conditions that favour the rapid loss of care.

In summary, the results of our model provide testable predictions for when parental care is expected to be lost evolutionarily. Parental care of eggs is most likely to be lost when egg survival is high, adult mortality is low, individuals spend relatively little time in the egg stage, and the level of care is high. Juvenile survival rate and the duration of the juvenile stage are expected to have little-to-no impacts on the evolutionary loss of egg-only parental care. As egg maturation rate decreases (i.e. as eggs begin to develop more slowly), it becomes increasingly more costly to lose care than to gain it, suggesting that evolutionary hysteresis can impact the evolutionary dynamics of parental care. It would be interesting to test the predictions of this modelling work through phylogenetic comparative analyses to explore

how the loss of parental care relates to empirical patterns of life-history traits. In general, the loss of parental care is relatively under-studied in animals, and we suggest that additional empirical and theoretical work on the loss of parental care will provide a more complete understanding of patterns of parental care evolution. Further, the exploration of evolutionary hysteresis warrants further attention with respect to the evolutionary loss of behaviours. In some cases, evolutionary history might create dynamics that make it difficult for a behaviour to be lost.

Data accessibility. All code is publicly available at <https://osf.io/jcrnx/>. Data are provided in the electronic supplementary material [48].

Authors' contributions. I.N.U.: formal analysis, investigation, writing—original draft, writing—review and editing; M.B.B.: conceptualization, formal analysis, investigation, methodology, validation, writing—review and editing; H.K.: conceptualization, formal analysis, funding acquisition, investigation, methodology, project administration, supervision, validation, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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