

Master's Thesis

Is it better to protect paternity than to provide care?

Maaria Kangasniemi



University of Jyväskylä

Department of Biological and Environmental Science

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Supervisors: Academy Research Fellow Jussi Lehtonen and
Senior Researcher Lutz Fromhage

Tarkastajat: Postdoctoral Researcher Petri Rautiala and
Academy Professor Otso Ovaskainen

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The variation in parental care in the animal kingdom and even within one population or breeding season is great. Despite extensive research, this variation and the evolution of parental care remain intriguing, incompletely understood, and widely debated topics. In theoretical biology, game theoretic methods help to identify the evolutionarily stable strategies in situations where other individuals' actions affect the outcome for one individual. Parental care is an example of such a scenario: the fitness of one parent depends not only on their own caring decision but also on the other parent's decision. One of the most researched questions about parental care is when we should expect care to be female-only, male-only, or biparental. Results from studies addressing this question are not unanimous, which keeps this an interesting research topic. One common assumption in parental care models is a trade-off between mating and caring, which means that caring males miss out on additional mating opportunities. This and partial paternity are two of the most common explanations for female-biased care. However, male care is widespread in birds, for example, even in the presence of partial paternity. In this work, I built two models explaining parental care when there is partial paternity but no mating-caring trade-off. In the first model, I assumed that all the females share the same strategy and used a traditional game theoretical method to find the evolutionarily stable strategies for males. I found out that both pure strategies (only caring or only deserting) could be evolutionarily stable, depending only on other parameter values. In the second model, I allowed the female strategy to evolve and searched for evolutionarily stable strategy pairs with the help of adaptive dynamics. In this model, all the evolutionarily stable strategy pairs were also pure strategy pairs, and it depended only on the parameter values and the population strategy of the opposite sex. According to my results, a better ability to protect one's paternity may be enough to select for male desertion even if there is no mating-caring trade-off.

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Vanhempien tarjoaman huolenpidon tyyppi vaihtelee lajien välillä, mutta myös yhden populaation sisällä tai lisääntymiskauden aikana. Kattavasta tutkimuksesta huolimatta yleispäteviä selityksiä huolenpidon evoluutiolle ei ole löytynyt, minkä vuoksi se pysyykin kiehtovana tutkimusaiheena. Vanhemman tarjoama huolenpito on esimerkki tilanteesta, jossa populaation muiden yksilöiden käyttäytyminen vaikuttaa yhden yksilön fitness-hyötyyn. Tällaisissa tilanteissa on peliteoreettisia menetelmiä hyödyntäen mahdollista selvittää parhaan lopputuloksen tuottava toimintatapa eli evolutiivisesti tasapainoinen strategia. Yleinen huolenpitoon liittyvä tutkimuskysymys koskee sitä, kumman vanhemman kannattaisi huolehtia jälkeläisistä. Tutkimustulokset eivät ole aivan yksimielisiä, minkä vuoksi tämä on edelleen mielenkiintoinen tutkimuskysymys ja inspiroi siten myös tätä työtä. Yleinen oletus huolenpitoa kuvaavissa malleissa on ollut huolehtivien koiraiden jääminen paitsi ylimääräisistä lisääntymismahdollisuuksista. Tätä sekä isyyden epävarmuutta on käytetty selityksenä naarasvoittoiselle huolenpidolle. Kuitenkin esimerkiksi linnuilla esiintyy paljon myös koiraan tarjoamaa huolenpitoa isyyden epävarmuudesta huolimatta. Tässä työssä muodostin kaksi mallia, joissa otin huomioon isyyden epävarmuuden ja oletin, että sekä huolehtivat että hylkäävät koiraat kohtaavat yhtä todennäköisesti ylimääräisiä lisääntymistilaisuuksia. Ensimmäisessä mallissa oletin, että kaikki naaraat käyttävät samaa strategiaa (huolehtivat) ja etsin evolutiivisesti tasapainoista strategiaa vain koiraille. Ensimmäisessä mallissa sekä huolehtiminen että hylkääminen voivat molemmat olla evolutiivisesti tasapainoisia strategioita koiraille, jolloin lopputulos riippuu muiden parametrien arvoista. Toisessa mallissa annoin myös naaraan strategian muuttua ja etsin evolutiivisesti tasapainoista strategiaparia. Tässä mallissa kaikki puhtaat strategiaparit saattoivat olla evolutiivisesti tasapainoisia, riippuen muista parametrien arvoista ja vastakkaisen sukupuolen populaatiostrategiasta. Tulosteni mukaan hylkääminen voi olla koiraille parempi strategia, mikäli hylkäävät koiraat ovat parempia puolustamaan isyyttään.

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TERMS AND ABBREVIATIONS

Terms

Anisogamy	The size difference between male and female gametes
Game theory	Field of mathematics that deals with interactions between individuals and helps to find the best behavior in a specific situation
Evolutionary game theory	Game theory applied in evolutionary biology context
Strategy	The probabilities that an individual chooses different options expressed as a vector
Pure strategy	A strategy where the individual always chooses one option with probability 1
Mixed strategy	A strategy where the individual chooses different options with some probabilities p_1, p_2, \dots, p_n so that $0 < p_i < 1$ and $\sum_{i=1}^n p_i = 1$
Population strategy	A strategy that is adopted by every individual of the population
Payoff	The fitness obtained by using some strategy
Evolutionarily stable strategy	A strategy that cannot be replaced by another strategy under natural selection
Evolutionarily stable strategy pair	A pair of strategies that consists of a male and a female strategy that are evolutionarily stable
Extra-pair copulation	A copulation that does not occur between a mated pair

Abbreviations

ESS	Evolutionarily stable strategy
ESS pair	Evolutionarily stable strategy pair
EPC	Extra-pair copulation

1 INTRODUCTION

The evolution of parental care is one of the many intriguing mysteries in evolutionary biology because the observed variation of parental care is abundant. In some species, there is no observable parental care, whereas in other species both parents provide extensive care for the young. In addition to that, the methods of parental care also vary across species.

Parental care can be broadly defined as any type of investment made by the parent, which increases the number of surviving offspring and inflicts some cost to the carer (Smiseth *et al.* 2013). This general definition of parental care allows it to include multiple types of investments that enhance the survival probability of the offspring. According to this definition, parental care can be as subtle as allocating more resources to gametes to enhance the offspring's survival (Smiseth *et al.* 2013). One could argue that the females always provide parental care in this sense, as the gametes produced by the females are commonly bigger than the ones produced by the males and require more resources. Another form of parental care that occurs before fertilization is the courtship behavior the males (or females in some cases) of some species may express. Providing the female with good resources may increase the survival probability of the offspring or the number of eggs the female produces. For example, a study with green-veined white butterflies (*Pieris napi*) shows that increasing the amount of nutrients the male provides before fertilization increases the number of eggs the female produces (Wedell and Karlsson 2003). Other pre-fertilization behaviors, like choosing the breeding site, nesting site, or oviposition site, can be classified as parental care if the choice affects the offspring's survival (Smiseth *et al.* 2013).

Despite the examples above, parental care is often seen as behavior that is expressed directly towards the eggs or living offspring. This definition of parental care limits it to happen after fertilization and even after the offspring are born. Parental care after fertilization can include attending to the eggs, which protects them from environmental hazards such as predators (Smiseth *et al.* 2013). For example, the males of two frog species *Hylophorbus rufescens* and *Oreophryne* sp. A, express parental care by attending to the eggs (Bickford 2004). In addition to just staying with the fertilized eggs, parents can also carry the developing young externally or internally (Smiseth *et al.* 2013). In amphibians, parents can carry the eggs from one place to another in their dorsal pouches, vocal sacs, or stomachs (Crump 1996). An extreme version of carrying the fertilized eggs is viviparity. In viviparous animals, the fertilized eggs develop inside the female's reproductive tract, and the offspring are born alive (Campbell *et al.* 2015). This is an effective way to protect the eggs from environmental hazards and is prevalent in mammals (Smiseth *et al.* 2013). Attending to and carrying the offspring may occur at any time during offspring development and may therefore be directed towards eggs, hatched offspring, or live-born young. One of the most general

types of parental care is provisioning food to the offspring after hatching or birth (Smiseth *et al.* 2013), which is common in birds and mammals.

Not only does the form of parental care vary across the animal kingdom, but so does the caregiver's sex. Most of the parenting tasks can theoretically be performed by either of the parents, but sometimes they are more easily performed by one particular parent. For example, female mammals provide milk for the young, which is not something that males are generally capable of doing. Exceptions are found in the Dayak fruit bats (*Dyacopterus spadecius*) and the masked flying fox (*Pteropus capistrastus*). In these species, male lactation has been observed, although the adaptivity of that behavior could not be confirmed and it could instead be caused by a pathogen (Kunz and Hosken 2009).

How common is parental care across the animal kingdom, and which parent provides care? In mammals, the offspring always receive parental care because the females always provide milk for the young (Balshine 2013). The most common form of mammalian parental care is female-only care (90% of species), and the remaining 10% is biparental care (Gross 2005). Cantoni & Brown (1997) found that male presence is essential for offspring survival in California mice (*Peromyscus californicus*) when foraging for food was required. Another example of biparental care in rodents is found in a study with Campbell's dwarf hamster (*Phodopus campbelli*), which shows that the males assist the female during birth by cleaning and staying with the offspring (Jones and Wynne-Edwards 2000).

Only a few bird species do not provide parental care, including brood parasites such as the common cuckoo (*Cuculus canorus*), while 81% of the species provide biparental care (Cockburn 2006). Only 8% of the species provide female-only care, and 1% male-only care (Cockburn 2006). Bird species that provide male-only care include, for example, the emu (*Dromaius novaehollandiae*), the spotted sandpiper (*Tringa macularia*), and the Eurasian dotterel (*Charadrius morinellus*) (Owens 2002).

In species with biparental care, the parenting tasks could be the same for both parents or they could be divided somehow between the parents. Dark-eyed junco (*Junco hyemalis*) is an example of a bird species with biparental care but differing parental tasks. Dark-eyed junco males feed and protect the offspring but other parental tasks are performed by the female (Ketterson and Nolan Jr 1994). The division between parental duties has been observed also in the emperor penguin (*Aptenodytes forsteri*). After mating, emperor penguin females leave to the ocean to feed, and males are left behind to incubate the eggs (Stonehouse 1952). Females return at the time of hatching to feed newly hatched chicks (Jouventin *et al.* 1995).

In theory, parental care duties could be divided equally between the parents, and both parents could continue providing sufficient care even if the other one disappears. However, that is not always the case, as Schmutz *et al.* (2014) found in their observations on ferruginous hawks (*Buteo regalis*), rough-legged hawks (*Buteo lagopus*), and great horned owls (*Bubo virginianus*). They found that as males were used to bringing the food to the nest, they did not adapt to feeding the chicks when females were absent. Males did react to chicks begging for food,

but only by bringing more food and not attempting to feed the chicks (Schmutz *et al.* 2014).

In fishes, any type of parental care occurs in only about 20% of the species, half of that being male-only care and 30% female-only care (Gross 2005). A well-known but extreme example of a fish providing male-only care is the seahorse, as seahorse males are the ones that carry the fertilized eggs and care for them until releasing them (Vincent and Sadler 1995). An extraordinary form of biparental care is observed in Discus fish (*Symphysodon* sp.) that feed the offspring with mucus secretions (Buckley *et al.* 2010). Buckley *et al.* (2010) found that the offspring were never left alone in the first two weeks, although sometimes care was provided by both parents and sometimes by one parent.

Research on amphibian parental care is not nearly as comprehensive as the research on avian or mammalian parental care, but new information about amphibian parental care is accumulating rapidly. Some estimates suggest that parental care occurs in around 10% - 20% of amphibian species (Schulte *et al.* 2020). For example, Rosenberg's tree frog (*Hyla rosenbergi*) males and one population of Blacksmith tree frog (*Boana fiber*) males guard the fertilized eggs when male density is high, and by doing so, protect them from other males (Martins *et al.* 1998).

The form of parental care does not vary only between the species, but it also varies within species and populations of the same species. Environmental changes can affect the form of parental care, and it could change even within the individual according to the quality of the individual (Webb *et al.* 1999). In fact, environmental factors have been used to explain the emergence of parental care, along with different life-history characteristics (Klug *et al.* 2013). For parental care to evolve, it must increase the parent's fitness, the trait expressing parental care must be heritable, and the trait must be able to spread in a population under the influence of natural selection (Klug *et al.* 2013).

Questions regarding parental care do not focus only on the question "Should parental care be provided?" but also on the question "Who should provide parental care?". The difference in gamete sizes (termed anisogamy) has been used to explain female-only care. As females already invest more in the gametes, they should ensure that they do not invest for nothing and thus provide care for the offspring (Trivers 1972). However, this is not an entirely valid explanation for female-only care as the caring decision should be based on future investment instead of past investment (Dawkins and Carlisle 1976). Both parents obtain the same benefit from the offspring even if their initial investment is not equal and the benefit depends only on the future investment the offspring receives. Even though the argument by Trivers is criticized, anisogamy has still been accounted for in models for parental care. Due to expensive eggs, females can produce only a limited number of them, and egg production may trade-off with parental care (Maynard Smith 1982; Iyer *et al.* 2020). Males can produce almost a limitless number of tiny sperm, making their reproductive success dependent on the availability of females (Iyer *et al.* 2020). To maximize their offspring number, males should try to mate with as many females as possible.

Typically, a mating-caring trade-off has been assumed as a cost of caring, meaning that caring males miss out on additional mating opportunities. This trade-off has been thought to drive the evolution of parental care towards female care (Trivers 1972; Queller 1997).

Other possible explanations for the prevalence of female care arise from internal fertilization and paternity uncertainty. When fertilization occurs inside the female, males can never be sure that the offspring are indeed his biological offspring (Queller 1997). Male parental care has been suggested to occur more commonly in species with external fertilization, which allows males to defend their paternity more easily (Benun Sutton and Wilson 2019). To defend this argument, external fertilization is the norm in fishes, and half of the parental care found in fishes is indeed male-only care, while only 30% is female-only care. A correlation between fertilization mode and parental care type has been found in teleosts and amphibians (Gross and Shine 1981). Paternity uncertainty due to internal fertilization seems a reasonable explanation for female care, but male care is also found among birds that have internal fertilization. Clearly, paternity uncertainty does not rule male care out, so there must be some other factors that also affect the distribution of parental care roles.

Explanations for male care include increasing one's paternity by guarding the female and sexual selection. Females could prefer males who provide parental care, which makes them gain more additional mating opportunities instead of missing out on them (Alonzo 2012). Females could also be more loyal toward caring males, as has been seen in savannah sparrows (*Passerculus sandwichensis*). Freeman-Gallant (1996) found that most of the females mated to caring males were more loyal to their mates during their second breeding event, which means that the males had higher paternity in their second brood. This type of behavior may result from female preference or male guarding. Caring males could be better at keeping an eye on the female and preventing other males from mating with the same female (Kvarnemo 2006). Interestingly, males are not the only ones capable of guarding their mates, females have also been seen doing that. Female red-winged blackbirds (*Agelaius phoeniceus*) are aggressive towards other females, especially towards those who show interest in mating (Yasukawa and Searcy 1982). By guarding their mate from other females, they ensure undivided parental care by their mate (Yasukawa and Searcy 1982).

Parental care is defined in multiple ways and different terms describing parental care have been used in literature. Other terms commonly used in parental care research are parental effort and parental investment. Trivers (1972) defined parental investment as any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring". This definition also included pre-fertilization care, like the allocation of more resources to the gametes. Parental effort has been defined similarly, but it excludes the negative effects of providing care (Stiver and Alonzo 2009). Klug et al. (2013) addressed the struggle of defining parental care and defined parental

care as any behavior that occurs after fertilization and increases the offspring's lifetime reproductive success.

Since the terms and definitions used in the literature vary, it is crucial to define parental care clearly in every study regarding parental care. In this work, I define parental care as any behavior that occurs after fertilization, increases the offspring's survival probability, and is directed toward the eggs/offspring. This definition is important to remember throughout this thesis since it directly affects the assumptions I make in my models.

In the following section, I will provide a brief overview of game theory and its use in evolutionary biology. After that, I will discuss some previous theoretical work that has inspired this thesis and present the research questions and hypotheses.

1.1 Game theory and its applications in evolutionary biology

Game theory is a relatively young field of mathematics developed to explain reasonable frequency-dependent human actions in the economic setting (Neumann and Morgenstern 1947). Later game theory has been applied to evolutionary biology (e. g. Maynard Smith, 1982). Games in a game theoretic context are decision-making situations between two or more participants. Each participant decides independently what to do and tries to choose the option that yields the best payoff from the situation.

In evolutionary game theory, the game is often between two individuals who have some options from which to choose. Individuals can adopt a pure strategy, which means that they will always choose the same option, or they can adopt a mixed strategy, which means that they will choose different options with different probabilities (McNamara and Weissing 2010). Strategies are expressed mathematically as vectors, where the behavioral options are the components of that vector. If an individual has two options from which to choose, their strategy could be denoted by the vector $(p, 1 - p)$, which means that the individual will choose the first option with probability p and the second option with probability $1 - p$. If $0 < p < 1$, this strategy is called a mixed strategy.

In this thesis, I will use the term population strategy to refer to the strategy the population has adopted. In models including only two pure strategies, this can be interpreted as the mean strategy of the population. For example, if the population strategy is $(\frac{2}{3}, \frac{1}{3})$, this could mean that all the individuals choose the first option with probability $2/3$ and the second option with probability $1/3$. This could also mean that $2/3$ of the population always chooses the first pure strategy and $1/3$ always chooses the second pure strategy. In my models, both ways of interpreting the population strategy are equally correct in terms of the outcome because the models include exactly two pure strategies, and the individuals interact randomly with each other (Maynard Smith 1982).

Game theory gives tools that help to find the best strategy to maximize the individual's fitness, given the strategies of other individuals in the population. This strategy is also the strategy towards which the population strategy is

expected to evolve under natural selection. Traditional game theory has focused on finding the theoretical ESSs and has commonly assumed that all the trait values in the strategy set are equally possible. However, this may not be the case in nature since advantageous mutations rarely happen as large changes, and some theoretical ESSs may even be impossible to achieve under natural selection (McNamara and Weissing 2010). Due to this, and due to the mathematical convenience of modeling mutations of small effect (δ -weak selection (Wild and Traulsen 2007; Lehtonen 2018)), evolutionary dynamics under small effect mutations are commonly considered when searching for the ESS using modern game theoretical methods such as adaptive dynamics (also known as e.g. sequential invasion analysis) (Dieckmann and Law 1996; Otto and Day 2007; Avila and Mullan 2023). These methods also provide tools for modeling the coevolution of multiple traits, which will be useful in my second model when I study the coevolution of male and female strategies.

When applying game theory to parental care, the game is between a female and a male who have mated and must decide whether to care or desert (Maynard Smith 1977). The fitnesses are usually the number of surviving offspring or the expected lifetime reproductive success. Parental care research is an excellent application for game theory since fitness is usually affected by both parents' strategies. Fitnesses can be presented in matrix form (Maynard Smith 1977, 1982; Iyer and Shukla 2021), but I have just listed them separately in tables. The objective of solving the game is to find an evolutionarily stable strategy (ESS). Maynard Smith & Price (1973) defined an ESS as a strategy that "if most of the members of a population adopt it, there is no "mutant" strategy that would give higher reproductive fitness". This means that a population where all individuals use the ESS cannot be invaded by a mutant using any other strategy, but it also means that changing strategy unilaterally in a situation where both have adopted an ESS is not wise as it results in a lower payoff for the changer.

I have noticed that the use of the term ESS can be confusing as in some cases, it refers to a single strategy, and in some cases, it refers to a strategy pair. In some cases, the ESS could be the same for both players, but due to the asymmetrical nature of games regarding parental care, the ESSs might be different for each player. Because I deal with two different models, one having only one player and the other having two players, I define an evolutionarily stable strategy pair (ESS pair) as a strategy pair that includes the ESSs for males and females. Throughout this thesis, I use the term male-biased (or female-biased) ESS pair to denote an ESS pair where the proportion of caring males is higher than caring females (or vice versa).

1.2 Previous theoretical research regarding parental care

Parental care is not by any means a new topic for theoretical research, but instead many mathematical models regarding parental care have been developed. Among the most influential models are Maynard Smith's (1977) game theoretical frameworks that explain the distribution of parental roles. Instead of parental

care, he used the term parental investment and used the same definition as Trivers (1972) did. He constructed three models with slightly varying assumptions. In all the models, he assumed that the survival probability of the offspring depends on the number of caregivers, which is a basic feature of models regarding parental care. In the first and second models assuming discrete breeding seasons, he incorporated a mating-caring trade-off by assuming that only deserting males may mate a second time with another female. In his later work, he changed this assumption and let also caring males to mate again (Maynard Smith 1982), but this modification did not alter his fundamental findings. In the second model, he assumed that deserting females could lay more eggs and thus included the trade-off between fecundity and caring for females. In the third model, he assumed continuous breeding. He found that in the first two models, all the pure strategy combinations can be ESS pairs depending on the parameters, but he did not address any mixed strategy pair as an ESS pair. In the third model, he found two possible ESS pairs that were both uniparental care (Maynard Smith 1977).

Maynard Smith's Model 2 (1977) has inspired much further work and has been a very influential model about parental care evolution. Despite its usefulness, it has met some criticism. The lack of self-consistency, meaning that the females for additional mating attempts seem to appear out of thin air, has been pointed out on several occasions (Wade and Shuster 2002). Further work has focused on self-consistent versions of this model, and some mixed results have been achieved (Queller 1997; Webb *et al.* 1999; Fromhage *et al.* 2007; Iyer *et al.* 2020; Iyer and Shukla 2021).

Webb *et al.* (1999) criticized some other assumptions of the Model 2. They argued that the individual quality or the stage of the breeding season could affect the payoff. They then built a two-stage model in which they assumed that the individuals could mate only two times in the breeding season, and they could change their caring strategy between. In their baseline model with fixed remating probabilities, they found the same ESS pairs as Maynard Smith, and allowing the remating probability to depend on the frequency of deserting females also yielded mixed ESS pairs. They found mixed ESS pairs also when they included the individual's quality as a factor. They concluded that the relationship between caring decisions and the probabilities for achieving additional matings must be considered. Iyer and Shukla (2021) allowed the remating probability to depend on the proportions of deserting females and males. Fromhage *et al.* (2007) assumed that any additional matings happen as extra-pair copulations (EPCs) and let the remating probability depend on the proportion of deserting males. I will explain the details of their model in Section 2 as I am expanding and modifying their model in my work.

As Webb *et al.* (1999) noted, the stage of the breeding season could affect the outcome. McNamara *et al.* (2000) modeled the evolution of parental care over the breeding season. They found that the best behavior changed during the breeding season and at the end of the season, the best option was always caring. In his model, the future expected payoff affected the best decision at the given

moment. The number of deserters affected the remating probability, and the stage of the breeding season affected the expected number of broods possible to rear in the remaining season. At the end of the breeding season, neither of the parents can expect to be able to rear any more broods, so it is beneficial to care for the last brood to increase their own fitness by enhancing the survival probability of the offspring (McNamara *et al.* 2000).

Iyer *et al.* (2020) built several models on Maynard Smith's model 2 and investigated the effect of anisogamy on parental care evolution. Like Maynard Smith, they assumed that due to expensive eggs, females could lay more eggs if they did not put resources into caring. They constructed three different games. In the first game, they assumed that caring males missed completely out on additional mating opportunities. In this game, they found that biparental care and biparental desertion could both be ESS pairs, and they also found a symmetric mixed ESS pair. In the second game, they weakened the mating-caring trade-off but gave deserting males an advantage at remating. In addition to biparental care and biparental desertion being ESS pairs, they found two different male-biased ESS pairs in this game. In the third game, they assumed a strict mating-caring trade-off and that deserting females lay more eggs in the first brood than caring females. In the last game, biparental desertion and biparental care were ESS pairs again, and in addition to these, one strategy pair biased to male care was an ESS pair. They also did some agent-based simulations, where they relaxed the assumption of breeding synchrony. In these simulations, they could obtain female-biased care as an ESS pair. They concluded that anisogamy is not a sufficient explanation for female-biased care if there are no other factors.

Later, they expanded their model by adding partial paternity and constructed four different theoretical models (Iyer and Shukla 2021). In Game 1, they assumed that both caring and deserting males were equally likely to obtain extra-pair copulations (EPCs), but only deserting males could mate with other deserting females, who laid the additional eggs in new nests. In this situation, paternity uncertainty did not affect the ESS pair. In Game 2, they assumed that a caring male has higher paternity than a deserting male and found two mixed ESS pairs that were male-biased. In Game 3, they assumed a strict mating-caring trade-off and found two mixed ESS pairs that all were female-biased. In Game 4, they introduced variables for the remating probabilities and found all pure strategy pairs to be ESS pairs together with some mixed strategy pairs. They concluded that paternity uncertainty itself was not enough to weaken the selection for male care and a trade-off between mating and caring was necessary for an ESS pair to be female-biased (Iyer and Shukla 2021).

However, as a mating-caring trade-off might not be as significant as previously thought, or caring males could even be preferred by females, I argue that some other factors may drive the selection for male desertion. Iyer and Shukla (2021) found that in their model paternity did not affect the ESS pair when a mating-caring trade-off was excluded. In this case, caring did not inflict any cost for the males but generally, some form of cost should be incorporated in the

model. What if the cost of caring is a reduced ability to protect one's paternity and deserting males on average have higher paternity in their broods?

1.3 Objectives and predictions

In this thesis, my objective was to explore further how partial paternity affects the ESS in the absence of a mating-caring trade-off and if better ability to protect paternity could select for male desertion. I built two game theoretic models using the model by Fromhage et al. (2007) as a base model but assumed that there is no mating-caring trade-off and that deserting males are better at guarding their paternity. In the first model, I assumed according to Fromhage et al. (2007), that all the females share the same strategy, and thus the main objective was to find ESSs for males. I hypothesized that allowing deserting males to be better at guarding their paternity is enough for female-biased care to evolve.

The second model is an expanded version of the first model and allows the female strategy to evolve. Most of the models regarding parental care, including models by Iyer and Shukla (2021) and Maynard Smith (1977), allow both male and female strategies to evolve. Since they usually affect each other and evolve together, including the female strategy also in my model was crucial. With this model, I investigated how the female strategy affects the outcome and if male desertion could still be an ESS.

I used a traditional game theoretic method to solve the first model and find analytical conditions for male desertion. To make these conditions more comprehensible, I used MATLAB (Mathworks 2020) to illustrate the effect of the parameters on the possible ESSs. I searched for analytical conditions for each possible ESS pair also in the second model. In addition to that, I used adaptive dynamics (Dieckmann and Law 1996; Avila and Mullan 2023) to model the simultaneous evolution of male and female strategies, their co-evolutionary trajectories, as well as the resulting ESS pairs.

2 METHODS

I used a game theoretical approach to find the evolutionarily stable strategies for parental care when males do not suffer from mating-caring trade-off and deserting males are better at guarding their paternity. I built my models using the same basic principles and assumptions as Maynard Smith (1977) and Fromhage et al. (2007) used in their models.

As explained in Subsection 1.1, the game regarding parental care is usually between the individuals of a mated pair, and the behavioral options from which to choose are caring and deserting. Any individual could use a pure strategy, which means that they always choose one of the options, or a mixed strategy, which means that they choose one option with some probability p and the other with some probability $1 - p$. If this mixed strategy is an ESS, the population having caring individuals at frequency $1 - p$ and deserting individuals at

frequency p is also stable. This generalization does not always hold but is the case when there are exactly two pure strategies (Maynard Smith 1982).

The population in my models had a large population size, an even sex ratio, and synchronous breeding, meaning that all the individuals breed simultaneously. I also assumed that all individuals find a mating partner, which means that after the breeding event, all the individuals have mated. Even if females could desert, I assumed they would not lay another batch of eggs in another nest, meaning that all the additional mating opportunities after the main breeding event happened as extra-pair copulations (EPCs) when males could mate with another male's mate and obtain some paternity share in their brood. I assumed that only one successful EPC attempt could happen per brood, and any following attempts were automatically unsuccessful. This means that there was only one nest per breeding pair, but one nest could contain offspring sired by two different males.

Because I assumed the absence of a mating-caring trade-off, both caring and deserting males were free to seek EPCs and were equally likely to succeed in their EPC attempts. The success probability of an EPC attempt depended only on the strategy of the male whose female was involved in an EPC. Since I assumed that deserting males were better at guarding their paternity, the probability of a successful EPC attempt was lower when the EPC attempt was targeted toward a deserting male's mate than when it was targeted toward a caring male's mate.

To make these assumptions understandable, I will introduce some biological explanations for them. I defined parental care as any behavior that happens after breeding, is directed towards the offspring, and increases the offspring survival probability. In my models, parental care could include, for example, incubating or protecting the eggs or feeding the young. Two parents provide better care than just one, for example, because then either one of the parents could be always attending to the eggs, even if the parents must leave the nest occasionally. Desertion is characterized by ignorance towards the offspring. Deserting females are free to roam around and forage without time restrictions and as a result, could allocate more resources towards egg production and produce a larger batch of eggs. Deserting males allocate their time and energy to guarding the female instead of caring for the offspring. Males guarding their mate could follow her and express hostile behavior towards other males to prevent EPCs.

I built two models, the second being a broadened version of Model 1. In Model 1, females shared the same strategy which did not evolve, but in Model 2, they could choose their strategy. My previously stated assumptions hold in both models. In the following sections, I will describe my models in detail and introduce necessary mathematical expressions.

2.1 Model 1: Only the male strategy can evolve

Model 1 is a modification of the model Fromhage et al. (2007) constructed. According to their assumptions, I assumed that all the females share the same

strategy, but males can make their caring decisions after mating, meaning that some males might care for the offspring, and some might desert. Fromhage et al. (2007) used ρ to denote the proportion of deserting males, whereas I used m_d to be more consistent throughout my work.

I allowed both caring and deserting males to seek additional mating opportunities, meaning that every male has his own brood and a possibility for achieving extra-pair copulations (EPCs). Caring males missing out on additional mating opportunities is a common assumption (e.g., Fromhage et al., 2007; Maynard Smith, 1977). However, the mating-caring trade-off may not be as significant as thought, and caring males can be equally as good at getting additional mating opportunities, or there could even be a positive correlation between caring and mating (Stiver and Alonzo 2009).

Since any additional matings happen as EPCs, the intruder's payoff from a successful EPC must inflict a corresponding loss to the primary male's fitness. To account for the paternity loss and gain due to an EPC, Fromhage et al. (2007) introduced functions α and β for deserting male's expected paternity through EPCs with females whose partner is a caring male or a deserting male. Due to the formulation of these functions, they could also allow different probabilities for successful EPC attempts with a carer's mate and a deserter's mate. As this feature was already in the functions, modifying the functions to fit the scenario where deserting males were better at protecting their paternity was straightforward.

The parents' caring decisions affected the offspring survival probability, as two parents are better than one, and one is better than none. The offspring survival probability depended also on the EPC occurrence. I used the same variables for offspring survival probability as Fromhage et al. (2007) did. The variable V_c denoted the survival probability of the offspring when the male cares and an EPC did not occur, and V_{epc} was the survival probability in the cases where an EPC occurred. There is some evidence that males may reduce their caring effort if an EPC has occurred and the brood contains unrelated young, which is why I included three different survival probabilities (e.g., Møller & Cuervo, 2000).

Explanations for all parameters and functions are in Table 1. The functions from the model by Fromhage et al. (2007) and my modified functions and expressions for parameters are listed in Table 2 for comparison. I used parameters γ_c and γ_d instead of function $\gamma(\rho)$ to make differences between fitnesses for caring males and deserting males more distinguishable. I used γ_c to denote the proportion of caring males' broods in where an EPC occurs, as $\gamma(\rho)$ denoted before. In addition to that, I used γ_d to denote the proportion of deserting males' broods where an EPC occurs. These differ slightly from $\gamma(\rho)$, as these are not functions of m_d like γ was the function of ρ . This is because in my model, all the males were allowed to make EPC attempts, thus the number of EPC attempts did not depend on the ratio of deserting males to caring males.

Table 1 Explanations of parameters and functions used in Model 1.

m_d	The proportion of deserting males
V_c, V_{epc}, V_d	The offspring survival probability when male cares and no EPC has occurred, male cares and an EPC has occurred, male deserts
x	Paternity share obtained through a successful EPC
w	The number of eggs the female lays
$\alpha(m_d)$	Expected paternity obtained through successful EPCs with partners of caring males
$\beta(m_d)$	Expected paternity obtained through successful EPCs with partner of deserting males
p_A	The probability that an EPC attempt succeeds when it is directed towards a caring male's partner
p_B	The probability that an EPC attempt succeeds when it is directed towards a deserting male's partner
γ_c	The proportion of caring males' broods where an EPC occurs
γ_d	The proportion of deserting males' broods where an EPC occurs
$H_c(m_d)$	Fitness of a caring male
$H_d(m_d)$	Fitness of a deserting male

As Fromhage et al. (2007), I also used the Poisson distribution to determine the proportion of females experiencing any given number of EPC attempts. The Poisson distribution gives the probabilities for discrete events that happen in a specific time interval and do not depend on each other (Otto and Day 2007). In this case, the event was an EPC attempt, and any female could potentially experience many EPC attempts, but the expected number of EPC attempts experienced was n . That was because every male made n EPC attempts, and the sex ratio was equal, making the average number of EPC attempts experienced by one female also n . The probability that any given female experiences j EPC attempts is given by

$$poisson(n, j) = e^{-n} \frac{n^j}{j!}.$$

Using this probability for a female to experience j attempts, I calculated the value for γ_c as follows:

$$\gamma_c = 1 - \sum_{j=0}^{\infty} e^{-n} \frac{n^j}{j!} (1 - p_A)^j.$$

The sum is the probability that the female experienced zero attempts (which were not successful), or one attempt that was not successful, or two attempts that were not successful, et cetera. Thus, γ_c is the complementary event of the situation where none of the attempts were successful, meaning that γ_c denotes the probability that at least one attempt was successful. Equivalently, it is also the proportion of carers' broods in which an EPC occurred. I calculated the value for γ_d in the same way as for γ_c :

$$\gamma_d = 1 - \sum_{j=0}^{\infty} e^{-n} \frac{n^j}{j!} (1 - p_B)^j.$$

Calculating the sum simplifies the expressions for γ_c and γ_d to the ones in Table 2. These are incorporated in functions α and β , which give the paternity obtained through successful EPCs with the partners of caring males and deserting males. The expression for function α is formulated by multiplying the proportion of females mated to caring males ($1 - m_d$), the probability for a successful EPC with a caring male's mate ($1 - e^{-np_A}$), and the paternity share possible to obtain through an EPC (x). The expression for function β forms similarly, but $1 - m_d$ is replaced by m_d and p_A is replaced by p_B .

I then used the parameters γ_c and γ_d and the functions α and β to build the fitness functions for purely caring (H_c) and purely deserting (H_d) males. Every caring male could potentially have $V_c w$ surviving offspring in his brood, but the probability of a successful EPC attempt must be accounted for in the fitness functions. There is a probability of $1 - \gamma_c$ that an EPC does not occur and a probability of γ_c that an EPC occurs, meaning that any caring male can, on average, expect to have $V_c(1 - \gamma_c)w + V_{epc}\gamma_c w$ surviving offspring in his brood. However, due to an EPC, all the surviving offspring in his brood are not his biological offspring. Therefore, the number of surviving offspring sired by another male should be subtracted from the overall number of surviving offspring, leaving the number of surviving biological offspring, which is $V_c(1 - \gamma_c)w + V_{epc}\gamma_c w - \gamma_c x V_{epc} w$. Because every male is now able to make EPC attempts, also caring males could expect some offspring through successful EPC attempts. They could have these with the partners of caring males ($\alpha(m_d)V_{epc} w$) and/or deserting males ($\beta(m_d)V_d w$). By adding these to the number of surviving biological offspring in their own brood, the overall number of a caring male's surviving biological offspring is

$$H_c(m_d) = V_c(1 - \gamma_c)w + V_{epc}\gamma_c w - \gamma_c x V_{epc} w + \alpha(m_d)V_{epc} w + \beta(m_d)V_d w.$$

I built the expression for the function H_d the same way, except in that case, the offspring survival probability does not change if a successful EPC has occurred. For a deserting male, the number of surviving offspring in his own brood is $V_d w$, and from that is subtracted the number of offspring sired by other males ($\gamma_d x V_d w$). To the number of deserting male's surviving biological offspring is then added the number of offspring obtained through successful EPCs ($\alpha(m_d)V_{epc} w + \beta(m_d)V_d w$). An essential feature of this model is that this number is the same for both deserting and caring males due to the assumption that they are equally as good at obtaining EPCs.

The final forms of these expressions are listed below in Table 2, with expressions by Fromhage et al. (2007). Some differences between the two models are worth addressing. First, I used γ_d to denote the proportion of deserting male's broods in which an EPC occurs, while Fromhage et al. (2007) did not use anything to denote this even though it is included in their model. Second, the expressions for functions α and β are different because I assumed that all males make EPC attempts. In their model, Fromhage et al. (2007) assumed that only deserting males make EPC attempts, which means that for each EPC-attempting male (ρ), there were $(1 - \rho)/\rho$ females mated to caring males. My model assumed $1 - m_d$ females mated to caring males for each EPC attempting male.

The expressions for fitness functions also differ, mainly because caring males could also gain additional offspring through EPCs. The loss terms that denote the number of offspring sired by another male look different between my model and the model by Fromhage et al. (2007) because they included the function α in their loss term. However, including the notation α is not necessary and I decided not to include it to simplify the expressions. Fromhage et al. (2007) could have also omitted α , as

$$\frac{\rho}{1 - \rho} \alpha(\rho) V_{epc} = \frac{\rho}{1 - \rho} \frac{1 - \rho}{\rho} (1 - e^{-n\rho p_A}) x V_{epc}$$

when substituting the expression for function α . Since the factors $\rho/(1 - \rho)$ and $(1 - \rho)/\rho$ cancel out each other, the loss term further simplifies to

$$\gamma(\rho) x V_{epc},$$

as $1 - e^{-n\rho p_A}$ is the expression for $\gamma(\rho)$. In their function H_d , the loss term disappears because it cancels out with the benefit obtained through EPCs with deserting males' partners. The loss term does not cancel out in my function, which is why it is still visible in the expression for function H_d .

Table 2 Comparison of expressions for functions used in my model and in model by Fromhage et al. (2007).

My model	Fromhage et al. (2007)
$\gamma_c = 1 - e^{-np_A}$	$\gamma(\rho) = 1 - e^{-n\rho p_A}$
$\gamma_d = 1 - e^{-np_B}$	$1 - e^{-n\rho p_B}$
$\alpha(m_d) = (1 - m_d)(1 - e^{-np_A})x$	$\alpha(\rho) = \frac{1 - \rho}{\rho} (1 - e^{-n\rho p_A})x$
$\beta(m_d) = m_d(1 - e^{-np_B})x$	$\beta(\rho) = (1 - e^{-n\rho p_B})x$
$H_c(m_d) = V_c(1 - \gamma_c)w + V_{epc}\gamma_c w - \gamma_c x V_{epc} w + \alpha(m_d) V_{epc} w + \beta(m_d) V_d w$	$H_c = w \left(V_c(1 - \gamma(\rho)) + V_{epc}\gamma(\rho) - \frac{\rho\alpha(\rho)V_{epc}}{1 - \rho} \right)$
$H_d(m_d) = V_d w - \gamma_d x V_d w + \alpha(m_d) V_{epc} w + \beta(m_d) V_d w$	$H_d = V_d w + \alpha(\rho) V_{epc} w$

After I had defined and formulated all the parameters and functions properly, I continued to search for evolutionarily stable strategies (ESSs). I used the same approach as Fromhage et al. (2007) and searched for parameter conditions that were needed for inequality

$$H_d(m_d) > H_c(m_d). \quad (1)$$

When H_d is greater than H_c , deserting male's fitness is larger than caring male's fitness, meaning that deserting is more beneficial for the male and the ESS is to desert. If H_c is greater than H_d , it is better to provide care.

After deriving the analytical conditions for male desertion to be an ESS, I used the software MATLAB R2020b (Mathworks 2020) to illustrate how changing different parameters affected the result and how the conditions for desertion show in the outcome. By doing several numerical computations with varying parameter values, I was able to visualize the effect of different parameters and the analytical conditions derived from inequality.

2.2 Model 2: Both male and female strategies can evolve

Model 2 is an expanded version of Model 1, covering situations where also female strategy could evolve. I used the same basic principles and assumptions as in Model 1 but included the proportion of deserting females as Maynard Smith (1977) and Iyer and Shukla (2021) did in their models. I had to introduce a variable for the proportion of deserting females, which I named f_d to resemble the proportion of deserting males (m_d).

Males suffer from a decreased ability to protect their paternity as a cost from caring, whereas females suffer from reduced fecundity, meaning that caring females could lay fewer eggs (denoted by w). This is a general way to incorporate the cost of caring for females and is done similarly in other studies (Maynard Smith 1977, 1982; Iyer and Shukla 2021). I assumed that all the eggs are always laid in the same nest, meaning that even deserting females do not lay any additional eggs in another nest. This assumption differs from the one made by Iyer and Shukla (2021), as they assumed that deserting females could mate again and then lay any additional eggs in completely new nests. Because I assumed that all the additional mating opportunities happen as EPCs, it was reasonable to assume that instead of laying a second batch of eggs somewhere else, deserting females just lay more eggs (denoted by $W > w$) in the same nest. Maynard Smith (1977) did not specify where the deserting female lays the additional eggs, but his assumptions suggest that the female lays all her eggs in the same nest.

The means for obtaining additional matings differ between the models that have inspired this work. Maynard Smith (1977) assumed that only deserting males make additional mating attempts directed toward any female who has not mated yet. His formulation for payoffs suggests that deserting males may mate again with a probability p but with a female using the same strategy as the first female. For example, the payoff for a deserting male whose first mate cares is $wP_1(1 + p)$, where w is the number of eggs produced by the female and P_1 is the

offspring survival probability when only one parent cares. It is worth noting that the assumptions in his models are not perfectly justified, and the source for these additional females is not specified.

Iyer and Shukla (2021) noted this inconsistency in Maynard Smith's Model 2 (1977) and paid attention to that when building their models. In their first model (Game 1), they assumed that caring and deserting males could both obtain extra-pair offspring, but only deserting males may have completely another brood with a deserting female. With these assumptions, they specified the source for females available for a second mating and included a parameter for paternity, allowing them to incorporate paternity uncertainty. It is incorporated similarly in the model by Fromhage et al. (2007) and in my model. In addition to Game 1, they made other modifications in subsequent models, which allowed different paternities for caring and deserting males or excluded caring males from extra-pair matings. Although resembling the assumptions made by Fromhage et al. (2007), these allowed females to change their strategy and included the assumption that deserting females lay additional eggs in other nests.

Since I allowed females' strategies to change too, there were four different kinds of strategy pairs composed of female and male pure strategies. I used the notation (c, c) to denote the pair where both parents care, (c, d) to denote the pair where male cares and female deserts, (d, c) to denote the pair where male deserts and female cares, and (d, d) to denote the pair where both parents desert.

I used the same basic parameters as in Model 1 but modified the expressions to incorporate the varying female strategy and included additional parameters and functions. Instead of three different offspring survival probabilities, I used six different offspring survival probabilities in Model 2 (listed in Table 3). I assumed that $V_{c,c} > V_{epc,c} > V_{d,c} = V_{c,d} > V_{epc,d} > V_{d,d}$.

Table 3 The offspring's survival probabilities in Model 2.

$V_{c,c}$	The offspring's survival probability when both parents care and there is no EPC
$V_{epc,c}$	The offspring's survival probability when both parents care and there is an EPC
$V_{d,c}$	The offspring's survival probability when male deserts and female cares
$V_{c,d}$	The offspring's survival probability when male cares (no EPC) and female deserts
$V_{epc,d}$	The offspring's survival probability when male cares (there is an EPC) and female deserts
$V_{d,d}$	The offspring's survival probability when both parents desert

The proportions of caring males' broods and deserting males' broods in which an EPC occurs were calculated as in Model 1 since the female's strategy

did not affect the probability for a successful EPC, and all females experienced, on average, the same number of EPC attempts. The expressions for γ_c and γ_d are in Table 4.

Table 4 The expressions for the proportions of caring males' and deserting males' broods in which an EPC occurs.

$\gamma_c = 1 - e^{-np_A}$	The proportion of caring males' broods in which an EPC occurs
$\gamma_d = 1 - e^{-np_B}$	The proportion of deserting males' broods in which an EPC occurs

Due to four different types of mated pairs, I had to include two functions (α_c and α_d) that represent the paternity obtained through successful EPCs with the partners of caring males since any caring male could be mated to a caring female or deserting female and the female's strategy affects the expected number of offspring. For the same reason, I had to include two functions representing the paternity obtained through successful EPCs with the partners of deserting males (β_c and β_d). I modified the functions α and β from Model 1 to fit the scenario in Model 2. The new functions and their expressions are in Table 5.

Table 5 Paternities obtained through successful EPCs.

$\alpha_c(m_d, f_d) = (1 - f_d)(1 - m_d)\gamma_c x$	Paternity obtained through successful EPCs with the females of (c, c) pairs
$\alpha_d(m_d, f_d) = f_d(1 - m_d)\gamma_c x$	Paternity obtained through successful EPCs with the females of (c, d) pairs
$\beta_c(m_d, f_d) = (1 - f_d)m_d\gamma_d x$	Paternity obtained through successful EPCs with the females of (d, c) pairs
$\beta_d(m_d, f_d) = f_d m_d \gamma_d x$	Paternity obtained through successful EPCs with the females of (d, d) pairs

I then determined the expected fitnesses (expressed as the number of surviving biological offspring) separately for females and males for all four strategy combinations. The fitness functions for males are in Table 6. In the fitness functions for males, I used the function

$$epc(m_d, f_d) = w \cdot (\alpha_c(m_d, f_d)V_{epc,c} + \beta_c(m_d, f_d)V_{d,c}) + W(\alpha_d(m_d, f_d)V_{epc,d} + \beta_d(m_d, f_d)V_{d,d})$$

to denote the fitness acquired from successful EPCs. Any male could now achieve EPCs with any female, so all possible situations must be included in the expression for function epc . The number of extra-pair offspring is the same for all males similarly like in Model 1.

Table 6 Fitness functions for males in Model 2.

$H_{c,c,m}(m_d, f_d) = w \cdot V_{c,c}(1 - \gamma_c) + w \cdot V_{epc,c}\gamma_c - \gamma_c \cdot x \cdot V_{epc,c} \cdot w + epc(m_d, f_d)$	Fitness for male from (c, c) -type brood
$H_{c,d,m}(m_d, f_d) = W \cdot V_{c,d}(1 - \gamma_c) + W \cdot V_{epc,d}\gamma_c - \gamma_c \cdot x \cdot V_{epc,d} \cdot W + epc(m_d, f_d)$	Fitness for male from (c, d) -type brood
$H_{d,c,m}(m_d, f_d) = w \cdot V_{d,c} - \gamma_d \cdot x \cdot V_{d,c} \cdot w + epc(m_d, f_d)$	Fitness for male from (d, c) -type brood
$H_{d,d,m}(m_d, f_d) = W \cdot V_{d,d} - \gamma_d \cdot x \cdot V_{d,d} \cdot W + epc(m_d, f_d)$	Fitness for male from (d, d) -type brood

Fitness functions for males are built similarly as in Model 1 but hold some differences. The fitness for a male consists of the benefit from his own brood (in the form of surviving offspring), the loss from his own brood (offspring sired by another male), and the benefit from successful EPCs. The number of surviving biological offspring is affected by the caring decisions of both parents since the offspring survival probability is dependent on those and females lay different number of eggs depending on their caring decision. The fitness functions for females (listed in Table 7) are constructed similarly, but females do not have any loss from their brood, and neither do they have any extra-pair offspring in someone else's nest. All the offspring in her nest are her biological offspring, thus the number of surviving biological offspring is affected only by the caring decisions and the probability of a successful EPC attempt.

Table 7 Fitness functions for females in Model 2.

$H_{c,c,f}(f_d) = w \cdot V_{c,c}(1 - \gamma_c) + w \cdot V_{epc,c}\gamma_c$	Fitness for female from (c, c) -type brood
$H_{c,d,f}(f_d) = W \cdot V_{c,d}(1 - \gamma_c) + W \cdot V_{epc,d}\gamma_c$	Fitness for female from (c, d) -type brood
$H_{d,c,f}(f_d) = w \cdot V_{d,c}$	Fitness for female from (d, c) -type brood
$H_{d,d,f}(f_d) = W \cdot V_{d,d}$	Fitness for female from (d, d) -type brood

To check the self-consistency of the model, I checked that the overall number of offspring for males and females was equal. Then, I ensured that this model is compatible with Model 1 when females always care. I did this by setting $f_d = 0$ and checking that the resulting fitness functions for male are equal to the fitness functions in Model 1. After these necessary steps to ensure that Model 2 is consistent with Model 1, I searched for evolutionarily stable strategy pairs (ESS pairs) by adaptive dynamics (sometimes alternatively referred to as evolutionary

invasion analysis). Adaptive dynamics is an extension of game theory, which can help to find a strategy that can resist invasions (ESS), if there is one (Dieckmann and Law 1996; Otto and Day 2007; Avila and Mullon 2023). I used the male fitness functions from different types of broods to build a probability-weighted sum function describing the overall fitness of a male using strategy $(\widehat{m}_d, 1 - \widehat{m}_d)$ in a population where other males use strategy $(m_d, 1 - m_d)$. These strategies indicate that the desertion probability for the focal (deviant) male is \widehat{m}_d and for a resident male it is m_d . The overall fitness function for the male is:

$$H_m(\widehat{m}_d, f_d, m_d) = (1 - \widehat{m}_d)(1 - f_d)H_{c,c,m} + \widehat{m}_d(1 - f_d)H_{d,c,m} + (1 - \widehat{m}_d)f_dH_{c,d,m} + \widehat{m}_df_dH_{d,d,m}.$$

In the same way, I used the female fitness functions to build a sum function describing the overall fitness of a female using strategy $(\widehat{f}_d, 1 - \widehat{f}_d)$ in a population where other females use strategy $(f_d, 1 - f_d)$. The overall fitness function for the female is:

$$H_f(m_d, \widehat{f}_d, f_d) = (1 - m_d)(1 - \widehat{f}_d)H_{c,c,f} + m_d(1 - \widehat{f}_d)H_{d,c,f} + (1 - m_d)\widehat{f}_dH_{c,d,f} + m_d\widehat{f}_dH_{d,d,f}.$$

I could then search for the maximum value for a male's fitness by differentiating the male fitness function H_m with respect to \widehat{m}_d and finding the root of the derivative. I repeated the same process with the female fitness function H_f . If some values of \widehat{m}_d and \widehat{f}_d turned out to be the root of the derivatives, these strategy values indicate possible maximum fitnesses and thus could potentially be ESSs and compose an ESS pair (Otto and Day 2007).

In addition to searching for a mixed strategy that could potentially be an ESS, I also checked for conditions for any of the pure strategy pairs being an ESS pair. Maynard Smith (1977) did this simply by comparing the fitnesses obtained by using pure strategies. This approach disregards the possibility of a mixed ESS, but it is not problematic in his case since the fitness functions in his model are linear, and therefore no mixed ESSs are possible. I solved the conditions by differentiating the fitness functions, setting the opposite sex's strategy equal to zero (always caring) or one (always deserting), and then examining the sign of the derivative. A positive derivative indicated that the ESS would be achieved with higher values of the desertion probability and vice versa with a negative derivative. By repeating this process for both derivatives H'_m and H'_f , I could find the analytical conditions for each pair type to be an ESS pair. My method was essentially the same as the one Maynard Smith used but allowed me to find mixed ESS pairs if there were any.

Because the analytical conditions are challenging to interpret on their own, I also modeled the coevolution of female and male strategies using adaptive dynamics (Dieckmann and Law 1996; Otto and Day 2007; Avila and Mullon 2023), which allowed me to visualize their evolutionary trajectories and endpoints. In principle, the results using adaptive dynamics should be modeled using relative fitness, or equivalently the derivative of logarithmic fitness. However, the choice of using absolute versus relative fitness does not affect the results presented in this thesis. When solving the ESS analytically as described above, the sign of the

derivative is affected only by the numerator which is the derivative of the absolute fitness. In the adaptive dynamics models, the choice of absolute vs. relative fitness again makes no difference, because the mean fitness for males and females must be the same due to an even sex ratio, which implies that the evolutionary trajectories are not affected since the derivatives of both fitnesses are divided by the same mean fitness. Despite this fact, I still used the relative fitness when modeling the coevolution using adaptive dynamics in MATLAB R2020b (Mathworks 2020) but used the absolute fitness when solving the ESSs analytically.

3 RESULTS

In this section, I present the findings of my models. The results of Models 1 and 2 are presented separately since they required partly different approaches and thus yielded different types of results. I will start with the results of Model 1 and continue to the results of Model 2.

3.1 Model 1: Only the male strategy can evolve

I searched the conditions for desertion to be an ESS by manipulating the inequality $H_d(m_d) > H_c(m_d)$. In that process, m_d canceled out of the equation, meaning that the proportion of deserting males did not affect the ESS. Thus, no mixed strategy could be an ESS, but either one of the pure strategies could be an ESS, depending on the other parameters. I then continued manipulating the inequality (1) to find some parameter conditions for desertion to be an ESS. As a result, I got

$$\gamma_c x V_{epc} w - \gamma_d x V_d w > V_c(1 - \gamma_c)w + V_{epc}\gamma_c w - V_d w. \quad (2)$$

This inequality means that for desertion to be an ESS, the loss from a caring male's brood must be greater than the loss from a deserting male's brood and significant enough to counteract the better offspring survival probability in a caring male's brood. As the loss is directly affected by the probability of a successful EPC attempt, the value of the parameter p_B (the probability that an EPC attempt is successful when directed towards a deserting male's partner) is significant. From the inequality (2), I was able to find a maximum value for variable p_B , as follows:

$$p_B < -\frac{1}{n} \log \left(\frac{V_c(1 - \gamma_c) + \gamma_c V_{epc} - x\gamma_c V_{epc} - V_d}{xV_d} + 1 \right). \quad (3)$$

For this expression to make sense, $n \neq 0$, $x \neq 0$, and $V_d \neq 0$. All of these are reasonable conditions. If $n = 0$, no EPC attempts are made, meaning that it is more beneficial to care since desertion can be favorable only if deserting males lose significantly less paternity through an EPC. If $x = 0$, no paternity share is

gained through a successful EPC, so caring is again beneficial. If $V_d = 0$, the only surviving offspring a deserting male gets are from EPCs, and a caring male gets this same number of offspring in addition to the offspring from his own brood, so it is better to care. In addition to these conditions, the limit must belong between zero and one for it to be reasonable. The formulation of the limit seems like it would be negative, but it is, in fact, positive when $V_c(1 - \gamma_c) + \gamma_c V_{epc} - x\gamma_c V_{epc} - V_d$ is negative because then the logarithm gives out negative values that are multiplied by $-1/n$, making the result positive.

Note that the expanded expression for γ_c includes the parameters p_A and n , so the maximum value for p_B depends logarithmically on the values of parameters p_A, x, n , and survival probabilities. When V_d or x increases, the limit for p_B also increases. When V_{epc} gets closer to V_c , the limit for p_B decreases.

Because the conditions in symbolical form can be abstract and the effect of different parameters can be challenging to comprehend, I did several numerical computations in MATLAB to illustrate the effect of some parameters. In the following sections, I present three cases where I have changed the values of V_d, x, p_A and p_B since these were the main parameters that affected the analytical conditions. The limit for p_B is especially illustrated in Subsection 3.1.2 and the effect of varying paternity is addressed in Subsection 3.1.3. The values for parameters that remained constant across all these cases are listed below (Table 8). Note that I used a constant desertion probability m_d since my analytical results indicated that the proportion of deserting males does not affect the ESS.

Table 8 The general parameter values used in all cases.

m_d	0.5
w	5
n	10

3.1.1 Case 1: The offspring survival probabilities change

Since the relative magnitude of offspring survival probabilities clearly affects the ESS, I explored how much of an effect variation in parameter V_d has together with variation in parameter p_B . In this case, I let p_B vary from 0 to 0.5 as p_A was set equal to 0.5, and let V_d vary from 0 to 0.9 as V_{epc} was equal to 0.9. The MATLAB script I used in this case is in Appendix 1.

The outcome of this computation is presented in Figure 1. Blue marks the parameter combinations that yield caring as the ESS. For example, with $V_d = 0.4$ and $p_B = 0.2$, caring is an ESS. Yellow then marks the parameter combinations when deserting was the ESS. The figure shows that as V_d increased, p_B could get closer to p_A , and desertion was still an ESS. In this case, V_d must be at least around 0.45 for deserting to be an ESS, even when p_B is zero. This means that even if deserting males are able to protect their paternity completely, desertion is still not favorable if the survival probability of the offspring is too low.

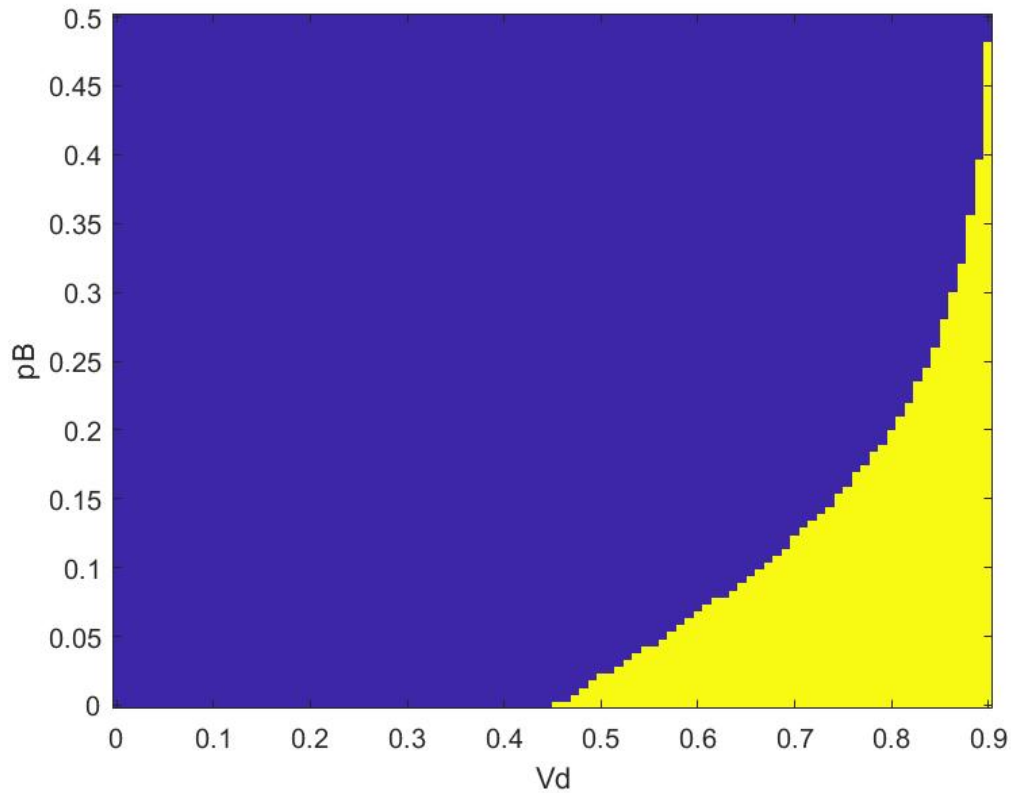


Figure 1. The distribution of ESSs when p_B changes from 0 to 0.5 and V_d changes from 0 to 0.9. Caring is the ESS in blue regions, and in yellow regions, deserting is the ESS. Other parameter values: $p_A = 0.5, V_c = 1, V_{epc} = 0.9, x = 0.5$.

Changing the paternity share possible to obtain through a successful EPC (x) also influenced the results. I set $x = 0.8$ and found that the boundary between blue and yellow regions follows a different kind of curve (Figure 2). Higher paternity share from an EPC allows V_d to be lower without making desertion unfavorable. It also allows p_B to be closer to p_A while keeping desertion as an ESS.

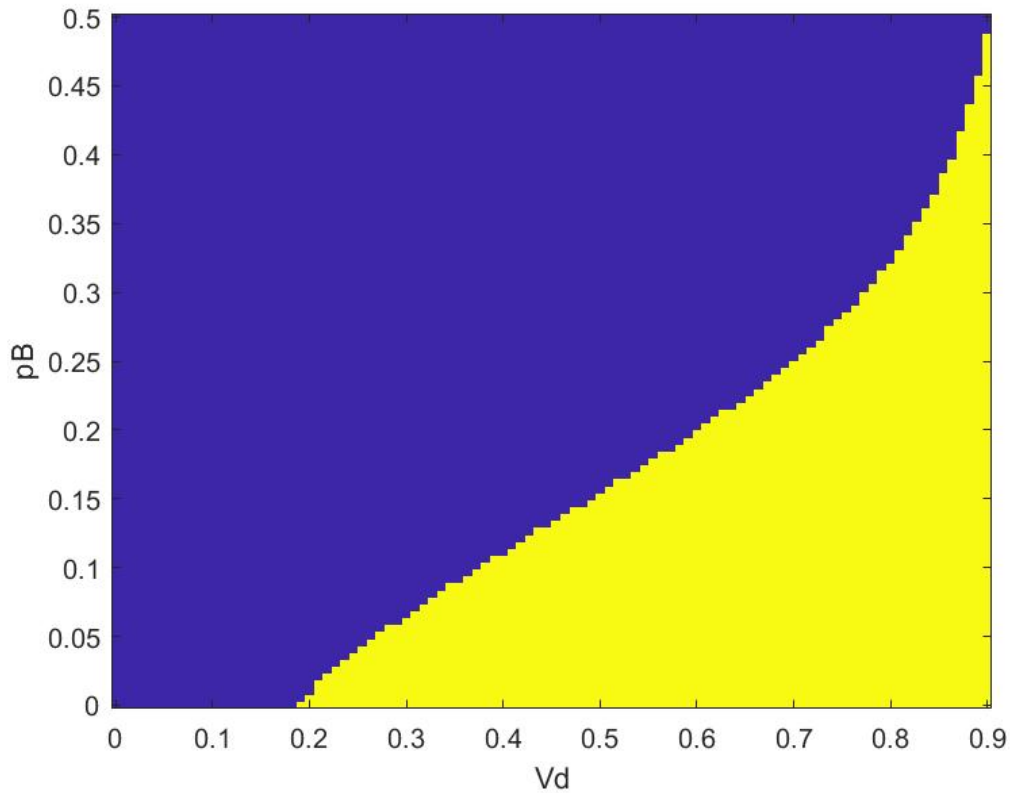


Figure 2 ESS distribution V_d changes from 0 to 0.9 and p_B changes from 0 to 0.5. In blue regions caring is an ESS and in yellow regions deserting is an ESS. Other parameter values are the same as in Figure 1, except that x is equal to 0.8.

3.1.2 Case 2: Probabilities for succeeding in EPC attempts change

Next, I wanted to illustrate the analytical limit (3) I got for p_B , that is how much advantage deserting males should have at protecting their paternity for desertion to be more beneficial than caring. To accomplish this, I let the probabilities of successful EPC attempts (p_A and p_B) vary from 0 to 1 and kept the other parameters constant. The MATLAB script I used in this case is in Appendix 2.

Figure 3 shows the results of this case by illustrating the limit for p_B . It makes visible the fact that even when p_A gets close to 1, p_B could only increase to some extent for desertion to be an ESS. Note that the regions above the black line should be ignored because p_A is smaller than p_B in those regions, conflicting with my initial assumptions.

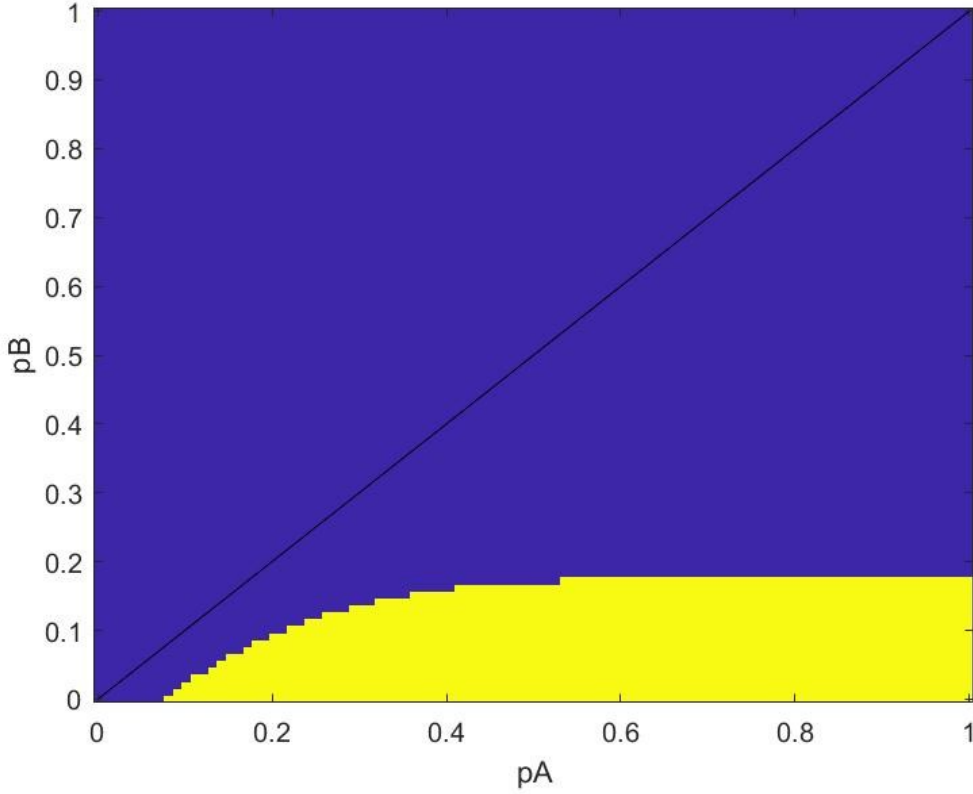


Figure 3. The distribution of ESSs when both p_A and p_B change from 0 to 1. Caring is the ESS in blue regions, and in yellow regions, deserting is the ESS. Other parameter values: $V_c = 0.8, V_{epc} = 0.7, V_d = 0.5, x = 0.7$.

When I changed V_d to equal V_{epc} , I found that p_B could increase linearly while p_A increased, although it still had to be smaller than p_A (Figure 4). This indicates a situation where cuckolded males do not provide care even if their initial strategy is to care, which is the case in model 2 by Maynard Smith (1977) and addressed also by Fromhage et al. (2007). With further manipulations of the inequality (2), I found that the difference between p_A and the maximum p_B depended on the difference between V_c and V_d . I solved p_B from the inequality (2) and found a limit for the parameter p_B as follows:

$$p_B < p_A - \frac{1}{n} \log \left(\frac{V_c - V_d}{xV_d} + 1 \right).$$

For this expression to make sense, $n \neq 0$, $x \neq 0$, and $V_d \neq 0$. If any of these parameters would equal 0, it would be beneficial to care, so finding the maximum p_B for desertion would be irrelevant. When $V_{epc} = V_d$, the limit for p_B does not depend logarithmically on p_A but depends logarithmically on the difference between V_c and V_d and the paternity share possible to obtain through a successful EPC (x). When the difference between V_c and V_d increases, the limit for p_B decreases. When either V_d or x increases, the limit for p_B also increases.

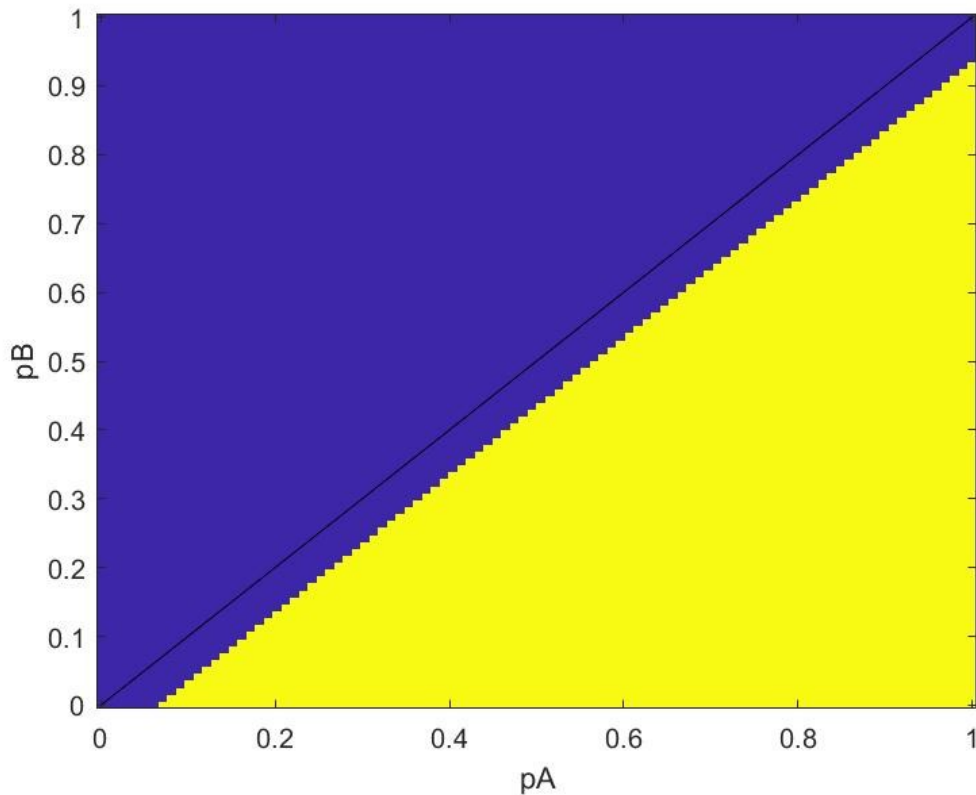


Figure 4. The distribution of ESSs when p_A and p_B change from 0 to 1 and $V_d = V_{epc} = 0.5$. Caring is the ESS in blue regions, and in yellow regions, deserting is the ESS. Other parameter values are the same as in Figure 3.

3.1.3 Case 3: The paternity share obtained through a successful EPC changes

I already found out in Case 1 that changing the paternity share possible to obtain from a successful EPC attempt affects the results. In this case, I explored further how changing x and p_B together affects the outcome. I let p_B vary from 0 to 0.7 as p_A was set to 0.7, and I let x vary from 0 to 1. The MATLAB script I used in this case is in Appendix 3.

The results are presented in Figure 5, which shows that with higher values of x , p_B can get closer to p_A , and it is still better to desert. The maximum value of p_B increases significantly when x approaches 1. However, with low values of x , caring remains the better strategy even if p_B is zero.

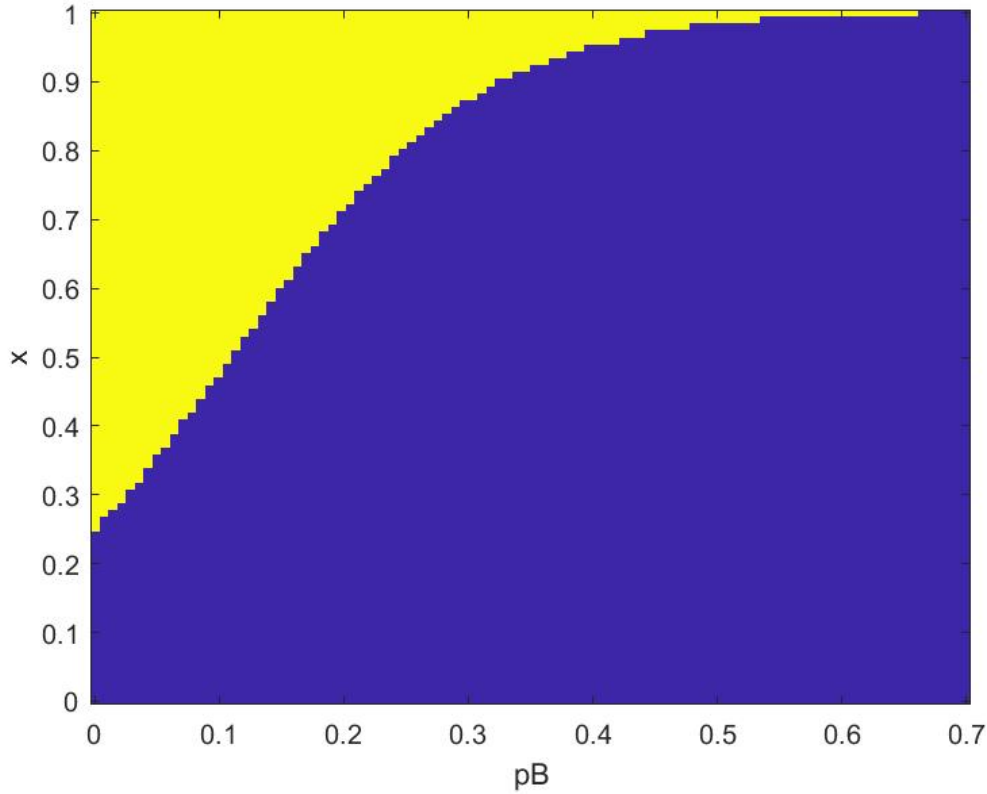


Figure 5 The distribution of ESSs when P_B changes from 0 to 0.7 and x changes from 0 to 1. Caring is the ESS in blue regions, and in yellow regions, deserting is the ESS. Other parameter values: $V_c = 0.9, V_{epc} = 0.8, V_d = 0.6, p_A = 0.7$.

3.2 Model 2: Female strategy can also evolve

In Model 2, I allowed the female strategy to evolve, which made me change my approach to solving ESSs. To investigate if any deviant male using strategy $(1 - \widehat{m}_d, \widehat{m}_d)$ could invade the population where other males use strategy $(1 - m_d, m_d)$ and females use strategy $(1 - f_d, f_d)$, I differentiated the overall fitness function H_m (Otto and Day 2007). As the derivative of function H_m , I got

$$\begin{aligned}
 H'_m(\widehat{m}_d, m_d, f_d) &= (1 - f_d)(V_{d,c}W - \gamma_d x V_{d,c}W) + f_d(V_{d,d}W - \gamma_d x V_{d,d}W) \\
 &\quad - (1 - f_d) \left((1 - \gamma_c)V_{c,c}W + \gamma_c V_{epc,c}W - \gamma_c x V_{epc,c}W \right) \\
 &\quad - f_d \left((1 - \gamma_c)V_{c,d}W + \gamma_c V_{epc,d}W - \gamma_c x V_{epc,d}W \right).
 \end{aligned}$$

If the derivative had contained the variables \widehat{m}_d or m_d , I could have then proceeded to find out the root of the derivative by setting \widehat{m}_d equal to m_d and then solving the equation $H'_m(\widehat{m}_d, m_d, f_d) = 0$ with respect to m_d . However, in this case, the derivative did not depend on the strategy of the focal (deviant) male or the resident male, meaning that no mixed strategy could be an ESS for males. Only possible ESSs were then pure strategies, and the outcome depended on the parameter values and the strategy of the opposite sex. I searched for the parameter conditions for both ESSs by setting the derivative positive or negative

depending on the strategy. A positive derivative means that the fitness function is increasing with respect to \widehat{m}_d , meaning that the highest fitness is achieved with the largest value of \widehat{m}_d , which would be 1, making desertion the best strategy for males. If the derivative is negative, the fitness function is decreasing, meaning that the highest fitness is achieved with the lowest \widehat{m}_d , which would be 0.

I repeated the same process with the overall fitness function for a deviant female using strategy $(1 - \widehat{f}_d, \widehat{f}_d)$ in a population where other females use strategy $(1 - f_d, f_d)$ and all the males use strategy $(1 - m_d, m_d)$. As the derivative of the function H_f , I got

$$H'_f(\widehat{f}_d, m_d, f_d) = W \left((1 - m_d) \left((1 - \gamma_c)V_{c,d} + \gamma_c V_{epc,d} \right) + m_d V_{d,d} \right) - w \left((1 - m_d) \left((1 - \gamma_c)V_{c,c} + \gamma_c V_{epc,c} \right) + m_d V_{d,c} \right).$$

As in the case of male overall fitness, the derivative of female overall fitness did not depend on the strategy of the focal (deviant) female or on the strategy of the resident female. The ESS for females was then also either one of the pure strategies, depending on the parameter values and the male population strategy.

As I mentioned, both derivatives depended on the strategy of the opposite sex. It was possible to find a value for f_d that makes the derivative H'_m equal to zero. This situation means that all male strategies yield the same payoff, making any strategy equally beneficial. It does not mean that the value of f_d would indicate any stability but shows that with some parameter combinations and female population strategy, it is possible to have a situation where the male strategy does not matter and the fitness for males is the same despite the strategy they use. This type of situation (the only difference is that the female strategy does not matter) is illustrated in Figure 7 and is discussed in detail later.

Since I found no mixed strategies as ESS candidates, only the pure strategy pairs could be ESS pairs. I obtained the parameter conditions for each ESS pair from the derivatives by setting the desertion probability of the opposite sex equal to 1 or 0. Conditions for each pure strategy pair to be an ESS pair are listed in Table 9. The conditions for male desertion are basically the same as the conditions I obtained from Model 1, including only minor modifications in parameter names. The conditions for males and females differ in that for males, the paternity loss from their own brood in relation to survival probabilities is significant, and for females, the ratio of egg quantities compared to the ratio of survival probabilities is significant.

Table 9. The conditions for each pure strategy to be an ESS pair in Model 2.

pair type	conditions for male	conditions for female
(c, c)	$V_{d,c} - \gamma_d x V_{d,c} < (1 - \gamma_c)V_{c,c} + \gamma_c V_{epc,c} - \gamma_c x V_{epc,c}$	$W \left((1 - \gamma_c)V_{c,d} + \gamma_c V_{c,d} \right) < w \left((1 - \gamma_c)V_{c,c} + \gamma_c V_{epc,c} \right)$

(c, d)	$V_{d,d} - \gamma_d x V_{d,d}$ $< (1 - \gamma_c)V_{c,d}$ $+ \gamma_c V_{epc,d}$ $- \gamma_c x V_{epc,d}$	$W \left((1 - \gamma_c)V_{c,d} + \gamma_c V_{epc,d} \right)$ $> w \left((1 - \gamma_c)V_{c,c} \right)$ $+ \gamma_c V_{epc,c}$
(d, c)	$V_{d,c} - \gamma_d x V_{d,c} > (1 - \gamma_c)V_{c,c}$ $+ \gamma_c V_{epc,c} - \gamma_c x V_{epc,c}$	$WV_{d,d} < wV_{d,c}$
(d, d)	$V_{d,d} - \gamma_d x V_{d,d}$ $> (1 - \gamma_c)V_{c,d}$ $+ \gamma_c V_{epc,d}$ $- \gamma_c x V_{epc,d}$	$WV_{d,d} > wV_{d,c}$

From these conditions, I could have derived the limits for p_B like I did while solving analytical conditions in Model 1. Similarly, I could have derived some conditions for other parameters, but these were not useful due to their complexity. That is why I only offer the general conditions here and focus on modeling the adaptive dynamics in MATLAB. Figure 6 contains four figures illustrating the evolutionary trajectories of male and female strategies. The arrows show the direction of higher relative fitness, and the circles represent the ESSs, so the figure shows which direction the strategies are presumed to evolve under evolutionary forces. The figure includes representations of all four pure strategy ESS pairs.

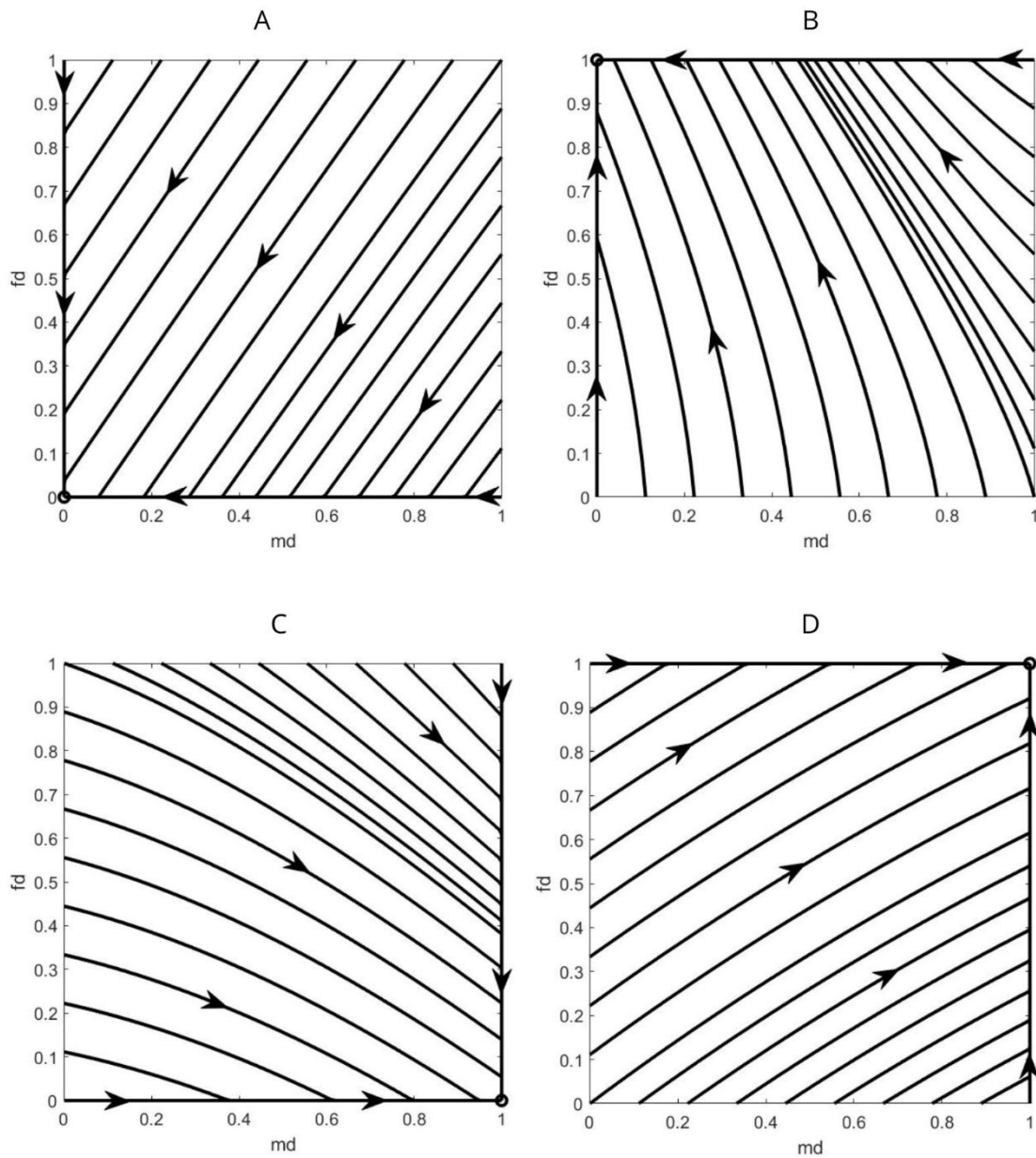


Figure 6 The evolutionary trajectories of male and female strategies in different parameter spaces. The arrows of the vector fields show the presumed direction of evolution and circles represent the ESS pairs. Figure **A** illustrates the situation when (c, c) is an ESS pair. Figure **B** shows that (c, d) is an ESS pair. Figure **C** shows that (d, c) is an ESS pair. Figure **D** shows that (d, d) is an ESS pair. Parameter values used to obtain these figures are listed in Table 10.

The parameter values used to obtain the vector fields in Figure 6 are listed below in Table 10. Some parameter values are the same in all figures, and I aimed to achieve distinct differences with as small changes to parameter values as possible. Figure A illustrates the situation where biparental care is an ESS pair, and for that to change towards male-only care, I increased the offspring survival probabilities and W . Increasing the number of eggs laid by a deserting female made desertion more favorable for females, and greater survival probabilities enhanced that

effect. To switch to female-only care, I decreased W and p_B and increased x . Decreasing W made desertion less beneficial for females, and lower p_B , together with higher x , made desertion more favorable for males. To obtain biparental desertion as an ESS pair, I increased $V_{d,d}$ and W , which made desertion again favorable for females (as it was already favorable for males).

Table 10 Parameter values I used to obtain the results in Figure 6.

A	$V_{c,c} = 1$	$V_{epc,c} = 0.9$	$V_{c,d} = 0.6$	$V_{d,c} = 0.6$
	$V_{epc,d} = 0.5$	$V_{d,d} = 0.3$	$x = 0.5$	$n = 5$
	$p_A = 0.8$	$p_B = 0.5$	$w = 5$	$W = 7$
B	$V_{c,c} = 1$	$V_{epc,d} = 0.9$	$V_{c,d} = 0.8$	$V_{d,c} = 0.8$
	$V_{epc,d} = 0.7$	$V_{d,d} = 0.5$	$x = 0.5$	$n = 5$
	$p_A = 0.8$	$p_B = 0.5$	$w = 5$	$W = 9$
C	$V_{c,c} = 1$	$V_{epc,c} = 0.9$	$V_{c,d} = 0.8$	$V_{d,c} = 0.8$
	$V_{epc,d} = 0.7$	$V_{d,d} = 0.5$	$x = 0.7$	$n = 5$
	$p_A = 0.8$	$p_B = 0.1$	$w = 5$	$W = 6$
D	$V_{c,c} = 1$	$V_{epc,c} = 0.9$	$V_{c,d} = 0.8$	$V_{d,c} = 0.8$
	$V_{epc,d} = 0.7$	$V_{d,d} = 0.6$	$x = 0.7$	$n = 5$
	$p_A = 0.8$	$p_B = 0.1$	$w = 5$	$W = 8$

In all figures in Figure 6, the vector fields seem to converge quite neatly to one corner, but this was not always the case. As I mentioned previously while presenting the analytical solution, it was possible to analytically derive an expression for the opposite sex' strategy that would make the derivative equal to zero. This kind of situation is illustrated below in Figure 7, where the male strategy seems to evolve towards complete desertion while the female strategy evolves towards caring, but with a high proportion of deserting males, the difference between fitnesses for caring and deserting females approaches zero. This means that either of the strategies is equally beneficial for females, making the female population unaffected by evolutionary forces. Basically, in this situation $H_{d,c,f} = H_{d,d,f}$, because $w/W = V_{d,d}/V_{d,c}$. This situation is highly unlikely in nature and even in this theoretical model the female strategy probably has enough time to fixate on caring, while the male strategy evolves toward desertion. However, it is theoretically possible that the female strategy could fixate on any strategy that is prevalent at the time when the male strategy reaches

equilibrium, or the female strategy could keep changing and never fixate in any strategy. That is why there are multiple circles representing ESS pairs in Figure 7, even though neither of those is an actual ESS pair in this case.

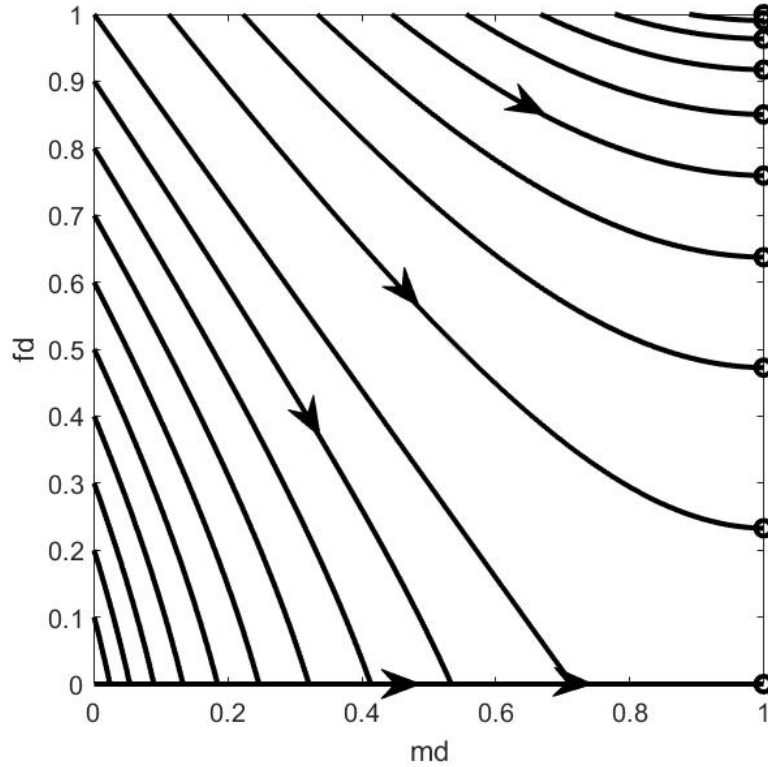


Figure 7. An illustration of the special case where the female fitness is the same regardless of their strategy after the male strategy has reached stability. Arrows indicate the presumed direction of evolution and circles represent the potential endpoints of the evolution. Parameter values: $V_{c,c} = 1, V_{epc,c} = 0.9, V_{c,d} = V_{d,c} = 0.7, V_{epc,d} = 0.6, V_{d,d} = 0.5, x = 0.5, n = 5, p_A = 0.7, p_B = 0.2, w = 5, W = 7$.

As this figure shows, the mating partner's strategy affects the benefit the focal individual gains by using different strategies. Due to this, different strategy pairs could be ESS pairs depending on the initial conditions. Figure 8 shows how the male population strategy influences the evolution of the female population strategy. With high values of m_d and relatively low values of f_d , females are selected to care and males to desert. However, female desertion and male care could also be an ESS pair, depending on the relationship between the initial values of m_d and f_d . In this situation, the ESS pair is always asymmetrical, meaning that the ESS is always uniparental care, but the caregiver's sex depends on the initial conditions.

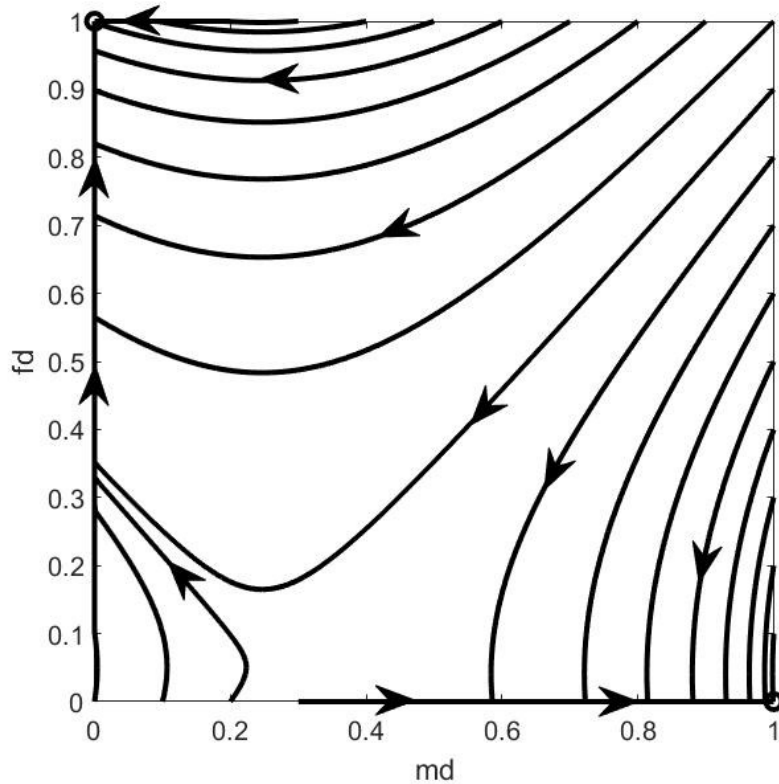


Figure 8. An illustration of the situation where the ESS depends on the initial proportions of deserting individuals. Arrows indicate the presumed direction of evolution and circles represent the possible ESS pairs. Parameter values: $V_{c,c} = 1, V_{epc,c} = 0.9, V_{c,d} = V_{d,c} = 0.8, V_{epc,d} = 0.7, V_{d,d} = 0.4, x = 0.3, n = 5, p_A = 0.8, p_B = 0.2, w = 5, W = 7$.

I even found a parameter combination that made both (c, c) and (d, d) possible ESS pairs (Figure 9). This situation is characterized by the relative inefficiency of uniparental care compared to biparental care. In this case, the offspring's survival probability when both parents desert is almost as good as when only one parent cares. If the initial desertion probabilities are, for example, $m_d = 0.8$ and $f_d = 0.4$, both strategies would eventually evolve towards desertion. However, if $m_d = 0.3$ instead of 0.8, both strategies would evolve towards caring. It seems that while changing the m_d , the ESS for males changes too. How is that possible if the population strategy for any given sex should not affect the ESS for that sex? I argued earlier that it is always better to choose either of the pure strategies, depending on the other parameters (including the behavior of the other sex). This argument still holds because the population strategy for any given sex does not affect the ESS for that sex directly. However, the initial population strategies determine the direction of evolution and thus achievable ESS.

In my example, changing m_d from 0.8 to 0.3 changed the ESS for males, but that is not a realistic change as the proportion of deserting males could not change so drastically in a stable environment, and this kind of change in population strategy is not even possible under natural selection. The proportion of deserting males could evolve only via small mutations and due to the effect of

female strategy, could never reach 0.3. The reason behind this is that when $m_d = 0.8$, the female strategy evolves towards desertion, and the male strategy evolves towards care for a while. However, as the proportion of deserting females increases, the beneficial strategy for males changes, and the population strategy starts to evolve towards desertion. When $m_d = 0.3$, both strategies evolve towards care, and the proportion of deserting males cannot increase under natural selection. Neither of the strategies evolves isolated from the other, and m_d cannot evolve from 0.8 to 0.3 without affecting the proportion of deserting females, which then affects the direction of male strategy evolution.

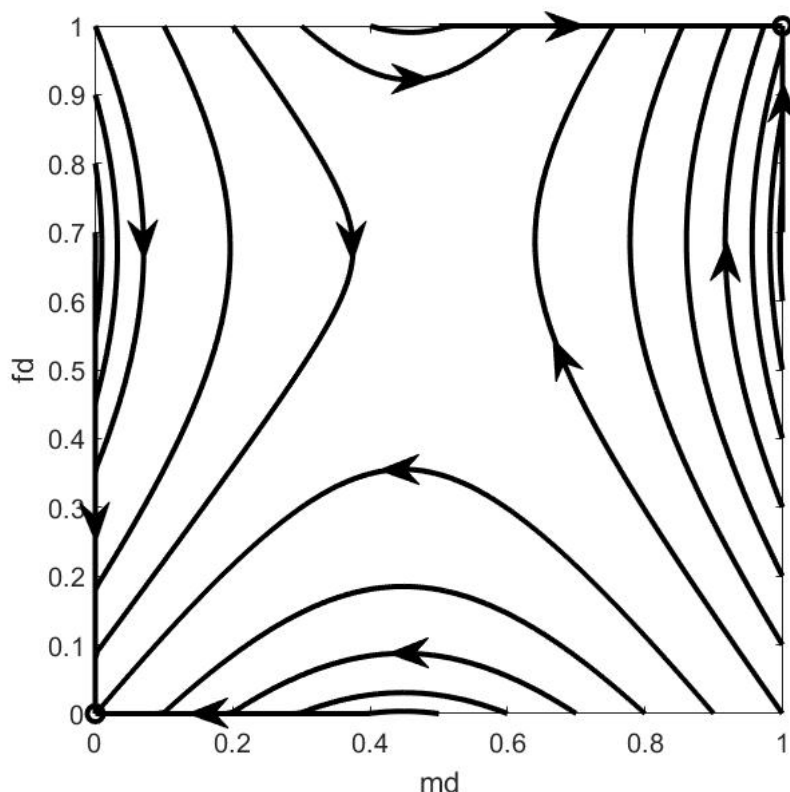


Figure 9. An illustration of the situation where strategy pairs (c, c) and (d, d) are both possible ESS pairs, and the outcome depends on the initial proportions of deserting individuals. Arrows indicate the presumed direction of evolution and circles represent the possible ESS pairs. Parameter values: $V_{c,c} = 1, V_{epc,c} = 0.9, V_{c,d} = V_{d,c} = 0.7, V_{epc,d} = 0.6, V_{d,d} = 0.55, x = 0.5, n = 5, p_A = 0.6, p_B = 0.3, w = 5, W = 7$.

4 DISCUSSION

Iyer and Shukla (2021) argued that in their models including partial paternity, a mating-caring trade-off was necessary for female-only care to be an ESS. In my models, I incorporated partial paternity similarly as Iyer and Shukla (2021) and Fromhage et al. (2007) did but assumed that there is no mating-caring trade-off and deserting males are better at protecting paternity. In my models, I was able

to find all pure strategies/strategy pairs to be evolutionarily stable, including female-only care. This indicates that the better ability to protect their paternity could be enough to select for male desertion even in the absence of a mating-caring trade-off.

Often caring males have been assumed to have higher paternity (Iyer and Shukla 2021). One explanation for higher paternity is that caring behavior could involve some behavior that simultaneously increases the carer's paternity (Kvarnemo 2006). However, assuming that deserting males could be better at protecting their paternity is not unreasonable. My definition of parental care excluded any kind of mate guarding from that, so the most straightforward way to assume paternity protection in my model is that deserting males allocate their resources to guarding the female. For the results of this thesis, it is unnecessary to specify how exactly deserting males are better at protecting their paternity since it could happen in many ways but offering some explanation might be helpful. In any real-life situations, the biological explanations and meanings should be thoroughly explained since discriminating parental care from other types of behavior can be challenging.

Due to the better ability to protect their paternity, desertion could readily be an ESS for males. What were the conditions for this to happen? From the analytical condition for desertion to be an ESS, I solved a limit for parameter p_B , which was the probability that an EPC attempt succeeds if it is directed towards a deserting male's partner. According to this limit, the parameter p_B could increase only to a certain level (without destabilizing desertion) as p_A (the probability that an EPC attempt succeeds when it is directed towards a caring male's partner) increased. Because the parameters p_A and p_B affect the probability of a successful EPC attempt, they directly affect the paternity loss males experience from their own broods.

Since caring and deserting males were both allowed to make EPC attempts and they were equally good at achieving those, the proportion of deserting males did not affect anything else than the fitness obtained through EPCs. This fitness was the same for both caring and deserting males, meaning that the fitnesses between deserting and caring males did not differ due to the proportion of deserting males and the proportion of deserting males did not affect the ESS. This also causes the only difference between fitness expressions for caring and deserting males to be the benefit obtained from their own brood. In Model 1, only the focal male's own strategy affects this benefit, and the evolutionary stability of a given strategy depends on the difference between offspring survival probabilities and the amount of paternity lost due to an EPC. For a deserting male to have higher fitness than a caring male, the loss from a caring male's brood should be large enough to outweigh the lower offspring survival probability in a deserting male's brood after the loss due to an EPC is considered.

The loss is affected by the offspring survival probabilities, the probabilities that an EPC attempt succeeds, and the paternity share possible to obtain through an EPC. When the paternity share obtained by EPC increases, the maximum limit for p_B increases, meaning that deserting is an ESS even when the difference

between p_A and p_B decreases. Especially with extremely high values of x , deserting becomes more and more beneficial, and p_B could get close to p_A . That is because with high values of x , the loss from a caring male's own brood becomes significantly more than the loss from a deserting male's brood. As the loss is the only term that could make fitness for a caring male lower than the fitness for a deserting male, and higher values of x make the loss greater, desertion is more favorable with high values of x . Higher x affects the deserting male's loss too, but not as much since other parameters that are multiplied by x are smaller in value than in the loss for a caring male. The significance of x is illustrated in Figure 10, which shows that the loss for the carer becomes significantly greater when x increases (while other parameters stay constant).

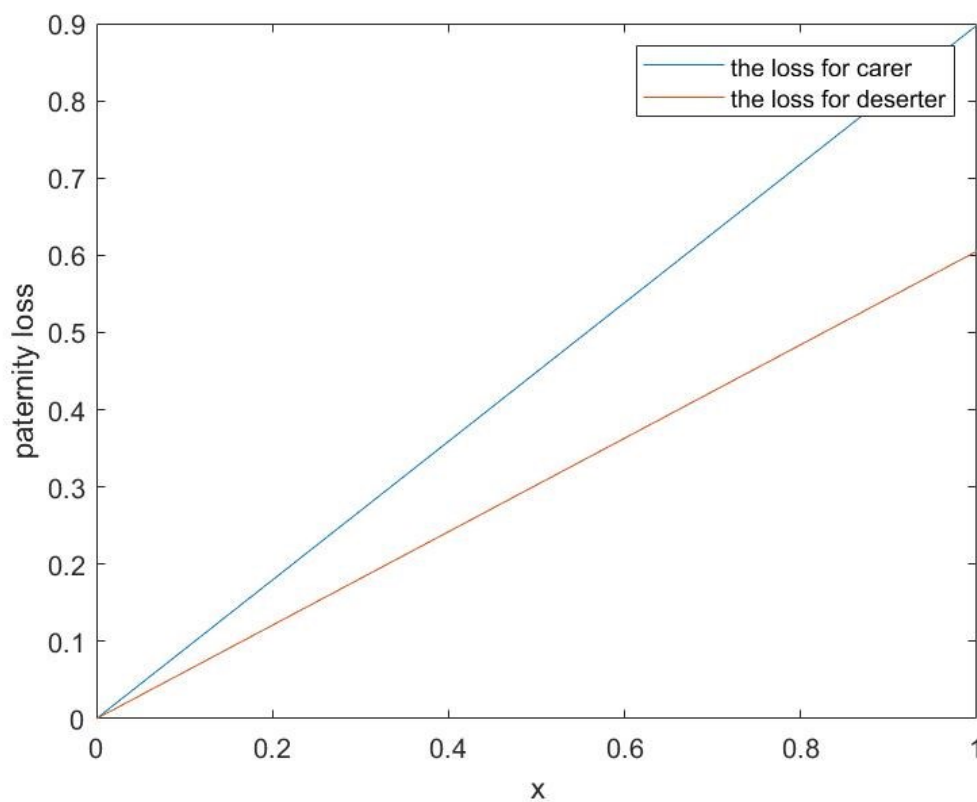


Figure 10. Increasing the value x increases the amount of paternity loss more for a caring male.

In my first model, the ESS was always a pure strategy, and it did not depend on the male population strategy. Fromhage et al. (2007) used the same approach as I did in Model 1 to search for conditions when males are selected to care. They found that the ESS depended on the proportion of deserting males, and a mixed ESS could be obtained. They compared their conditions for desertion with conditions obtained by Maynard Smith (1977) and concluded that by aligning their assumptions with Maynard Smith's assumptions, they arrived at the same conditions for male care as Maynard Smith did, even though he did not specify the source for additional females. The main difference between the conditions is that the conditions given by Maynard Smith (1977) for male care did not depend

on the proportion of deserting males or the proportion of deserting females, even though he incorporated the female strategy also in his model. In the model by Maynard Smith (1977), the proportions of deserting individuals are not incorporated in any way in the fitness expressions, so it makes sense that they do not affect the ESS.

Differing from these results, Iyer and Shukla (2021) found several mixed strategy pairs to be ESS pairs, and all pure strategy pairs were not ESS pairs in all their models. They allowed both caring and deserting males to attempt EPCs and took into account the paternity loss that a successful EPC attempt inflicts. However, they also assumed that deserting females are free to mate again with only deserting males and lay any additional eggs in a new nest. The difference between my Model 2 and the models by Iyer & Shukla is that in my model, the deserting female lays more eggs in the same nest and does not seek another male to sire her additional offspring. This implies that in Iyer & Shukla's model, the benefit for deserting males is greater as they can expect another brood in addition to some extra-pair offspring in other male's broods.

In the second model, the population strategy of the same sex did not affect the ESS for males or females (similarly as in Model 1), and only the population strategy of the other sex affected that. The ESS for males was mainly dependent on the offspring survival probabilities, the paternity share gained through a successful EPC attempt, the probabilities for succeeding in EPC attempts, and the proportion of deserting females. The ESS for females was mainly dependent on the egg numbers, the offspring survival probabilities, and the proportion of deserting males. In the second model, the conditions for ESSs for males were like the ones in the first model, only including more parameters. A sufficient difference between p_A and p_B was necessary for desertion to be favorable, and higher values of x made desertion more favorable. Figure 10 is relevant also in the second model, even though it is constructed with the loss terms of the first model. The loss terms are similar between the two models, and only the offspring survival probability changes according to the female strategy.

In the first model, all the females were assumed to share the same fixed strategy but allowing them to change their strategy did not affect the outcome for males. Both female care and female desertion could be ESSs with appropriate parameter values, and this adding the female strategy did not make some form of care impossible. Although the population strategy of the opposite sex affected the ESS, the ESS was still always pure strategy, and the ESS pair was always a pure strategy pair. Remember that Fromhage et al. (2007) obtained a mixed ESS with a similar model structure. That is due to the assumption that caring males do not make any EPC attempts, which causes the fitness functions to differ with respect to the fitness obtained through EPCs and fitness lost due to an EPC.

Since the population strategy of the opposite sex affected the ESS in my second model, achieving two different ESS pairs with the same parameter values was possible, depending on the initial proportions of deserting individuals. This is an interesting feature since it also means that the population might evolve towards an ESS pair that gives lower fitness than some other ESS pair. This

illustrates the situation where some ESS pair might be unattainable because the population cannot evolve towards that under natural selection.

Because the offspring in a caring male's brood are more likely to survive and an EPC attempt is more likely to succeed with a caring male's partner, any male can expect more surviving extra-pair offspring per EPC attempt in a caring male's brood versus a deserting male's brood. Could this drive for more EPC attempts to be made towards caring males' partners? I did not allow the number of EPC attempts to evolve but that could be an interesting question to explore further, assuming males could somehow distinguish between caring and deserting males' mates.

It would have been also possible to let the probability of succeeding in an EPC attempt vary according to the female caring decision. I did not incorporate this in my Model 2, but it is an interesting question to explore further. For example, it would be reasonable to assume that caring females are less receptive towards EPC attempts, and that lowers the probability for succeeding in those. In addition to that, it would also be possible to allow a different number of EPC attempts to be made towards a caring female than a deserting female. Both would be intriguing modifications to add to Model 2.

Since the models by Iyer and Shukla (2021) assumed that deserting females mate again and lay the resulting additional eggs in new nests, modifying my Model 2 according to that assumption would be interesting. This would allow a more direct comparison of our results, and the addition of second nests would make the probability of remating dependent on the proportions of deserting individuals and may yield mixed ESS pairs as a result. The benefit for deserting males could be drastically different depending on the proportion of deserting females and therefore the female population strategy could have a much stronger effect on the male ESS.

In all these models, breeding is assumed to be synchronous, and every individual finds a mating partner. This leads to the situation where there are no unmated individuals left after the mating. In real life, this is not usually the case as in many species, all individuals do not mate at the same time or even find a mating partner. This assumption is made to simplify the models and make mathematical solutions attainable and is commonly made in other models too (Maynard Smith 1982; Fromhage *et al.* 2007; Iyer *et al.* 2020; Iyer and Shukla 2021). Numerical simulations may be a useful tool to investigate situations where this assumption has been relaxed, as Iyer *et al.* (2020) showed.

5 CONCLUSIONS

Since so much variation in parental care exists in nature, finding all pure strategy pairs as possible ESS pairs in my models is not surprising. The results show some fundamental dependencies between different parameters that affect the outcome. I showed that the better ability to protect one's paternity can be enough to select

for male desertion even if there is no mating-caring trade-off. The magnitude of paternity share possible to obtain through an EPC also affects the ESS, meaning that desertion cannot be favorable if the paternity share awarded is too small. My results from the second model also illustrate how the population strategy of the opposite sex affects the ESS and how different ESS pairs could theoretically be possible with the same parameter values but only one can be achieved depending on the initial population strategies.

A notable result is that there were no mixed ESS pairs, meaning that the beneficial strategy was strictly caring or strictly deserting. This results from the simplicity of my models as they did not include negative frequency dependence. That is why my model cannot explain polymorphic populations where multiple patterns of parental care emerge. Analyses with more complex models could obtain also mixed ESS pairs as previous studies have shown.

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Jyväskylä April 18, 2024
Maaria Kangasniemi

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APPENDIX 1. MATLAB SCRIPT (CASE 3.1.1)

In this script I have allowed p_B to change from 0 to 0.5 and V_d to change from 0 to 0.9. As a result, this script produces a matrix including information about the ESS in every value combination of parameters p_B and V_d and presents it as a figure.

```
% changing pB and Vd

clc
clear

md = 0.5; % the proportion of deserting males
n = 10; % the number of epc attempts per male
w = 5; % basic number of eggs
values = 100; % how many values of pB and Vd

Vc = 1; % the offspring survival probability when male cares and
there is no epc
Vepc = 0.9; % the offspring survival probability when male cares
and there is an epc
Vd = linspace(0,Vepc,values); % the offspring survival probabili-
tity when male deserts
x = 0.5; % the basic paternity share possible to obtain through
an epc
pA = 0.5; % the probability that an epc attempt succeeds with a
caring male's mate
pB = linspace(0,pA,values); % the probability that an epc at-
tempt succeeds with a deserting male's mate
deserts = zeros(values); % favorable strategies in a matrix form

for j = 1:length(Vd) % for each value of Vd
    for i=1:length(pB) % for each value of pB
        % fitnesses for caring and deserting male
        Hc = w*(Vc*(1-gamma_c(n,pA))+Vepc*gamma_c(n,pA)-1/(1-
md)*alfa(md,gamma_c(n,pA),x)*Vepc+alfa(md,gamma_c(n,pA),x)*Vepc+
beta(md,gamma_d(n,pB(i)),x)*Vd(j));
        Hd = w*(Vd(j)-
1/md*beta(md,gamma_d(n,pB(i)),x)*Vd(j)+alfa(md,gamma_c(n,pA),x)*
Vepc+beta(md,gamma_d(n,pB(i)),x)*Vd(j));
        deserts(i,j) = Hd > Hc; % 1 if deserting is more benefi-
cial and 0 if caring is more beneficial
    end
end

% drawing the figure
figure(1)
imagesc(Vd,pB,deserts)
set(gca, 'YDir', 'normal')
ylabel('pB')
xlabel('Vd')
```


APPENDIX 2. MATLAB SCRIPT (CASE 3.1.2)

In this script I allowed both p_A and p_B to change from 0 to 1. As a result, this script produces a matrix including information about the ESS in every value combination of the varying parameters and presents it as a figure.

```
% changing pA and pB

clc
clear

md = 0.5; % the proportion of deserting males
n = 10; % the number of epc attempts per male
w = 5; % basic number of eggs

Vc = 0.8; % the offspring survival probability when male cares
and there is no epc
Vepc = 0.7; % the offspring survival probability when male cares
and there is an epc
Vd = 0.5; % the offspring survival probability when male deserts
values = 100; % how many different values of pA and pB
x = 0.7; % the basic paternity share possible to obtain through
an epc
pA = linspace(0,1,values); % values for pA
pB = linspace(0,1,values); % values for pB
deserts = zeros(values); % matrix for favorable male strategies

for j = 1:length(pA) % for each pA value
    for i=1:length(pB) % for each pB value
        % fitness values for caring and deserting males
        Hc = w*(Vc*(1-gamma_c(n,pA(j)))+Vepc*gamma_c(n,pA(j))-
1/(1-
md)*alfa(md,gamma_c(n,pA(j)),x)*Vepc+alfa(md,gamma_c(n,pA(j)),x)*
*Vepc+beta(md,gamma_d(n,pB(i)),x)*Vd);
        Hd = w*(Vd-
1/md*beta(md,gamma_d(n,pB(i)),x)*Vd+alfa(md,gamma_c(n,pA(j)),x)*
Vepc+beta(md,gamma_d(n,pB(i)),x)*Vd);
        deserts(i,j) = Hd > Hc; % 1 if deserting is more benefi-
cial and 0 if caring is more beneficial
    end
end

% drawing figure
figure(1)
imagesc(pA,pB,deserts)
hold on
plot(pA,pB,'black') % plotting the line where pA and pB are
equal
set(gca,'YDir','normal')
ylabel('pB')
xlabel('pA')
hold off
```

APPENDIX 3. MATLAB SCRIPT (CASE 3.1.3)

In this script, I allowed p_B to change from 0 to 0.7 and x to change from 0 to 1. As a result, this script produces a matrix including information about the ESS in every value combination of the varying parameters and presents it as a figure.

```
% changing pB and x

clc
clear

md = 0.5; % the proportion of deserting males
n = 10; % the number of epc attempts per male
w = 5; % basic number of eggs

values = 100; % how many different values of x and pB
Vc = 0.9; % the offspring survival probability when male cares
and there is no epc
Vepc = 0.8; % the offspring survival probability when male cares
and there is an epc
Vd = 0.6; % the offspring survival probability when male deserts
x = linspace(0,1,values); % the basic paternity share possible
to obtain through an epc
pA = 0.7; % the probability that an epc attempt succeeds with a
caring male's mate
pB = linspace(0,pA,values); % the probability that an epc at-
tempt succeeds with a deserting male's mate

deserts = zeros(values); % favorable male strategies in a matrix
form

for i = 1:length(x) % for each value of x
    for j=1:length(pB) % for each value of pB
        % fitness values for caring and deserting males
        Hc = w*(Vc*(1-gamma_c(n,pA))+Vepc*gamma_c(n,pA)-1/(1-
md)*alfa(md,gamma_c(n,pA),x(i))*Vepc+alfa(md,gamma_c(n,pA),x(i))
*Vepc+beta(md,gamma_d(n,pB(j)),x(i))*Vd);
        Hd = w*(Vd-
1/md*beta(md,gamma_d(n,pB(j)),x(i))*Vd+alfa(md,gamma_c(n,pA),x(i)
))*Vepc+beta(md,gamma_d(n,pB(j)),x(i))*Vd);
        deserts(i,j) = Hd > Hc; % 1 if deserting is more benefi-
cial and 0 if caring is more beneficial
    end
end

figure(1)
imagesc(pB,x,deserts)
set(gca,'YDir','normal')
ylabel('x')
xlabel('pB')
```

APPENDIX 4. MATLAB SCRIPTS FOR MODEL 2

MATLAB script to set parameter values

In this script, the parameter values are set with the initial desertion values and the plotting function is called.

```
clear
clc

values = 10; % how many initial values

startingm = linspace(0,1,values); % initial md values
startingf = linspace(0,1,values); % initial fd values
iterations = 10000; % how many iterations or "generations"

% PARAMETER VALUES
Vcc = 1;
Vepcc = 0.9;
Vcd = 0.8;
Vdc = 0.8;
Vepcd = 0.7;
Vdd = 0.6;
x = 0.7;
n = 5;
pA = 0.8;
pB = 0.1;
gammac = 1 - exp(-n*pA);
gammad = 1 - exp(-n*pB);
w = 5;
W = 8;

% LOOPS FOR PLOTTING
for i=1:length(startingm)
    model2plot(Vcc, Vepcc, Vcd, Vdc, Vepcd, Vdd, x, gammac, gam-
mad, w, W, startingm(i), 0, iterations);
    model2plot(Vcc, Vepcc, Vcd, Vdc, Vepcd, Vdd, x, gammac, gam-
mad, w, W, startingm(i), 1, iterations);
end

for i=1:length(startingf)
    model2plot(Vcc, Vepcc, Vcd, Vdc, Vepcd, Vdd, x, gammac, gam-
mad, w, W, 0, startingf(i), iterations);
    model2plot(Vcc, Vepcc, Vcd, Vdc, Vepcd, Vdd, x, gammac, gam-
mad, w, W, 1, startingf(i), iterations);
end
```

MATLAB script for plotting function

This is the script for the plotting function that plots the evolutionary trajectories of males and females in Figures 6-9.

```

% function for plotting the evolutionary trajectories in model 2

function [ desertion_prob ] = model2plot(Vcc, Vepcc, Vdc, Vcd,
Vepcd, Vdd, x, gammac, gammad, w, W, md0 ,fd0,iterations)

desertion_prob = zeros(2,iterations); % contains all desertion
probabilities from all iterations
desertion_prob(:,1) = [md0,fd0]'; % setting the first desertion
probabilities as the initial md and fd given as parameters
i = 2;

while i <= iterations

    md = desertion_prob(1,i-1);
    fd = desertion_prob(2,i-1);

    % the relative fitness change for male
    dm = (((-1)+fd).*((-1)+gammac).*((-1)+md).*Vcc.*w+(-1).*gam-
mac.*Vepcc.*w+fd.* ... %Mathematicasta kopioidut deri-
vaatat (haluat varmaankin kopioida omasi tänne)
gammac.*Vepcc.*w+(-1).*fd.*Vcd.*W+fd.*gammac.*Vcd.*W+(-
1).*fd.*gammac.* ...
Vepcd.*W+md.*(((-1)+fd).*Vdc.*w+gammac.*Vepcc.*(w+(-
1).*fd.*w)+fd.*( ...
Vcd+(-1).*Vdd).*W+fd.*gammac.*((-1).*Vcd+Vepcd).*W)).^(-
1).*(((-1)+ ...
fd).*((-1)+gammac).*Vcc.*w+gammac.*Vepcc.*w+(-
1).*fd.*gammac.*Vepcc.*w+fd.* ...
Vcd.*W+(-1).*fd.*gammac.*Vcd.*W+(-
1).*fd.*Vdd.*W+fd.*gammac.*Vepcd.*W+ ...
(-1).*gammac.*Vepcc.*w.*x+fd.*gam-
mac.*Vepcc.*w.*x+fd.*gammad.*Vdd.*W.*x+(-1) ...
.*fd.*gammac.*Vepcd.*W.*x+(-1).*((-1)+fd).*Vdc.*w.*((-
1)+gammad.*x));

    % the relative fitness change for female
    df = ((-1).*md.*Vdc.*w+(-1).*((-1)+md).*(((-1)+gam-
mac).*Vcc+(-1).*gammac.* ...
Vepcc).*w+md.*Vdd.*W+((-1)+md).*(((-1)+gammac).*Vcd+(-
1).*gammac.*Vepcd) ...
.*W).*((-1).*((-1)+fd).*md.*Vdc.*w+(-1).*((-1)+fd).*((-
1)+md).*(( ...
(-1)+gammac).*Vcc+(-1).*gam-
mac.*Vepcc).*w+fd.*md.*Vdd.*W+fd.*((-1)+md).*(( ...
((-1)+gammac).*Vcd+(-1).*gammac.*Vepcd).*W).^(-1);

    fitgrad = [dm,df]'; % fitness gradient
    dp = 0.01/max(abs(fitgrad)); % the "resolution" of figure,
tells how big changes in desertion probabilities are allowed

```

```

    desertion_prob(:,i) = min(1,max(0,(desertion_prob(:,i-
1)+fitgrad*dp))); % setting the new desertion probabilities, not
allowing them below 0 or over 1

    i = i+1;
end

% plotting
figure(1);
axis square;
plot(desertion_prob(1,:),desertion_prob(2,:), 'k', 'LineWidth',2);
hold on;
plot(desertion_prob(1,iterations),desertion_prob(2,iterati-
ons), 'ok', 'LineWidth',2); % circles at the end points
xlabel('md')
ylabel('fd')
hold on;

```