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Crusaders, monks and family fortunes: evolutionary models of male homosexuality and related phenomena

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The fraternal birth order effect (FBOE) is a well documented preponderance of older brothers among gay men. Until now, it has lacked a proper formal treatment in light of evolutionary theory. In this article, we propose two related mathematical models based on the rigorous application of the inclusive fitness concept. The models examine sibling rivalry and resource allocation within families. One of the models assumes that the laterborn's reproductive ability is not compromised by the manipulation that leads to the exclusive allocation of family resources to the firstborn. The other model posits that this manipulation may lower the laterborn's direct fitness to zero. Both models suggest that the FBOE arises primarily from the older brother's manipulation, as the firstborn's inclusive fitness may increase, while the mother's decreases, but not *vice versa*. However, under certain conditions, the mother should support an activity that discourages division of family resources, and in extreme cases, the younger brother's homosexuality may be the best available reproductive strategy for his genes. The models also provide insight into the cultural evolution of primogeniture and explain how manipulation between relatives could evolve before the emergence of substantial economic inequality.

1. Introduction

The evolutionary origins of male homosexuality, understood here as an exclusive attraction to persons of the same sex, have long intrigued scientists. Homosexual individuals tend to have lower fecundity than heterosexuals [1–3], which raises questions about the factors that maintain this trait across generations. Several hypotheses have been proposed to explain male homosexuality. The antagonistic pleiotropy hypotheses suggest that homosexuality is a negative side effect of an otherwise beneficial gene or genes [4–6]. The same-sex affiliation hypothesis proposes that homosexuality serves a function unrelated to reproduction, primarily maintaining long-term alliances among men [7]. The bisexuality byproduct hypothesis views homosexuality as an unintended consequence of genes favouring bisexuality, which itself could offer reproductive advantages [8]. Although empirical data provide substantial support for some of these hypotheses, conclusive evidence remains elusive.

The parental manipulation hypothesis was offered as an alternative understanding of why male homosexuality continues to persist in the population [9,10]. According to this old hypothesis, male homosexuality is not a biological adaptation but a xenoadaptation, i.e. a trait controlled by genes present in the genome of a different individual (either of the same or a different species) and serving the interests of that different individual [11].

The hypothesis suggests that mothers may benefit from influencing the development of laterborn sons in a way that makes them more likely to be homosexual.

The idea is anchored in the concept of inclusive fitness, which contrasts with direct fitness. Direct fitness is best defined as the number of offspring that reach adulthood and have a chance to reproduce themselves. Inclusive fitness, on the other hand, accounts for an individual's alleles passed to the next generation through offspring and alleles transmitted via relatives.

The parental manipulation hypothesis posits that a woman can achieve a higher number of grandchildren (and, consequently, a higher number of copies of her alleles) if her laterborn sons are less likely to seek reproduction. This is presented as a scenario that maximizes the allocation of family resources to the eldest brother.

The parental manipulation hypothesis has two important (often unexpressed) assumptions: (i) The additional offspring is male only 50% of the time, and parents cannot predict the sex of children in advance. (ii) Male homosexual offspring are not net consumers of family resources. If they do not reproduce themselves, they aid the reproduction of relatives. If these assumptions do not hold, it is more beneficial to terminate the production of male offspring rather than increase their chances of being gay.

With each additional older brother, the probability that a man will exhibit homosexual orientation, indeed, increases. This phenomenon, referred to as the *fraternal birth order effect* (FBOE; [12–16]), has been firmly established and supported by meta-analyses [17,18]. The FBOE could be understood as an indirect support for the parental manipulation hypothesis.

Initial research conducted in the 1930s at German workplaces focused on the observation that homosexual men have more brothers than sisters [19], whereas independent studies carried out in the 1960s England noted that male homosexuals have more older siblings than heterosexuals [20]. It was not until the 1990s that Canadian research demonstrated that these observations were manifestations of the increased likelihood of homosexuality in men with older brothers [21]. This effect is not culturally specific and has been found in samples from the Greece [13], Mexico [15], Samoa [16], The Netherlands [12], Czechia [14] and other geographically diverse regions. A recent meta-analysis concluded that homosexual men show greater odds of having an older brother than heterosexuals (odds ratio = 1.28) [22]. The effect is present regardless of whether the brothers lived together or were separated after birth and, moreover, only biological brothers, not stepbrothers, show this effect [23].

The mechanism behind the hypothesized manipulation is largely unknown. The mother's body may alter the son's future sexual orientation during embryonic development, for example, through the effects of certain hormones on the developing nervous system or the expression of specific genes in neural cells. The existence of previous male offspring can be recognized through the presence of high-affinity antibodies against male embryo-specific antigens [24]. A 2018 study suggests that the maternal antibody-mediated immunological response to the Y-chromosome-linked protein neuroligin 4 (NLGN4Y) contributes to the development of male homosexuality [25].

A significant limitation of the parental manipulation hypothesis is, in our opinion, that the postulated manipulation can enhance parental inclusive fitness only if the relationship between resources and direct fitness is one of increasing returns (where each additional unit of available resources increases reproductive success more than the previous unit). If the direct fitness returns diminish with the amount of already invested resources (see figure 1A), parents maximize their inclusive fitness by securing an equal split of resources between their offspring.

We believe, therefore, that wherever the parental manipulation hypothesis is implied, another hypothesis that has a capacity to explain the FBOE should be postulated:

The sibling manipulation hypothesis suggests that genes within the older brother's embryo orchestrate the younger brother's transition to homosexuality [26]. Apostolou [27] is hinting towards this hypothesis by arguing that after the transition to agriculture, homosexuality in younger brothers is selected in order to decrease sibling competition over parental resources. This hypothesis has the capacity to explain all effects commonly attributed to parental manipulation and perhaps more.

When the mother benefits from allocating more resources to the firstborn, the firstborn benefits even more in terms of inclusive fitness. This is because the firstborn is, on average, twice as related to his own children as his mother is, while they are both equally related to the laterborn's offspring. If the laterborn's homosexuality is of cost C to his direct fitness but of benefit B to the direct fitness of the firstborn, it benefits parental inclusive fitness when $B > C$. It, however, benefits the inclusive fitness of the firstborn when $B > 0.5C$. This may happen even when the relationship between resources and reproductive success exhibits diminishing returns (figure 1).

If one is sceptical about the likelihood of such xenoadaptations, he/she may subscribe to *The alternative reproduction strategy hypothesis*. This hypothesis, related to the previous two, suggests that a similar effect to the FBOE could potentially be directed by the genes of laterborns themselves. If the benefits to the firstborn outweigh the costs to the laterborn more than twice ($0.5B > C$), the laterborn may willingly forgo reproduction to maximize his inclusive fitness. Such a scenario may occur in societies with pronounced social stratification, where people are divided into multiple hierarchically ordered groups based on their wealth and social status. In such societies, reproductive success was closely tied to wealth [28].

If this hypothesis was correct, then the mother's immune reaction against specific antigens unique to male embryos could be, rather than a means of manipulation, a cue that embryos of younger brothers use to switch to a more advantageous reproductive strategy. The alternative reproduction strategy hypothesis stems from the same roots as Wilson's [29] kin selection hypothesis. Recent overview [30] permits interpretation of the FBOE along this line.

In this paper, we introduce two limiting-case models (see §2c) that result from a consistent application of the inclusive fitness concept. They allow the three aforementioned informal hypotheses to be aligned in a single formal system (see electronic supplementary material, S1 for mathematical details) where the actors (firstborn, mother, laterborn) may conditionally shift their strategies based on current constraints and opportunities. In essence, the models explain how the costs and benefits in this specific incarnation of Hamilton's rule arise and further implications thereof.

2. Methods

A concrete example illustrating the constitutive elements of our models is shown in figure 1. In general, the utility of manipulation to each actor depends on:

(a) The importance of rival and non-rival resources

Rival resources must be divided; one offspring's gain cannot benefit the other (e.g. land, money). Non-rival resources can be passed to all offspring in equal measure (e.g. good genes, reputation, socially transmitted hunting skills). When discussing rival and non-rival wealth, researchers usually emphasize resources that flow from parents to offspring [31]. In this article, these terms also encompass resources obtained by the siblings. This allows contextualization of the results with theories that assume that non-reproducing individuals actively support their siblings' offspring. Any resource that can be easily transferred between siblings without a loss in value but can be converted into reproductive success by only one of them should be considered a rival resource. For instance, wild crops collected on a daily basis should be counted as a rival resource if siblings live nearby, but non-rival if siblings disperse.

We assume that two siblings compete for rival resources, which makes the maths elegant. The extension to larger sibship sizes is trivial and does not qualitatively change any conclusions of the analysis. Moreover, the scenario where two siblings of a single mother reach adulthood is parsimonious, as it implies a stable population size. A similar approach has already been utilized and advocated elsewhere [32].

We denote the total rival resources r and assume that the rival resources obtained by the two siblings are r_1 and r_2, where $r_1 + r_2 = r$. Additionally, each sibling obtains non-rival resources $n \geq 0$, which are unaffected by the other sibling's consumption. Without loss of generality, we can set $r = 1$ and interpret n as the relative importance of non-rival to rival resources. We then assume asymmetric manipulation opportunities and set $r_1 \in [0.5, 1]$. Thus, $r_2 \in [0, 0.5]$. This is the only thing that distinguishes firstborns from laterborns in the models. We believe the age gap and *in utero* sequentiality justify a 'first-mover' advantage, making a 'fair split of rival resources' the worst-case scenario for the firstborn and the best-case scenario for the laterborn. Relaxing this assumption would not change the main results but would complicate their interpretation. It would be necessary to emphasize that the optimal strategy for both brothers is identical—allocating the majority of rival resources to self—though it may shift if either brother gains an advantage for any reason.

(b) Function $f(x)$ that describes the relationship between obtained resources and the direct fitness

We can interpret $f(x)$, for instance, as a continuous rate λ in a Poisson distribution that determines the number of adult offspring that an individual with total resources x raises over a lifetime. For simplicity, and because very few humans reach the peak of their theoretical reproductive capacity, we assume no upper bound to $f(x)$. We also assume that direct fitness increases with available resources, i.e. that the first derivative of $f(x)$ is positive ($f'(x) > 0$). Some conclusions can be derived from these constraints alone, but creating visualizations and formulating specific predictions requires choosing a concrete function for use in the models.

In the main article, we work with a power function $f(x) = x^a$, where a is a positive real number. In this expression, $f(x)$ represents the direct fitness, i.e. the number of offspring that reach adulthood. x stands for the total sum of rival and non-rival resources available to an individual and convertible to offspring (e.g. $r_1 + n$). The returns exponent a determines whether the function translates resources into offspring with diminishing returns ($a < 1$), linear returns ($a = 1$), or increasing returns ($a > 1$). The power function has several advantages: (a) it fulfils the stated requirements, being differentiable and increasing (for $a > 0$); (b) it encompasses a continuum of diminishing (e.g. $f(x) = x^{0.5} = \sqrt{x}$) and increasing returns functions (e.g. $f(x) = x^2$); and (c) most functions can be locally approximated by a power series while the behaviour of a function represented by a power series can be captured by the term with the highest exponent for sufficiently large x (see electronic supplementary material, S3.4). This is relevant to our case, as we represent n relative to r, which allows the assumption that $r + n$ is arbitrarily large. Therefore, most conclusions drawn from this tractable model can be generalized to other functions that fulfil the stated requirements (see electronic supplementary material, S1.2.3 for an alternative using the exponential function).

By using a function that operates on the sum of rival and non-rival resources, we assume interchangeability of resources. Any added rival resource (or its 'common currency' equivalent that may be converted to offspring) contributes equally to any added non-rival resource. This does not, however, imply that their effects are additive, as they may exhibit synergistic interactions (see electronic supplementary material, S3.5 for a specific elaboration). Potential synergies—when combined resources yield greater benefit than the sum of both contributing individually—are reflected in the returns exponent a and do not require an additional parameter ($a > 1$ may be interpreted as indicating a high frequency of synergistic effects). A model where resources are interchangeable but not additive assumes that synergies between any two rival resources, two non-rival resources, and one rival and one non-rival resource occur with equal probability. Only the model with linearly increasing returns assumes additive effects of resources. Diminishing returns ($a < 1$) suggest that compensatory interactions between resources outweigh the synergies. If resources can substitute for each other, a resource added to a large pool contributes less than it would contribute in isolation.

As we demonstrate in electronic supplementary material, S1.1.3, function $f(x) = bx^a + c$ behaves identically for any values of b and c, so we conduct the analysis with $f(x) = x^a$, but plot the results on an arbitrary scale. In all figures, we scale the direct fitness to $f(0) = 0$ and $f(r + n) = 5$ to foster a biological interpretation of the direct fitness as an average number of offspring surviving into adulthood.

(c) The nature of manipulation

When f_1 is the direct fitness of the firstborn and f_2 is the direct fitness of the laterborn, the firstborn's inclusive fitness is $F_1 = f_1 + \frac{1}{2}f_2$, the laterborn's inclusive fitness is $F_2 = \frac{1}{2}f_1 + f_2$, and the inclusive fitness of the mother in the generation of grandchildren is $F_M = \frac{1}{2}f_1 + \frac{1}{2}f_2$.

We assume that the direct fitness of an individual who does not face manipulation towards an unfair share of rival resources (the firstborn) is always $f_1 = f(r_1 + n)$. The laterborn's direct fitness depends on how the manipulation of rival resource consumption is implemented on the cultural and physiological levels. Here, we recognize and henceforth distinguish two limiting case models.

In the first model, the laterborn's ability to convert non-rival resources into offspring is unaffected by the manipulation. If the manipulation is maximal and the firstborn manages to monopolize all rival resources, the laterborn's direct fitness is $(f_2 | r_2 = 0) = f(n)$. We name this model 'Crusader' to appeal to popular imagination and inspire the thought that *primogeniture* is a typical representative of a cultural practice that fits this model. Primogeniture leaves the laterborn landless ($r_2 = 0$) and prone to dispersion. The dispersion may prevent the reallocation of newly obtained resources to the firstborn's offspring (keeping n larger). In the Crusader model, it is useful to write r_1 as $\frac{1}{2} + \delta$, where δ is the deviation from the fair split of rival resources. The direct fitness of the laterborn is then $f_2 = f\left(\frac{1}{2} - \delta + n\right)$.

In the second model, the laterborn's ability to convert non-rival resources into offspring decreases with the intensity of manipulation. If the firstborn manages to monopolize all rival resources in this model, the laterborn does not reproduce at all, i.e. $(f_2 \mid r_2 = 0) = 0$. In the context of the FBOE, this can be interpreted as a model of *exclusive homosexuality*, but we name this model 'Monk' as a vivid counterpart of Crusader. This acknowledges that there is more than one way to culturally contextualize individuals who forgo biological reproduction and specialize in increasing the reproductive success of kin and community. (We are aware that in many cultures, religious specialists do reproduce, but modelling the evolution of religious practices is not a focus of this article.) The label is also inspired by empirical work suggesting that celibate monks reliably increase the direct fitness of their brothers and the inclusive fitness of their parents [33,34]. In the Monk model, we label the manipulation parameter $m \in [0,1]$ (to distinguish it from δ in the Crusader model, which could be expressed as $\frac{m}{2}$). We link m with the utilization of both rival and non-rival resources by the laterborn. The direct fitness of the laterborn in the Monk model is, therefore, $f_2 = f\left(\frac{1}{2} - \frac{m}{2} + (1 - m)n\right)$, which is more convenient to write as $f\left(\frac{(1-m)(1+2n)}{2}\right)$ for the purpose of the analysis.

We used the resulting inclusive fitness functions to draw plots of manipulation benefits and to identify indifference boundaries: (a, n) parameter combinations for which maximal manipulation ($r_1 = 1$) promises the same inclusive fitness as the fair split of rival resources $\left(r_1 = \frac{1}{2}\right)$. We used the first derivatives of inclusive fitness functions to identify manipulation incentives at the fair split, to express critical points (minima or maxima) algebraically, and to find (a, n) boundaries of parameter space regions where finding critical points within $r_1 \in \left[\frac{1}{2}, 1\right]$ is possible. We used second derivatives to see where inclusive fitness functions are concave or convex. Details of the analysis can be found in electronic supplementary material, S1. All algebraic steps and code that can be used to replicate results of numerical methods and plot equivalent figures are at https://osf.io/m9uft/.

3. Results

We identified the conditions under which the model actors benefit, in terms of inclusive fitness, from the manipulation that favours the allocation of rival resources to the firstborn. The complete results are shown in figure 2. For algebraic details, see electronic supplementary material, S1.

All three actors are more likely to benefit from increasing the firstborn's share (r_1) as the returns exponent (a) increases. For any given importance of non-rival resources (n), there exists a returns exponent (a) large enough to make the exclusive allocation of rival resources to the firstborn ($r_1 = 1$) the most profitable strategy for the firstborn, the mother and the laterborn alike. If the reproductive returns are diminishing ($a < 1$), however, only the firstborn may be incentivized to manipulate the laterborn towards the lower consumption of rival resources.

The benefits of manipulation usually decrease with the growing importance of non-rival resources n. An exception is found in the Crusader model (where conversion of non-rival resources to offspring is unaffected by the manipulation) with diminishing returns ($a < 1$). There, counterintuitively, the firstborn's benefits from manipulation increase with the importance of non-rival resources.

In total, we identified six possible optimal strategies. These are determined by whether the inclusive fitness functions $F_i(r_1)$ are monotonic or contain a critical point between the fair split ($r_1 = 0.5$) and maximal allocation of rival resources to the firstborn ($r_1 = 1$), by whether the achievable critical point is a minimum or maximum, and by whether the fair split offers higher inclusive fitness than allocating all rival resources to the firstborn (table 1).

Only the firstborn in the Monk model shows the separation of the parameter space into all six strategies.

In the Crusader model, the firstborn always prefers deviation from the fair split (electronic supplementary material, S1.1). In the Monk model, all actors are aligned on the fair split if non-rival resources are important ($n > 0.5$) and reproductive returns are diminishing ($a < 1$).

Table 1. Overview of actor strategies.

strategy	inclusive fitness function $F_i(r_1)$ monotonic on $r_1 \in [0.5, 1]$	critical point	maximal manipulation better than the fair split, $F_i(r_1 = 1) > F_i(r_1 = 0.5)$	example
manipulate as much as possible	true	—	true	figure 2B, Crusader model, firstborn
optimize manipulation but favour the maximal manipulation over the fair split	false	max.	true	figure 1, Crusader model, firstborn
optimize manipulation but favour the fair split over the maximal manipulation	false	max.	false	figure 1, Monk model, firstborn
prefer allocating resources to the firstborn since the maximal manipulation tops the fair split	false	min.	true	figure 2B, Monk model, mother
counteract manipulation only up to a point but favour the fair split over the maximal manipulation	false	min.	false	figure 2B, Monk model, laterborn
always counteract manipulation	true	—	false	figure 1, Crusader model, laterborn

In the Crusader model, the mother prefers an equal split if the fitness returns are diminishing ($a < 1$). She, however, prefers primogeniture if the fitness returns are increasing with invested resources ($a > 1$). The importance of non-rival resources plays no role in her preferences.

For laterborn in both models and the mother in the Monk model, immediate deviation from the fair split decreases inclusive fitness (its first derivative is negative at $r_1 = 0.5$). However, allocating all rival resources to the firstborn may still prove to be the best available strategy, surpassing the fair split. This typically happens if returns increase sharply (large a) and non-rival resources are unimportant (small n).

The regions of parameter space where manipulation is beneficial are perfectly nested (which relates back to the Hamilon's rule inequalities $B > 0.5C$ for the firstborn, $B > C$ for the mother, and $0.5B > C$ for the laterborn). If the laterborn's inclusive fitness increases with further allocation of rival resources to the firstborn, both the mother's and the firstborn's inclusive fitness increase too. When the mother's inclusive fitness increases, so does the firstborn's, but there are no (a, n) parameter combinations where she would benefit from the manipulation but the firstborn would not. In both models, there are combinations of a and n where the mother and the laterborn are against further deviation from the fair split, but the firstborn is incentivized to deflect more rival resources to himself. More examples can be found in electronic supplementary material, S2.

4. Discussion

(a) Sibling and parental manipulation: theoretical insights and underlying mechanisms

We have established a hierarchy of the suggested hypotheses and identified the conditions under which each is applicable. The sibling manipulation hypothesis should apply in the widest range of societies, including those where the relationship between resources and reproduction shows diminishing returns. This hypothesis, therefore, clearly dominates the parental manipulation hypothesis, which is relevant only if the relationship between resources and reproduction shows increasing returns.

In extreme circumstances of sharply increasing returns and high importance of rival resources, the laterborn's transition to homosexuality may also be an adaptive strategy promoted by his genes. It is, however, a question what (if anything) can cause reproductive returns to increase so sharply. A pronounced social stratification would be one of the candidate causes (see electronic supplementary material, S3.4). Unequal distribution of wealth leads to a substantial inequality in reproductive success [28,35]. The primary cause of the stratification is the increasing returns between wealth and income, which may result from several subsistence strategies (see electronic supplementary material, S3). It is important to note that stratification, in turn, may increase the extent to which reproductive returns grow with wealth (providing the wealthy men are able to lock a substantial part of the male population out of reproduction). Thus, a positive feedback—leading to primogeniture along the way—may amplify random fluctuations in wealth between families.

The physiological mechanism behind the manipulation remains elusive. It might be associated with the mother's immunization against specific antigens unique to male embryos [25] or the activity of embryonic cells that infiltrate the maternal

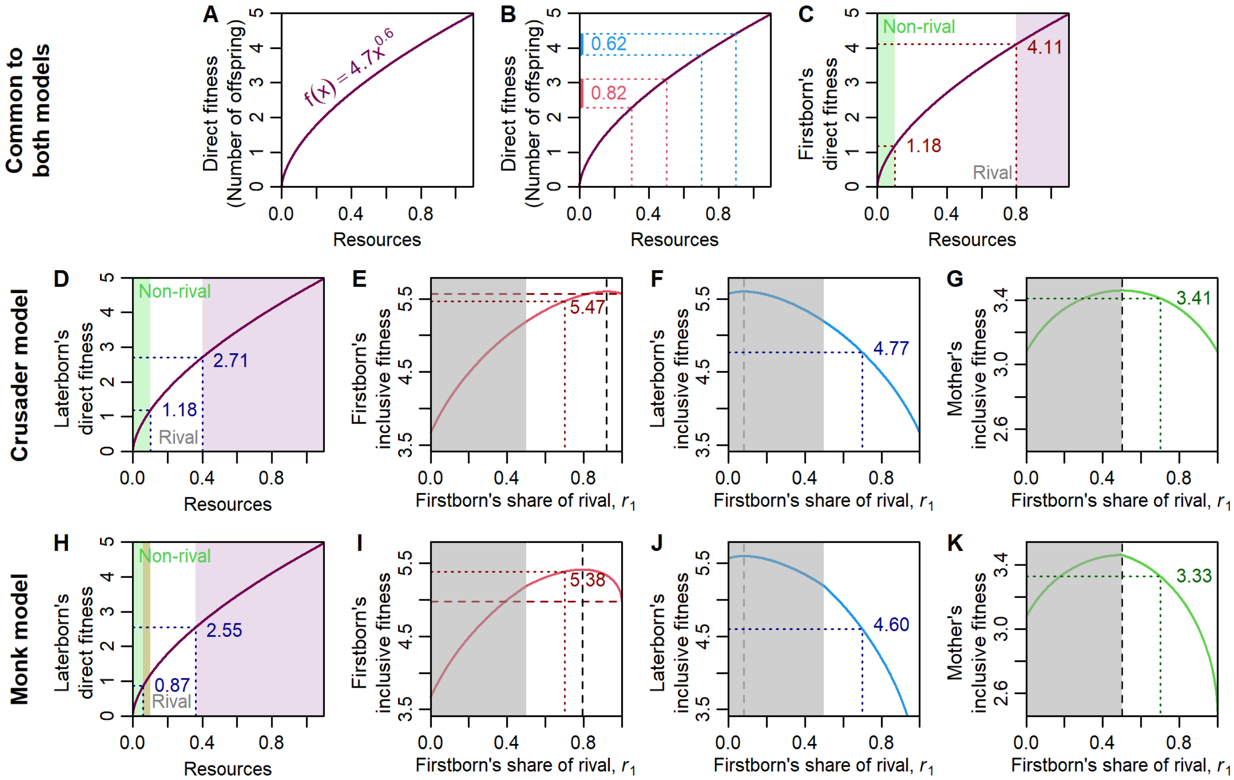

Figure 1. Direct fitness function and its implications for inclusive fitness: an illustration. This is an example of a direct fitness function $f(x) = bx^a$, which determines how obtained resources are converted into the expected number of offspring (A). In the expression, a, the 'returns exponent', determines the relative growth of direct fitness with increasing resources ($a < 1$: diminishing fitness returns; $a = 1$: linear returns; $a > 1$: increasing returns), while b scales the absolute value of direct fitness without altering the ratio $f(x_1)/f(x_2)$ for any x_1 and x_2. Here $b = 4.7$, so the function predicts realistic numbers of offspring, but as we show in electronic supplementary material, S1.1.3, b does not play any role in judging best strategies for different actors. The decisive parameter, returns exponent a, is set to 0.6 here, indicating diminishing returns in expected offspring with increasing resources. For instance, if 0.2 resources are added to 0.3, direct fitness increases by 0.82, but when 0.2 is added to 0.7, direct fitness increases by only 0.62 (A). Two brothers, firstborn (C) and laterborn (D), both obtain, by definition, the equal amount of non-rival resources (n), here $n = 0.1$, and convert them, on average, into 1.18 offspring each. Additionally, there is a budget of rival resources $r = 1$ that the brothers must split. The firstborn's share is labelled r_1 and the laterborn's share r_2 follows from $r_2 = 1 - r_1$. In this example, the firstborn secures $r_1 = 0.7$ of the rival resources, leaving the laterborn with the remaining 0.3. The firstborn is therefore expected to sire 4.11 offspring in total, while the laterborn can expect 2.71. Brothers share, on average, 50% of genetic alleles. The inclusive fitness of the firstborn is therefore $4.11 + 0.5 \times 2.71 = 5.47$ (E, dotted line) and the inclusive fitness of the laterborn is $0.5 \times 4.11 + 2.71 = 4.77$ (F, dotted line). By varying the amount of rival resources monopolized by the firstborn (r_1), we observe how the inclusive fitness would change for each brother. We can see that the firstborn would prefer further deviation from the fair split up to 0.92 (E, black dashed line), when his inclusive fitness would start to decline again, while the laterborn should push to decrease the inequality (F, flipping the advantage in favour of the laterborn—the grey area—is not allowed, so the laterborn's potential optimum at $r_1 = 0.08$, is marked by a grey dashed line). The mother, being equally related to both sons, should oppose any (further) deviation from the fair split. Fair split maximizes her inclusive fitness under the assumption of diminishing reproductive returns (G). This illustrates the core of the *Crusader model*, where the laterborn's ability to convert non-rival resources into offspring is unaffected by the manipulation that results in the uneven distribution of rival resources. In the *Monk model*, which assumes celibacy or exclusively homosexual activity in the extreme case $r_1 = 1$, the proportion of laterborn's non-rival resources converted into offspring also declines with the deviation from the rival resources' fair split. The firstborn's direct fitness at a 70 : 30 split remains unchanged (C), but the laterborn's direct fitness is expected to be 2.55 (H). Inclusive fitness functions change accordingly: the firstborn would now prefer to raise his share of rival resources only up to 0.79 and he would favour an equal split over monopolizing all rival resources (I, red dashed line). From the available alternatives (in white), the laterborn (J) and the mother (K) should still advocate for an equal split. By analysing the changes in the inclusive fitness functions with the returns exponent (a) and the relative importance of non-rival resources (n), we can partition the parameter space according to each actor's optimal strategy (figure 2).

organism during pregnancy [36]. Microchimerism, the transfer of cells from one individual to another, has been proposed as one of the potential sources of the antigen that causes maternal immunization [25]. However, it cannot be ruled out that microchimerism directly contributes to the development of homosexuality or other traits that lower the laterborn's interest in direct reproduction. It is known that during pregnancy some cells of the embryo are embedded in the maternal organism [37]. Likewise, somatic cells of the mother can become engrafted in the developing embryo [38], even in its brain [39]. It is also possible that the embryo is colonized by cells from a previously developing embryo [40,41]. Therefore, it is conceivable that the shift in sexual preferences is induced by cells of older brothers' embryos. Moreover, cells have the potential to carry out more complex and targeted modifications to brain development compared with the relatively simple action of IgG antibodies, which are known to cross the placenta.

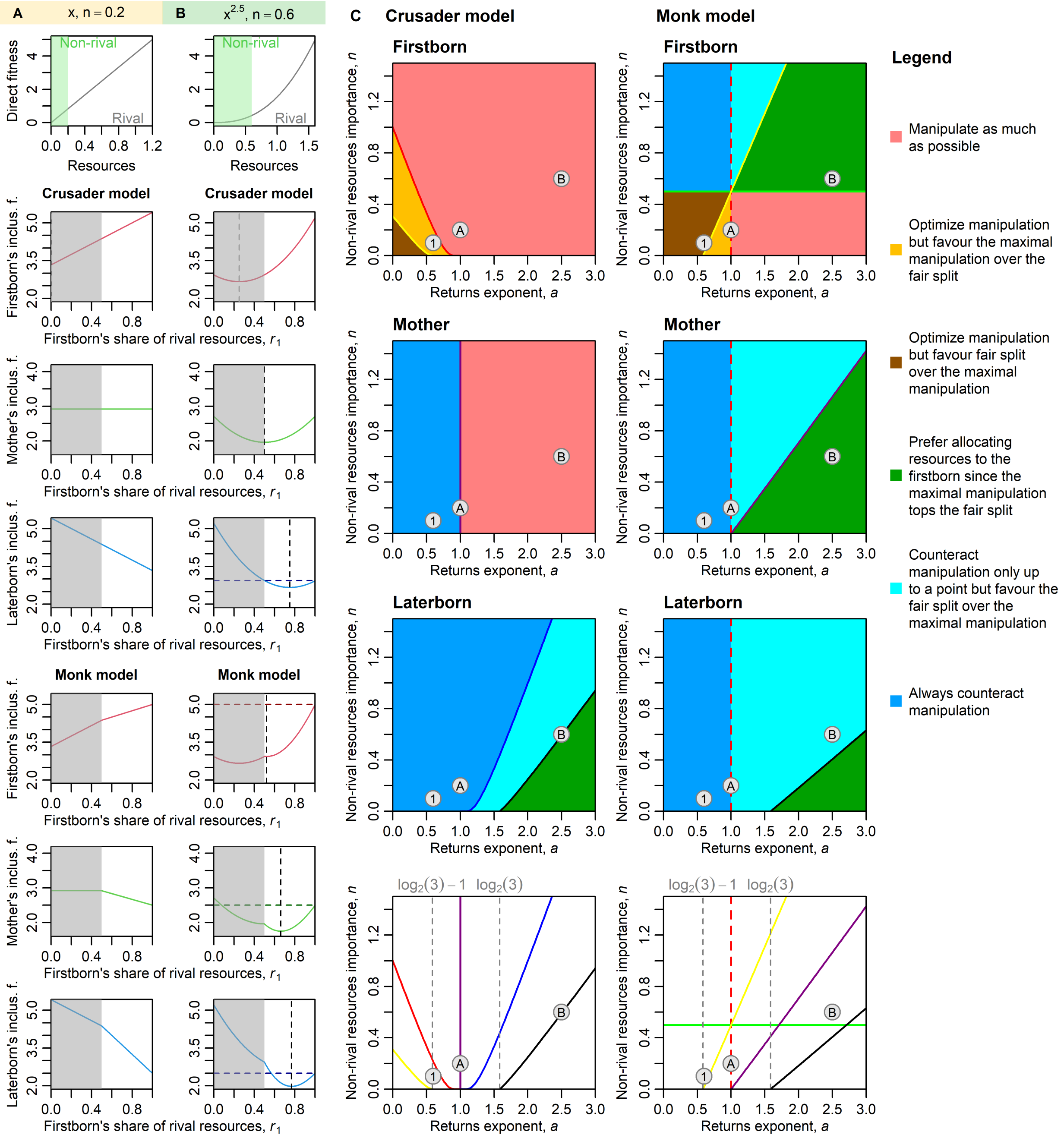

Figure 2. Fitness function examples and boundaries between optimal strategies for each model and actor. In examples A and B, the top panels display direct fitness function $f(x) = x^a$ for linear (A, $a = 1$) and increasing (B, $a = 2.5$) returns. Lower panels depict the dependence of the firstborn's, the mother's and the laterborn's inclusive fitness on the proportion of rival resources monopolized by the firstborn, $r_1 \in [0,1]$. When the local minimum or maximum of the function occurs between the fair split ($r_1 = 0.5$) and the exclusive allocation of all rival resources to the firstborn ($r_1 = 1$), i.e. when derivative 0 is achievable in $r_1 \in [0.5,1]$ (white region), we mark it with a black dashed line. In such cases, the extreme $F_i(1+n)$ is intersected with a horizontal line to mark the corresponding indifference point on the other side of the minimum or maximum. Unachievable scenarios $r_1 \in [0,0.5]$ are in grey. Segment C shows optimal strategies of the actors in the parameter space of a (returns exponent) and n (importance of non-rival relative to rival resources). The bottom panels show all boundaries plotted together. Number 1 and letters in white circles denote positions of examples in figure 1 and in segments A and B of this figure.

(b) Testing the hypotheses

A critical issue with the sibling manipulation hypothesis is that the older brother's manipulative actions might conflict with the optimal allocation of rival resources by parents. This allocation does not necessarily mean an equal distribution; optimal resource distribution depends on the family structure, inheritance systems and sex ratios at birth and in adulthood, among other factors. In the presented models, however, the mother always leans more towards the fair split than the firstborn. If the eldest brother manages to secure an unfair share in a situation of diminishing returns between resources and direct fitness, he lowers not only the inclusive fitness of his siblings but also that of his parents. Fifty years ago, Richard D. Alexander contended that parents, especially mothers, may be better positioned to enforce their interests against their offspring [42]. Offspring who carry an allele that promotes their interests at the expense of parents, argued Alexander, will eventually become parents themselves. Their children will inherit the allele, which ultimately harms them. This claim was, however, based on an inconsistent application of gene-centred views [43]. There is no reason to favour this conclusion over the alternative: 'Alleles that

Table 2. Overview of hypotheses based on the existence of the fraternal birth order effect.

hypothesis	localization of responsible genes	supposes economic inequality?	subsistence strategies	suggested mechanism
sibling manipulation	firstborn's genome	no	possibly all	microchimerism, immunization against male antigens
parental manipulation	maternal genome	yes	horticulture or any investment-based strategies	immunization against male antigens
alternative reproduction strategy	laterborn's genome	yes, substantial	complex combinatorial strategies	gene activity triggered by cues of male embryo precedence

favour parental interests over those of offspring cannot spread because all parents were once kids'. In fact, many alleles trade off benefits at one stage of life for benefits at another. What matters is the relative advantage—in terms of the average number of copies present in the next generation after a completed life cycle—that the allele has over competitors for the same locus.

There are at least three factors that potentially enable older sons to gain advantages. First, the manipulative behaviours of the older brother might not result from a single gene but could arise from epistatic interactions between alleles at different loci. In such a case, the manipulation would exhibit lower narrow-sense heritability, h^2, which reflects only additive genetic variance (as opposed to broad-sense heritability, H^2, which captures the total genetic determination of the trait). Consequently, manipulative firstborns might often avoid inclusive-fitness-lowering actions of their own sons [44]. (This explanation implies a testable prediction of standing genetic variation at the loci responsible for the manipulation.) Second, it may not always be technically feasible to defend against manipulation by offspring. For instance, if the embryo introduces its cells into the mother's body, which subsequently penetrate the younger brother's embryo and influence its brain development, the mother has limited ability to counteract these effects. Third, according to the so-called *life-dinner principle* [45], in scenarios where the interests of different biological entities conflict, the party most likely to assert their interests is typically the one with the most to gain, which, in this case, is likely the older brother. This intuition has a formal counterpart in our model. Regardless of the model type, the difference between the first derivatives of the firstborn's and the mother's inclusive fitness function is

$$\frac{dF_1}{dr_1} - \frac{dF_M}{dr_1} = \frac{1}{2} f'(r_1 + n),$$

where $f'(x)$ is the first derivative of the direct fitness function. Since the fitness function is set to be growing, its first derivative is always positive. So, when both actors are gaining with increased manipulation, the firstborn is gaining more. On the other hand, when inclusive fitness declines with further deviation from the fair split in both actors, the mother is losing more. She is therefore incentivized to prevent further deviation from her optimum. An equilibrium may be reached in the middle, when, in terms of inclusive fitness, the firstborn is gaining what the mother is losing ($\frac{1}{4} f'(r_1 + n)$). Other factors, such as the nature of the manipulation or bargaining power of the laterborn, may then decide the overall outcome.

Supporting the parental manipulation hypothesis over the sibling manipulation hypothesis may be challenging. The best option would be to demonstrate that the firstborn benefits only when the mother also benefits from the manipulation. Additionally, a detailed understanding of the physiological process behind the modification of the laterborn's sexual orientation could strengthen support for the parental manipulation hypothesis.

It is worth noting that if the laterborn's capacity to convert resources into offspring stays intact and the reproductive returns increase with invested resources, the mother's and firstborn's interests perfectly align. Although the mother is indifferent to which offspring monopolizes rival resources, she prefers exclusive allocation to one of them. The prevalence of primogeniture (or, more rarely, ultimogeniture) demonstrates that equal division of resources can be readily replaced by practices favouring a single heir at least through cultural evolution. Rarely, however, this practice is attributed to the agency of firstborns, while our Crusader model demonstrates that they are the actors most incentivized to establish it.

An alternative reproduction strategy gains support if firstborns and mothers benefit only when allocating all rival resources to the firstborn is the best option for the laterborn. This holds if the relationship between resources and fitness is sharply increasing and the importance of non-rival resources is low. All hypotheses and their assumptions are summarized in table 2.

In the near future, geneticists may extend genome-wide association studies [46,47] to include alleles located on family members' chromosomes. This approach will finally put all 'extended phenotype' narratives to the test. We hope this paper will inspire such a study on predisposition to homosexuality.

(c) Extensions and limitations

Recently, the potential presence of the FBOE in connection with homosexual orientation among women has come to light [12,14]. If the FBOE among lesbian women is confirmed, it could be explained as a mere side- effect of the maternal immunological reaction against male proteins. For example, the anti-NLGN4Y antibodies may simply cross-react with an X-based homologue, NLGN4X, as has already been suggested [25,48]. These findings, however, pose no challenge to our model, which is agnostic about the sex of siblings. It was primarily constructed as a model of competition between two brothers but it can be treated as a model for all siblings that compete for rival resources. Two brothers may typically represent a case where the relative size of the contested budget is large (small n). A brother and a sister occupy different social niches, and therefore may compete less, making non-rival resources more important (large n). An extension of our model could easily allow implementation of an additional exponent parameter a_2 that would allow distinction between sibling return profiles by sex. In such a model, parameters b_1 and b_2 would start modifying the results only to lead us to a well established Trivers–Willard conclusion that poor families can maximize their fitness by investing in daughters [49], while rich families should allocate rival resources to (firstborn) men.

Similarly, recent work suggesting the presence of an FBOE equivalent in rats [50] can be interpreted in the light of our results. Male offspring born to female lab rats that had previously been gravid multiple times displayed a higher proportion of homosexual behaviour and preference compared with males born to first-time mothers. This effect should be, in our opinion, attributed to sibling manipulation. Note that laterborn rats' expected fitness is not lowered all the way down to zero and that there may certainly be some rival resources that offspring of two related rats compete for (living space or sexual partners, for instance). Precise details depend on the relative severity of competition between offspring of siblings and offspring of unrelated individuals. If the former is relatively strong, the advantage of increasing one’s own fitness at the expense of a younger brother’s increases, and an FBO-like effect may arise as an adaptation. Extending this idea to humans, one can expect that strong institutions protecting family wealth against repeated contests from unrelated individuals contribute to an environment where sibling manipulation is incentivized.

We recognize that the proposed hypotheses may be applicable to only a subset of gay men. As a previous study suggests [51], there may be various subgroups of gay men with potentially distinct aetiologies. The maternal immunological reaction is hypothesized to cause homosexuality in one of these subgroups. It is, however, possible that another subgroup is influenced by microchimerism and yet another by their own genes—either as a result of an alternative mating strategy or in accord with the byproduct hypothesis. We hope that our conclusions will inspire further research in this area.

It can be argued that older brothers have more direct methods available, such as siblicide, to redirect resources from younger siblings to themselves. However, such actions overtly conflict not only with the biological interests of other family members and societal norms but also with the perpetrator’s own moral consciousness affecting his overall wellbeing and fitness [52]. In contrast, subtle embryonic manipulations mediated by the maternal organism are much harder for observers and ‘perpetrators’ themselves to recognize and address. Even if evolving to prevent the mother from future conceptions (of male embryos) was an option, it would not be likely to be favoured by natural selection. A sibling who does not aim to reproduce is better than no sibling. They may be easily convinced to invest transferable resources in nephews and nieces. Remember, that when siblings are willing and able to pool the resources, any resource that is easy to transfer is rival. Samoan *fa’afafines*, who make more money than average Samoan heterosexuals and exhibit tendencies to support their siblings’ children, are an exemplar ‘product’ of such a situation [53]. Mexican *muxes* also show elevated kin-directed altruism compared with their heterosexual counterparts [54].

(d) Implications for the evolution of the fraternal birth order effect

The real evolutionary outcome is bound to be more dynamic and fall between proposed extremes of the Crusader and Monk models. Conversion of non-rival resources to offspring is likely affected by the availability of rival resources, but not directly proportionally. Many poor men in stratified societies, if they reach adulthood, eventually do reproduce, as do many men with homosexual orientation. Although we linked it primarily with the Monk model in our narration, homosexuality, or rather bisexuality, could function as an adaptation to living in a prevalently male collective [7]. This would hint towards the Crusader model, in which manipulated laterborns are able to convert non-rival resources into offspring. Still, there is an implicit yet valid assumption that an increased same-sex attraction (even in bisexuals with unaffected attraction to the opposite sex) inevitably leads to spending less time with opposite-sex individuals. This reduced interaction consequently limits mating opportunities. Both limiting conditions $(f_2 \mid r_2 = 0) = f(n)$ and $(f_2 \mid r_2 = 0) = 0$ shall be treated as idealized abstractions.

Based on our models, one can speculate about the potential evolutionary trajectory that led to the current prevalence of male homosexuality. We have shown that if returns diminish with invested resources and the importance of rival resources is small but not null in the Crusader model, the firstborn benefits from manipulation of arbitrarily large intensity (top left corner of firstborn’s Crusader panel in figure 2C). In ancestral conditions, where human life-history strategies emerged, returns between hunted and gathered resources and reproduction were likely diminishing. The time that the grandmother can spend caring for grandchildren could emerge as a rival resource that can be either shared or monopolized [55]. In this scenario, while the mother prefers to distribute her attention equally among all grandchildren, the firstborn is incentivized to manipulate the laterborns towards greater dispersal, perhaps by increasing their explorative tendencies [56].

In such a situation, alleles present in the mother and the laterborn would benefit from de-incentivizing the manipulation. This can be, in principle, achieved by moving from the Crusader closer to the Monk model (see the overlap of dark-blue regions in the Monk column of figure 2C, which is still in the red region of ‘maximal manipulation’ in the firsborn’s best strategy in the Crusader model). Genes that link the manipulation to the lower conversion of non-rival resources to offspring in laterborns (perhaps by increasing attraction towards same-sex individuals) could, therefore, spread alongside genes that limit manipulative tendencies in firstborns. A hypothetical allele functionally equivalent to the statement: ‘If you force me to leave home empty-handed, I won’t reproduce and increase your inclusive fitness!’ would create an environment where manipulation is less favourable. The spread of such ‘blackmailing’ alleles is poorly understood, but currently we cannot rule out the possibility that they lock the setting closer to the Monk model. Subsequently, when subsistence strategies change towards the lower importance of non-rival resources (moving down along the y-axes in figure 2C), the firstborn’s best interests shift from ‘no manipulation’ to an ‘optimized manipulation’ and possibly even towards maximal manipulation with a switch from diminishing to increasing returns (moving right along the x-axes in figure 2C). Depending on the value of the returns exponent (a), this can be tolerated (turquoise region of the mother's Monk model panel) or even supported (green region) by genes that protect the inclusive fitness of the mother. Further along this direction, even laterborns may join efforts to avoid splitting the family's rival resources (green region of the laterborn's Monk model panel, figure 2C).

(e) Concluding remarks and next steps

Such explanations must currently be treated as partial. Today's data do not allow a clear distinction between the 'byproduct hypothesis' of antagonistic pleiotropy—i.e. that the same allele increases reproductive success in some individuals (women, firstborn men) to such an extent that its detrimental effects on laterborns' direct fitness can be tolerated [6,57]—and an adaptive explanation, in which the allele increases reproductive success *because* it nudges laterborn brothers towards homosexuality (even when coincidently present in 50% of them). Only the proposed family-wide genome-wide association studies (FWGWAS) could resolve this. In reality, byproduct and adaptive effects coexist and sometimes transition into one another. A byproduct may be co-opted and amplified to gain a function, while an adaptation may lose its value when environmental or societal conditions change.

The simplicity of our models is their great feature, but we should not forget that the real world is bound to be more nuanced. In many societies, return profiles may change with the total amount of resources that family members can obtain (see, for instance, S-shape function in electronic supplementary material, figure S4C). In such contexts, the predictions about the best allocation of rival resources differ depending on the total family wealth. The prestige bias [58], under which individuals imitate wealthier and more successful peers, can obscure the adaptive value of prevalent cultural practices. Everyone may adopt the same practice, even if it is detrimental to the less fortunate.

Further research is needed to illuminate the complicated interactions between physiology, sexual orientation and culture. Pirates, monks, crusaders, church-choir eunuchs, gays or asexuals may be recruited from similarly manipulated laterborns who are just socialized in different ways. On the other hand, there might be several manipulation paths that lead to the same culturally facilitated phenotypes. Our model suggests when and why biologically related actors may be incentivized to contribute to this manipulation.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Supplementary material, including all algebraic steps, is available online at https://osf.io/m9uft/.

Supplementary material is also available in Figshare [59].

Declaration of AI use. During the preparation of this work, the authors used Chat GPT-4 in order to improve grammar and style. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Authors' contributions. P.T.: formal analysis, investigation, methodology, software, validation, visualization, writing—original draft, writing—review and editing; J.Fo.: conceptualization, funding acquisition, investigation, project administration, validation, writing—original draft, writing—review and editing; J.Fl.: conceptualization, funding acquisition, investigation, methodology, resources, supervision, validation, writing—original draft, writing—review and editing.

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

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Supplementary materials for

Crusaders, Monks, and Family Fortunes: Evolutionary Models of Male Homosexuality and Related Phenomena

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1 Mathematical analysis

1.1 The Crusader model

With the deviation from the fair split of rival resources $\delta \in \left[0, \frac{1}{2}\right]$, we get the inclusive fitness of the firstborn

$$F_1 = f\left(\frac{1}{2} + \delta + n\right) + \frac{1}{2} f\left(\frac{1}{2} - \delta + n\right), \tag{1}$$

the inclusive fitness of the laterborn

$$F_2 = \frac{1}{2} f\left(\frac{1}{2} + \delta + n\right) + f\left(\frac{1}{2} - \delta + n\right), \tag{2}$$

and the inclusive fitness of their mother

$$F_M = \frac{1}{2} f\left(\frac{1}{2} + \delta + n\right) + \frac{1}{2} f\left(\frac{1}{2} - \delta + n\right). \tag{3}$$

1.1.1 The firstborn always prefers deviation from the fair split

Even without using power function specifically, we can prove that it is always beneficial for the firstborn to start manipulating the laterborn to lower the consumption of rival resources.

The first derivative of firstborn's inclusive fitness function is

$$\frac{dF_1}{d\delta} = f'\left(\frac{1}{2} + \delta + n\right) - \frac{1}{2} f'\left(\frac{1}{2} - \delta + n\right), \tag{4}$$

where at $\delta = 0$ we have

$$f'\left(\frac{1}{2} + n\right) - \frac{1}{2} f'\left(\frac{1}{2} + n\right) = \frac{1}{2} f'\left(\frac{1}{2} + n\right) > 0 \tag{5}$$

because $f'(x) > 0$. Thus, the inclusive fitness of the firstborn is always increasing at $r_1 = 0.5$, meaning it is always beneficial for the firstborn to manipulate the laterborn at least a little into reducing the consumption of rival resources. This is true even if the returns from the direct fitness function are diminishing, e.g. when the returns exponent $a < 1$ in $f(x) = x^a$ (Fig. 1, Fig. S1A).

1.1.2 The mother prefers equal split for diminishing returns and exclusive allocation for increasing returns

When we focus on the mother's inclusive fitness (3), we can show that the first derivative is always 0 at the fair split, because the function is symmetric with respect to the two offspring. The derivative is

$$\frac{dF_M}{d\delta} = \frac{1}{2} f'\left(\frac{1}{2} + \delta + n\right) - \frac{1}{2} f'\left(\frac{1}{2} - \delta + n\right), \tag{6}$$

and at $\delta = 0$ we have

$$f'\left(\frac{1}{2}+n\right) - f'\left(\frac{1}{2}+n\right) = 0. \tag{7}$$

The second derivative determines the mother's preference for resource distribution between the offspring. If it is positive, the mother prefers exclusive allocation to one offspring because the inclusive fitness function is convex at $\delta = 0$. When it is negative at $\delta = 0$, the inclusive fitness function is concave, and the mother prefers an equal split of resources between the two offspring.

When using $f(x) = x^a$, the first derivative of the Mother's inclusive fitness function is

$$\frac{dF_M}{d\delta} = \frac{1}{2}a\left(\frac{1}{2}+\delta+n\right)^{a-1} - \frac{1}{2}a\left(\frac{1}{2}-\delta+n\right)^{a-1}. \tag{8}$$

We observe that the condition $\frac{dF_M}{d\delta} = 0$ is also satisfied for any value of δ when $a = 1$. Thus, with a linear direct fitness function, the mother is entirely indifferent to the allocation of rival resources between offspring, as her inclusive fitness remains constant (Fig. 2A).

The second derivative of the function is

$$\frac{d^2F_M}{d\delta^2} = \frac{1}{2}a(a-1)\left(\frac{1}{2}+\delta+n\right)^{a-2} + \frac{1}{2}a(a-1)\left(\frac{1}{2}-\delta+n\right)^{a-2}. \tag{9}$$

Terms $\left(\frac{1}{2}+\delta+n\right)^{a-2}$, $\left(\frac{1}{2}-\delta+n\right)^{a-2}$, and a are always positive for $a > 0$, $n \geq 0$, and $\delta \in \left[0, \frac{1}{2}\right]$. Therefore, the sign of the second derivative is determined by the term $a - 1$ in each product. For $a < 1$ (diminishing returns, Fig. 1, Fig. S1A), the second derivative is negative, indicating that the mother prefers an equal split of resources between offspring. For $a > 1$ (increasing returns, Fig 2. B, Fig. S1C-E), the second derivative is positive, so the mother prefers an exclusive allocation of resources to a single offspring. The relative quantity of non-rival resources n does not affect the mother's perspective on the optimal allocation of rival resources in the Crusader model, because her inclusive fitness function is symmetrical with respect to each offspring.

1.1.3 When the laterborn stops resisting

By immediately deviating from an equal split, the younger brother's inclusive fitness always decreases. The situation is symmetrical to why the firstborn always benefits from at least a tiny deviation from the fair split. At $\delta = 0$,

$$\frac{dF_2}{d\delta} = -\frac{1}{2}f'\left(\frac{1}{2}+n\right). \tag{10}$$

For increasing returns functions, however, there may be a critical point where it becomes advantageous for the younger brother to stop resisting manipulation and instead collaborate in allocating more rival resources to the firstborn. This shift occurs when half of firstborn's gain from additional resources surpasses the full gain that the laterborn could expect (i.e. when the first derivative of laterborn's inclusive fitness function is equal to 0). We express this critical point with δ as the deviation from an equal split of resources,

$$\frac{1}{2}f'\left(\frac{1}{2}+\delta+n\right) > f'\left(\frac{1}{2}-\delta+n\right). \tag{11}$$

We will now show that the multiplication and addition in the general function $f(x) = x^a$ plays no role in the search for this critical point and other similar critical points further in the text.

Let us have direct fitness function $f(x) = bx^a + c$ and use it's derivative $f'(x) = ba(x)^{a-1}$. The derivative of $c = 0$, so we get

$$\frac{1}{2}ab\left(\frac{1}{2}+\delta+n\right)^{a-1} > ab\left(\frac{1}{2}-\delta+n\right)^{a-1} \tag{12}$$

The coefficient b disappears from the equation in the next step where both sides are multiplied by 2 and divided by ab,

$$\left(\frac{1}{2}+\delta+n\right)^{a-1} > 2\left(\frac{1}{2}-\delta+n\right)^{a-1}. \tag{13}$$

We can therefore look for critical points using $f(x) = x^a$, but plot the curves on arbitrary units ($b \neq 1$ in $f(x) = bx^a$) on the y axis. In all figures of this article, we scale the direct fitness functions to $f(0) = 0$ and $f(r+n) = 5$ to evoke a biological interpretation of direct fitness as the average number of offspring surviving into adulthood. (Most likely maximum out of 100 individuals at $\lambda = 5$ is 11 adult offspring with reproduction opportunities.)

We can continue the analysis by taking $a-1$ root of both sides and isolate δ on the left side of the expression to get

$$\delta > \frac{2^{\frac{2-a}{a-1}} - \frac{1}{2} + \left(2^{\frac{1}{a-1}} - 1\right)n}{2^{\frac{1}{a-1}} + 1}. \tag{14}$$

All algebraic steps of this and similar calculations, together with the code that allows to replicate numerical methods, can be found in R Markdown files (and knitted pdfs) at https://osf.io/m9uft/.

By adding this δ to $\frac{1}{2}$ and simplifying the expression, we find that the secondborn starts benefiting from further deviation from the fair split at

$$r_1 = \frac{2^{\frac{1}{a-1}} + \left(2^{\frac{1}{a-1}} - 1\right)n}{2^{\frac{1}{a-1}} + 1}. \tag{15}$$

The critical point is in the accessible range $r_1 \in \left[\frac{1}{2}, 1\right]$ if $\delta < \frac{1}{2}$ and therefore

$$n < \frac{1}{2^{\frac{1}{a-1}} - 1}. \tag{16}$$

We can see that as the importance of non-rival resources increases (Fig. S4P-S), the laterborn is less likely to benefit from the manipulation by the firstborn. It requires a steeper increase in returns (the right-hand-side of the inequality grows as a gets bigger) to allow finding δ for which the laterborn starts benefiting from the manipulation (Fig. S4K-N).

1.1.4 When the laterborn should "manipulate himself"

There are combinations of a and n for which the exclusive allocation of rival resources to the firstborn emerges as the optimal strategy within $r_2 \in \left[0, \frac{1}{2}\right]$ even for the younger brother (Fig. S1C). The condition

$$\frac{1}{2}\left(\frac{1}{2} + n\right)^a + \left(\frac{1}{2} + n\right)^a < \frac{1}{2}(1 + n)^a + n^a \tag{17}$$

is met if rival resources are sufficiently important, and returns are sharply increasing. In such situations, the inclusive fitness of all three actors is maximized when the firstborn gets everything. In the extreme instance of $n = 0$, which is a limiting case of both Crusader and Monk models,

$$\frac{3}{2}\left(\frac{1}{2} + n\right)^a = \frac{1}{2}(1 + n)^a + n^a \tag{18}$$

simplifies to

$$a = \log_2(3). \tag{19}$$

If rival resources alone increase reproduction, it pays off to the laterborn to completely forgo reproduction in favor of the firstborn if the increasing returns function is steeper than $x^{\log_2(3)}$ (Fig. S4O).

If, for instance, total non-rival resources utilized by siblings are half of the rival resources, i.e. $2n = \frac{1}{2}$, $n = \frac{1}{4}$, the critical value of a is impossible to find analytically, because

$$\frac{3}{2}\left(\frac{1}{2} + \frac{1}{4}\right)^a = \frac{1}{2}\left(1 + \frac{1}{4}\right)^a + \left(\frac{1}{4}\right)^a \tag{20}$$

leads onto transcedental equation

$$3^{a+1} = 5^a + 2, \tag{21}$$

which contains exponential functions of different bases. A numerical solution leads onto $a = 2$ (Fig. 3P). Similarly, all (a, n) pairs of secondborn's indifference between no and maximal manipulation can be found (Fig.2C).

We use the Limited-memory BFGS quasi-newton method as implemented in the *optim()* R function, which allows box constraints that contribute to the numerical stability of the search. We start at $n = 0$, where the solution of a_0 can be found analytically, and then look for $a_{n+\Delta}$ within $[a_n, a_n + \varepsilon]$ utilizing the fact that lower importance of rival resources would require steeper increase in returns to offset the difference, i.e. that $a_n < a_{n+\Delta}$ for $\Delta > 0$. We employed $\delta = 0.01$ and $\varepsilon = 1$, but any combination of ε >> Δ is equally valid and renders identical results.

1.1.5 When the maximal manipulation is not optimal for the firstborn

If a diminishing returns function describes the direct fitness (for instance when the food and other resources cannot be preserved over longer periods of time, when there is no trade, no means of production to be monopolized, or, alternatively, when there is a strict maximum of the number of wives one can marry) a different dynamic appears (Fig. S3I, M). We search where

$$f'\left(\frac{1}{2} + \delta + n\right) < \frac{1}{2} f'\left(\frac{1}{2} - \delta + n\right) \tag{22}$$

holds and therefore it is beneficial from the perspective of the firstborn’s inclusive fitness to resort from the manipulation and let the laterborn keep some of the rival resources. For the function $f(x) = x^a$ we arrive at

$$\delta > \frac{\frac{1}{2} - 2^{\frac{2-a}{a-1}} + \left(1 - 2^{\frac{1}{a-1}}\right) n}{2^{\frac{1}{a-1}} + 1} \tag{23}$$

Notice that the denominator is the same as in the case of the laterbon’s critical point formula above, but the sign of every term in the numerator is reversed. The functions (14) and (23) are symmetrical with respect to the vertical line $a = 1$.

The corresponding $r_1 = \frac{1}{2} + \delta$ is

$$r_1 = \frac{1 + \left(1 - 2^{\frac{1}{a-1}}\right) n}{2^{\frac{1}{a-1}} + 1} \tag{24}$$

and finding such a point in $\delta < \frac{1}{2}$ is possible if

$$n < \frac{2^{\frac{1}{a-1}}}{1 - 2^{\frac{1}{a-1}}} \tag{25}$$

1.1.6 When the maximal manipulation renders the same outcome as the fair split

Similarly as with laterborn's indifference to manipulation, we can define a situation where the firstborn's inclusive fitness is equal if he manipulates maximally (and monopolizes all rival resources) or not at all (which results in the fair split).

Solving

$$\frac{3}{2}\left(\frac{1}{2}+n\right)^{a} = (1+n)^{a} + \frac{1}{2}n^{a} \tag{26}$$

analytically is, again, impossible in most cases, but for $n = 0$ (Fig. 3L) we arrive at

$$a = \log_2(3) - 1 \tag{27}$$

Again, $n = \frac{1}{4}$ (Fig. S3J) and other cases lead onto transcendental equations, but their solutions can be found numerically. Here we employed Brent's method from the *optimize()* R function (prompted through *optim()*), which showed sufficient numerical stability. The same numerical methods can be used to find n for given a. For very small a, such as $a = 10^{-10}$, $n \approx 0.309$, but for $a = 0$ the equality (26) holds for any n. Note that the equation cannot be mirrored to match (a, n) solutions of (18).

Using expressions (9), (16), (18), (25), and (26) we can define boundaries between the regions of the (a, n) parameter space that define the optimal behaviour of each actor (Fig. 2, Fig. S2).

1.1.7 When returns increase exponentially

If the exponential function $f(x) = e^{x}$ is used in the Crusader model, most statements about increasing returns functions hold. It is possible to find a point where the laterborn benefits from the allocation of resources to the firstborn but, interestingly, this point no longer depends on the importance of non-rival resources n.

The derivative of e^{x} is e^{x} so when looking for a point where half of firstborn's benefit exceeds the full benefit of the laterborn (11), we get

$$\frac{1}{2}e^{\frac{1}{2}+\delta+n} > e^{\frac{1}{2}-\delta+n}, \tag{28}$$

where we can divide both sides by $e^{\frac{1}{2}}e^{n}$ to obtain

$$e^{\delta} > 2e^{-\delta}. \tag{29}$$

Now we can see, why exponential direct fitness function makes non-rival resources irrelevant in the Crusader model (Fig S1D,E).

We can find the solution of (29) by rewriting $e^{-\delta}$ as $\frac{1}{e^{\delta}}$ and simplifying to

$$\delta > \frac{\ln(2)}{2}. \tag{30}$$

The laterborn always stops resisting the manipulation at

$$r_1 = \frac{1 + \ln(2)}{2} \tag{31}$$

if the reproductive returns grow exponentially with resources and if the manipulation has no effect on the conversion of non-rival resources to offspring.

1.2 Monk model

We can arrive at similar conclusions with the Monk model. The Monk model reflects that manipulation of the laterborn may compromise his capacity to convert non-rival resources to offspring (e.g. when manipulation triggers exclusively homosexual preferences). Using the power function $f(x) = x^a$, the inclusive fitness functions of individual actors are:

$$F_1 = \left(\frac{1 + m + 2n}{2}\right)^a + \frac{1}{2}\left(\frac{(1 - m)(1 + 2n)}{2}\right)^a \tag{32}$$

$$F_2 = \frac{1}{2}\left(\frac{1 + m + 2n}{2}\right)^a + \left(\frac{(1 - m)(1 + 2n)}{2}\right)^a \tag{33}$$

$$F_M = \frac{1}{2}\left(\frac{1 + m + 2n}{2}\right)^a + \frac{1}{2}\left(\frac{(1 - m)(1 + 2n)}{2}\right)^a \tag{34}$$

And their first derivatives:

$$\frac{dF_1}{dm} = \frac{a}{2}\left(\frac{1 + m + 2n}{2}\right)^{a-1} - a \cdot \frac{1 + 2n}{4}\left(\frac{(1 - m)(1 + 2n)}{2}\right)^{a-1} \tag{35}$$

$$\frac{dF_2}{dm} = \frac{a}{4}\left(\frac{1 + m + 2n}{2}\right)^{a-1} - a \cdot \frac{1 + 2n}{2}\left(\frac{(1 - m)(1 + 2n)}{2}\right)^{a-1} \tag{36}$$

$$\frac{dF_M}{dm} = \frac{a}{4}\left(\frac{1 + m + 2n}{2}\right)^{a-1} - a \cdot \frac{1 + 2n}{4}\left(\frac{(1 - m)(1 + 2n)}{2}\right)^{a-1} \tag{37}$$

Notice that the symmetry of fitness functions is disrupted because the firstborn’s ability to utilize non-rival resources does not depend on m, but if $m = 1$, i.e. when the manipulation is maximal, the direct fitness of the laterborn is $f(0)$. In our model, the functions are scaled to $f(0) = 0$. Again, potential parameters b and c in the direct fitness function $f(x) = bx^a + c$ play no role in the analysis of critical and indifference points.

1.2.1 Critical points and their availability

By setting the first derivatives to zero, we can find critical points for each actor. We reveal that the critical points are at

$$m_{F_1} = 1 - \frac{2^{\frac{a}{a-1}}(1+n)}{2^{\frac{1}{a-1}} + (1+2n)^{\frac{a}{a-1}}}, \tag{38}$$

$$m_{F_2} = 1 - \frac{2^{\frac{a-2}{a-1}}(1+n)}{2^{-\frac{1}{a-1}} + (1+2n)^{\frac{a}{a-1}}}, \tag{39}$$

$$m_{F_M} = 1 - \frac{2+2n}{1 + (1+2n)^{\frac{a}{a-1}}}. \tag{40}$$

It is easy to show that $m < 1$ for any combination of a and n in all three equations. There is, however, always a region, where the critical point cannot be achieved because that would require negative m. For the firstborn, $m > 0$ when $a > 1$ and $n > \frac{1}{2}$ or when $a < 1$ and $n < \frac{1}{2}$. For $a = 0$, the m equations above and other related expressions are not defined because $a - 1$ implies division by 0 and there is no critical point for any of the actors.

The $a = 1$ line constitutes a sign flipping boundary for other actors as well. For laterborn, $m > 0$ when $n > -\frac{1}{4}$ and $a > 1$ or when $n < -\frac{1}{4}$ for $a < 1$. For the mother, $m > 0$ when $a > 1$ and $n > 0$ or when $a < 1$ and $n < 0$. Because n must be equal or greater than 0, a critical point (minimum) is always available in the laterborn's and mother's inclusive fitness functions for increasing returns ($a > 1$) and unavailabe otherwise.

Critical point for each m can be expressed on the scale of r_1 as

$$r_1 = \frac{1+m}{2} \tag{41}$$

which leads to

$$r_{1,F_1} = 1 - \frac{2^{\frac{a}{a-1}}(1+n)}{2^{\frac{a}{a-1}} + 2(1+2n)^{\frac{a}{a-1}}}, \tag{42}$$

$$r_{1,F_2} = 1 - \frac{2^{\frac{a-2}{a-1}}(1+n)}{2^{\frac{a-2}{a-1}} + 2(1+2n)^{\frac{a}{a-1}}}, \tag{43}$$

$$r_{1,F_M} = 1 - \frac{2+2n}{2 + 2(1+2n)^{\frac{a}{a-1}}}. \tag{44}$$

By analyzing second derivatives of inclusive fitness functions such as

$$\frac{d^2F_1}{dm^2} = \frac{a(a-1)}{4}\left(\frac{1+m+2n}{2}\right)^{a-2} + \frac{a(a-1)(1+2n)^2}{8}\left(\frac{(1-m)(1+2n)}{2}\right)^{a-2}, \tag{45}$$

(equivalent functions of other actors differ only in integer denominators of fractions before parentheses) it is possible to show that the only element that decides the sign of the whole expression is $a-1$ as in equation (9) of the Crusader model. All inclusive fitness functions are therefore convex for $a > 1$ and concave for $a < 1$. This fact can guide the interpretations of critical point availability in Fig. 2 without explicitly plotting the fitness functions (but we do this anyway in supplementary Fig. S5).

1.2.2 The indifference between the maximal and no manipulation

In the Monk model, indifference lines between the maximal and no manipulation can be found analytically (yellow, black, and purple boundary lines in the left columns of Fig. 2 and Fig. S2). Expressed as relationships between n and a, they are:

$$n_{F_1} = \frac{3^{\frac{1}{a}} - 2^{\frac{1+a}{a}}}{2^{\frac{1+a}{a}} - 2\cdot 3^{\frac{1}{a}}}, \tag{46}$$

$$n_{F_2} = \frac{2 - 3^{\frac{1}{a}}}{2\cdot 3^{\frac{1}{a}} - 2}, \tag{47}$$

$$n_{F_M} = \frac{1 - 2^{\frac{1-a}{a}}}{2^{\frac{1}{a}} - 1}. \tag{48}$$

We can solve given functions for $n = 0$ to find minimal a for which the equality can be achieved:

$$a_{n_0,F_1} = \log_2(3) - 1, a_{n_0,F_2} = \log_2(3), a_{n_0,F_M} = 1 \tag{49}$$

The results are equivalent to the Crusader model, because both models are identical for the $n = 0$ limiting case.

1.2.3 Exponential returns

In the Monk model, critical points do depend on non-rival resources n under the assumption of exponentially increasing returns (Fig S1D vs Fig. S1F). The reason is in the presence of the mn product in the laterborn's direct fitness. The exponential returns situation therefore resembles the power series with increasing returns. The critical points can be calculated from the following equations:

$$m_{F_1} = \frac{\ln\left(\frac{1+2n}{2}\right)}{1+n}, m_{F_2} = \frac{\ln(2+4n)}{1+n}, m_{F_M} = \frac{\ln(1+2n)}{1+n} \tag{50}$$

We will not pursue this line of analysis further, because the precise difference between models with power and exponential functions is not the focus of this paper.

2 Additional examples and visualizations

2.1 Limiting case examples ($n = 0$) and exponential returns examples

When there are no important non-rival resources ($n = 0$) both models are identical (Fig. S1, A-C).

If the exponential function is employed to represent increasing returns in the Crusader model, non-rival resources play no role (Fig. S1D, Fig. S1E). However, if the laterborn's ability to convert non-rival resources into offspring is influenced by the manipulation, as in the Monk model, non-rival resources (n) become influential again (Fig. S1D, Fig. S1F). Higher importance of non-rival resources decreases the benefits of manipulation as in the Monk model with the power function direct fitness (Fig. S5).

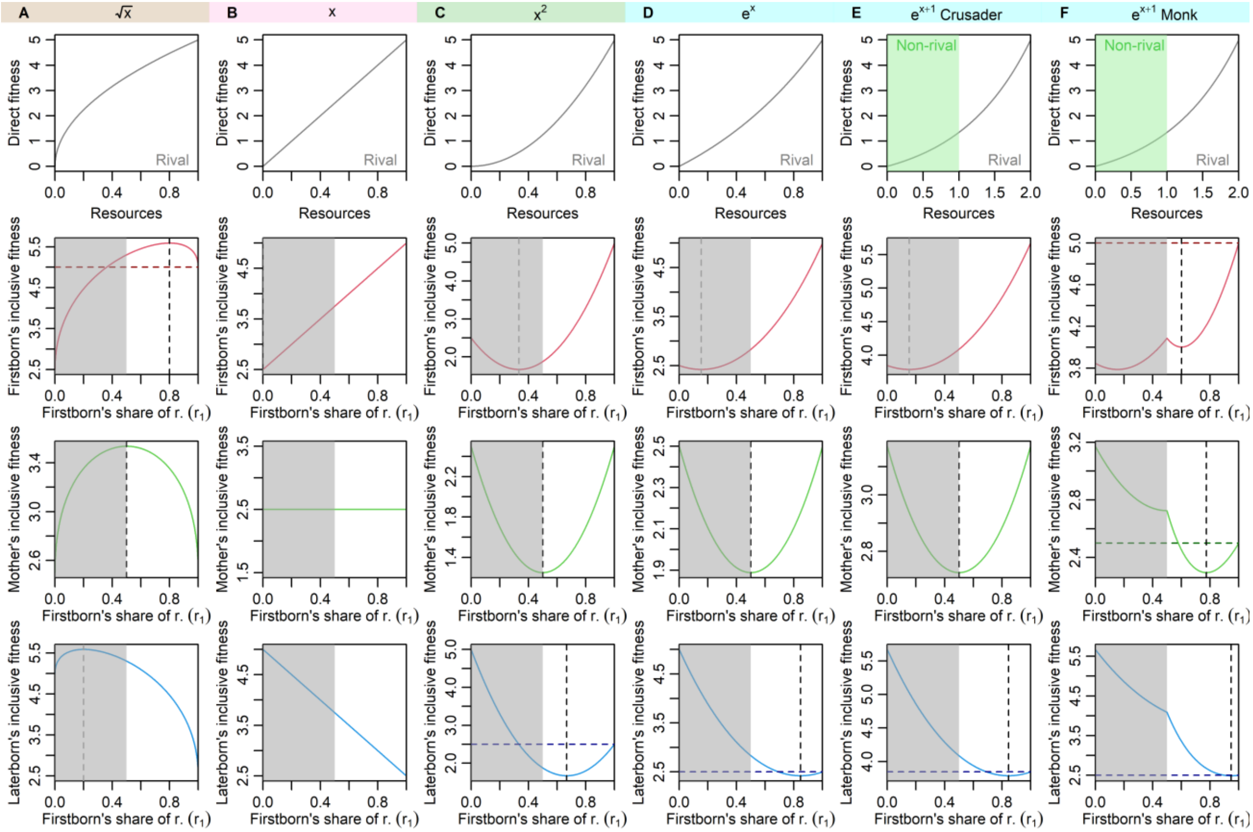


Fig. S1. Direct fitness functions and their implications for inclusive fitness in borderline cases with the exclusive importance of rival resources ($n = 0$, A-C) and exponentially increasing returns (D-F). The first row of panels displays direct fitness functions. It is the power function, that is, a function in the form $f(x) = x^a$ (A-C), or an exponential function $f(x) = e^x$ (D-F). This row illustrates the dependence of the number of offspring on the amount of resources available to an individual. The subsequent rows depict the implications of given direct fitness function for the inclusive fitness of the firstborn, the mother, and the laterborn over the range of values corresponding to the firstborn's rival resources share, $r_1 \in [0,1]$. When the critical point, a minimum or maximum ($F_i'(r_1 + n) = 0$), is achievable within $r_1 \in [0.5,1]$ (white), it is marked by a black dashed line. In each firstborn's or laterborn's inclusive fitness, the extreme $F_i(1 + n)$ is intersected with a horizontal line to mark the corresponding indifference point on the other side of the minimum or maximum. Unachievable scenarios $r_1 \in [0,0.5]$ (grey) are displayed for the clarity of functions' (a)symmetry.

2.2 The extended map of examples

This is an equivalent of Fig. 2 from the main article that shows, which points in the parameter space are occupied by examples in Supplement 2.

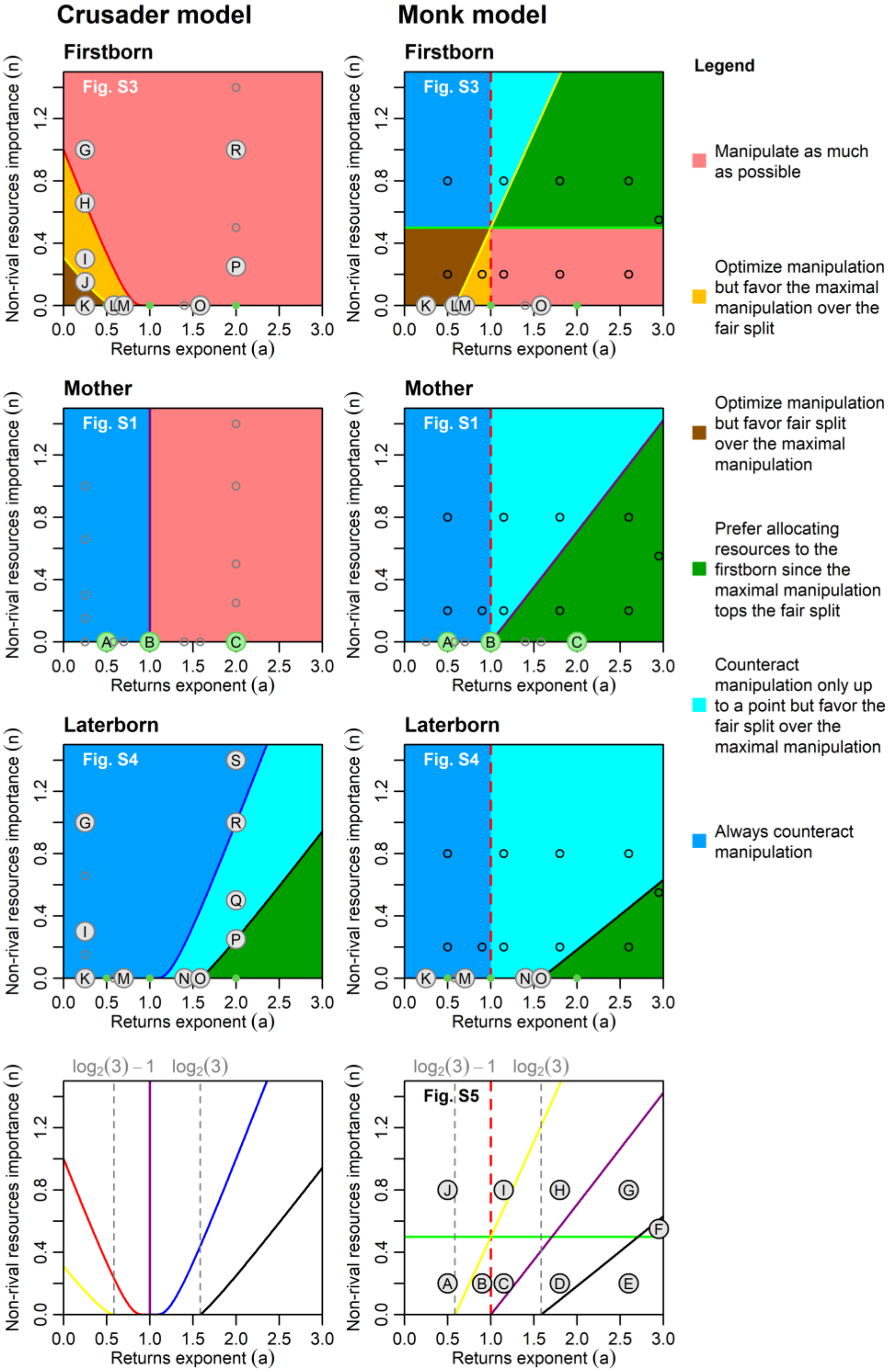


Fig. S2. Boundaries between optimal strategies for each model and actor in a parameter space of a (returns exponent in the direct fitness function $f(x) = x^a$) and n (importance of non-rival resources relative to rival resources $r = 1$) The bottom panels show all boundaries plotted together. Letters denote plots that are used to illustrate typical or borderline cases. **Crusader model:** U-shaped progression from the quadrant with important non-rival resources and diminishing returns through important rival resources and diminishing returns, important rival resources and increasing returns, and finally important non-rival resources and increasing returns. Cases in the mother's plot (A-C) are depicted for every actor in Fig. S1. Other cases (G-S) are shown for one of the brothers or both of them in Figs. S3-S4. Redundant or less interesting cases that are omitted to save space are presented as dots for easier orientation in the whole set of examples. **Monk model:** For $n = 0$ the model is equivalent to the Crusader and corresponding plots can be localized in Figures S1,S3, or S4 (see the top-right corner or each panel). Letters in the bottom panel (and black circles in the other panels) denote plots illustrating typical $n > 0$ cases for each delineated segment (Fig. S5).

2.3 Example inclusive fitness functions in the Crusader model

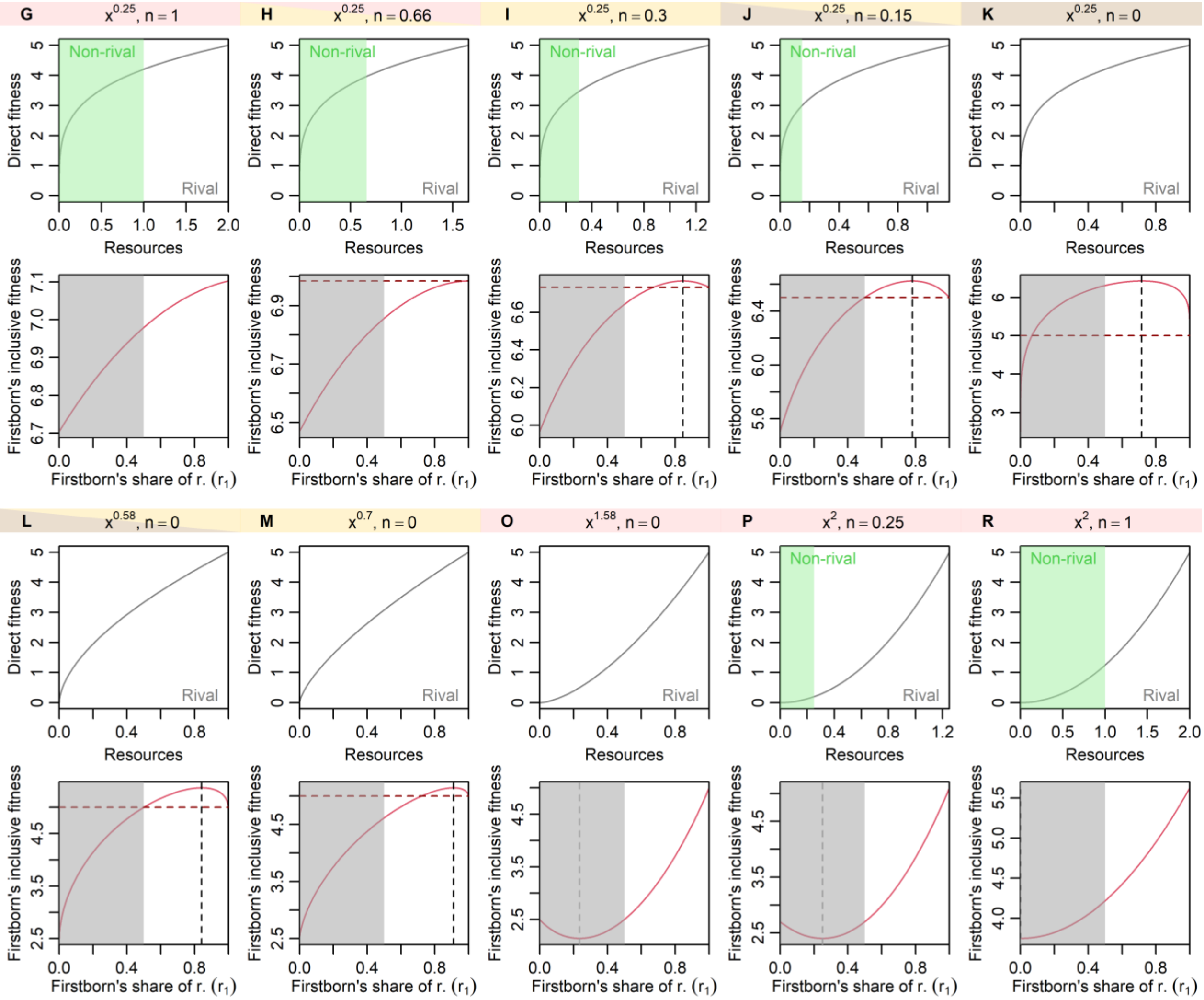


Fig. S3. Examples of the fitness function $f(x) = x^a$ for different values of a that illustrate typical and borderline optimal decisions of the firstborn in the Crusader model. Only direct fitness and firstborn's inclusive fitness are shown. See Fig. S2 for the positions of the examples in parameter space. In the case of diminishing returns ($a < 1$) and the high importance of non-rival resources (high n), firstborn has nothing to lose by diverting all rival resources from the laterborn to self (G). As rival resources gain importance, the critical point (maximum) at which it pays to refrain from manipulation and allow the laterborn to keep a part of rival resources emerges on the boundary (H) and gets within the achievable range (I) of the firstborn's inclusive fitness function. As the importance of non-rival resources decreases further, the firstborn becomes indifferent between no and maximal manipulation (J), and gradually starts preferring the former to the latter (K) because it promises higher inclusive fitness. Manipulation becomes a risky game then, but the firstborn's inclusive fitness first derivative is still positive at $r_1 = 0.5$, which suggests that there is an incentive to attempt an optimized manipulation of resource allocation. With the increase in a, this situation turns to manipulation-inviting indifference (L) and the preference of maximal manipulation over the fair split (M). With increasing returns ($a > 1$) the inclusive fitness function becomes convex and the firstborn starts preferring maximal manipulation over any intermediate strategy regardless of the importance of non-rival resources (O-R).

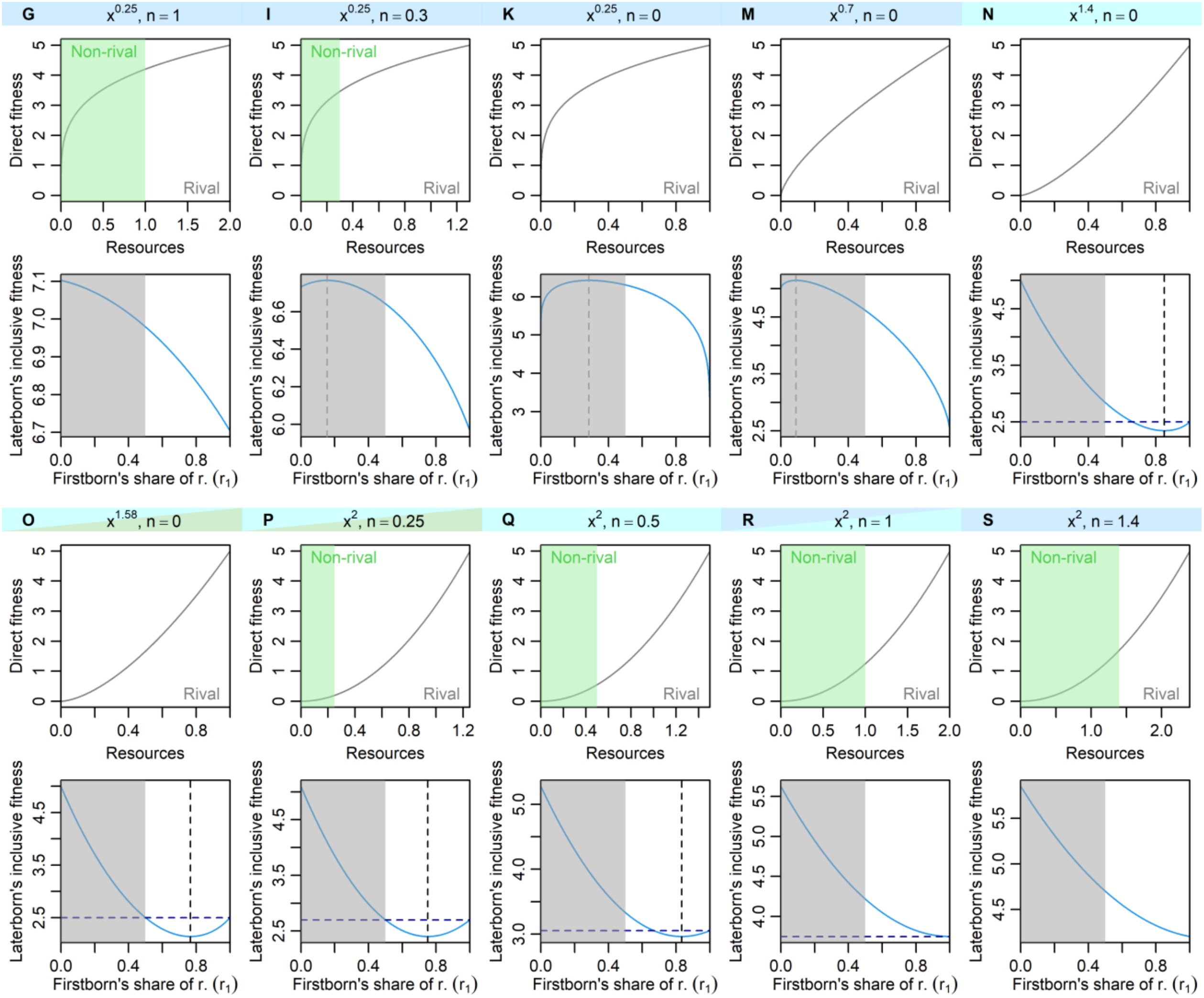
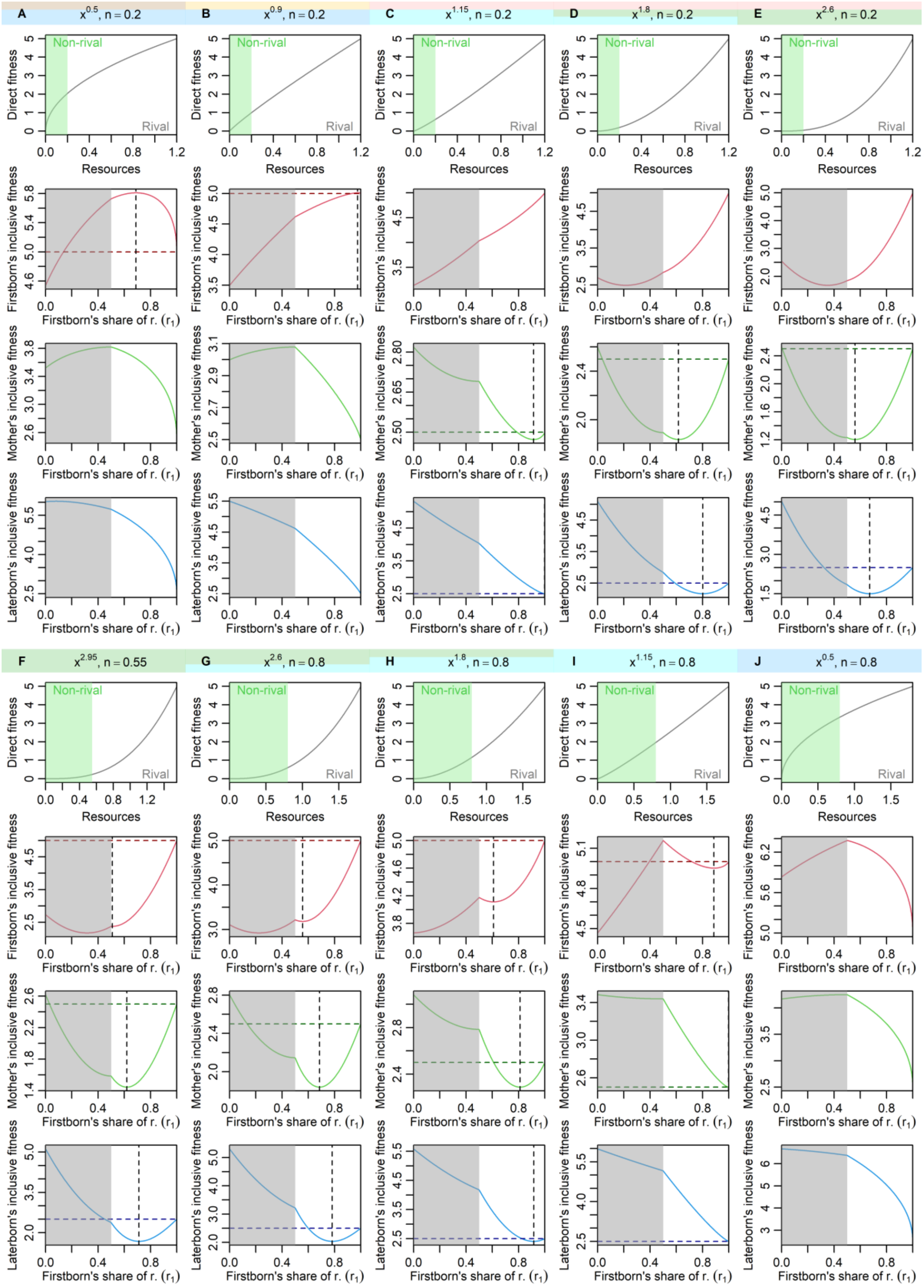


Fig. S4. Examples of the fitness function $f(x) = x^a$ for different values of a that illustrate typical and borderline optimal decisions of the laterborn in the Crusader model. Only direct fitness and the laterborn's inclusive fitness are shown. See Fig. S2 for the positions of the examples in parameter space. Regardless of the amount of non-rival resources (G-K), the laterborn does not benefit from the allocation of rival resources to the firstborn if the direct fitness function shows diminishing returns ($a < 1$, M) and should therefore attempt to resist the manipulation. If, however, an increasing returns function characterizes the direct fitness, it is often possible to find a critical point (minimum) after which the laterborn's inclusive fitness starts growing with a further deviation from the fair split (N). With even sharper increase in returns (higher a) the function's profile suggests the laterborn's indifference between the fair split and the maximal manipulation (O). If the importance of non-rival resources increases, a must also increase to keep the indifference (P). If a increases further at given n (Fig. S1C) the laterborn starts preferring maximal manipulation over the fair split. If the returns function does not change but the importance of non-rival resources increases, the indifference is lost in favour of the fair split (Q) and gradually, the critical point reaches the achievable boundary (R) before it gives way, again, to a function which implies incentive to universally resist potential manipulation (S).

2.4 Example inclusive fitness functions in the Monk model

Fig. S5. (Next page) Examples of fitness function $f(x) = x^a$ and their implications for inclusive fitness of all actors for different values of a and n in the Monk model. The examples illustrate typical cases for each delineated segment in Fig S2. Optimal strategies are indicated by the colour code in the heading (top: firstborn, middle: mother, bottom: laterborn). When fitness returns are diminishing ($a < 1$) with investment and the total non-rival resources obtained by the brothers ($2n$) are less than the rival resources they need to split, it does not pay for the firstborn to manipulate the laterborn's direct fitness to 0, rather there is a manipulation optimum between $m = 0$ and $m = 1$. This optimum is closer to the fair split for larger n and smaller a (A), but as the importance of non-rival resource decreases (n gets smaller) or returns diminish less (a gets larger), the maximal manipulation becomes more favourable of the two (B). For the laterborn and the mother, there is no change – they should resist any deviation from the fair split at this point. If the amount of non-rival resources does not change but returns start to increase with invested resources ($a > 0$) the incentive to manipulate as much as possible emerges for the firstborn (C), the laterborn and the mother do not share this incentive as they still prefer the fair split over the exclusive allocation of resources. A critical point, however, comes within reach of their fitness functions. If the firstborn can secure a share of rival resources beyond the critical point, their inclusive fitness starts growing again and they shall no longer resist further deviation from the fair split. Since the critical point (the minimum) is closer to the fair split in the mother's inclusive fitness, she quickly moves to a region of parameter space (with higher a or lower n) where maximal manipulation is preferred over the fair split regardless of the laterborn's direct fitness sacrifice (D). With further increase of rival resource importance (smaller n) of steeper increase in returns (larger a), the same becomes true even for the laterborn (E). In situations with very steep increase in returns and high importance of non-rival resources, we can observe the same function profile for all three actors (F), their inclusive fitness functions are convex and their derivation close to the fair split is negative. The critical minimum is, however, closest to the fair split in the firstborn's inclusive fitness, so he is still the one who is most incentivized to trade off all brother's reproduction for the opportunity to monopolize rival resources. With further increase in non-rival resource importance (larger n) and/or relative decrease in investment returns (lower a) first the laterborn (G), then the mother (H), and finally the firstborn himself (I) move to situation where the fair split would be preferred over the maximal manipulation. If the linear fitness function ($a = 1$) is crossed to the region of diminishing returns but the importance of non-rival resource remains high, we can find all relatives aligned stably on the fair split as it promises the highest inclusive fitness with a negative first derivative (J).


A
$x^{0.5}$, n = 0.2
B
$x^{0.9}$, n = 0.2
C
$x^{1.15}$, n = 0.2
D
$x^{1.8}$, n = 0.2
E
$x^{2.6}$, n = 0.2
F
$x^{2.95}$, n = 0.55
G
$x^{2.6}$, n = 0.8
H
$x^{1.8}$, n = 0.8
I
$x^{1.15}$, n = 0.8
J
$x^{0.5}$, n = 0.8
Non-rival
Rival
Direct fitness
Resources
Firstborn's inclusive fitness
Mother's inclusive fitness
Laterborn's inclusive fitness
Firstborn's share of r. (r_1)
0.0
0.4
0.8
1.2
0.5
1.0
1.5

3 Where may increasing returns come from

3.1 Investment

We will start with a straightforward example. Banks often offer clients better interest rates for larger investments. It is possible that many natural phenomena exhibit similar behavior for various reasons.

Let us denote the interest rate as I and model it as a growing function with a saturation value, represented by a part of a logistic function multiplied by $I_{\max}$:

$$I = I_{\max} \cdot \left(\frac{2e^{w}}{1+e^{w}} - 1\right), \tag{51}$$

where w is the wealth invested (Fig. S6A,D), we use $I_{\max} = 3$ in the figure so the maximal annual interest rate is 3%).

We assume that individuals invest all their wealth (everyone keeps constant resources for sustenance, so 0 does not imply starvation but rather no investment) and observe the returns after $t = 10$ years. We subtract the original wealth from the result so that the means of production remain unchanged and can be transferred to offspring. We assume that any additional profit is converted into reproductive success. The function we get is

$$F(w) = w \cdot \left(1 + \frac{I(w)}{100}\right)^{t} - w, \tag{52}$$

which is indeed an increasing returns function (Fig. S6B,E). Initially, it closely resembles a scaled power function x^2 because the growth of $I(w)$ is nearly linear for $w \in [0,1]$ (Fig. 62C). However, as w increases and $I(w)$ reaches $I_{\max}$, the function becomes linear (Fig. S6F).

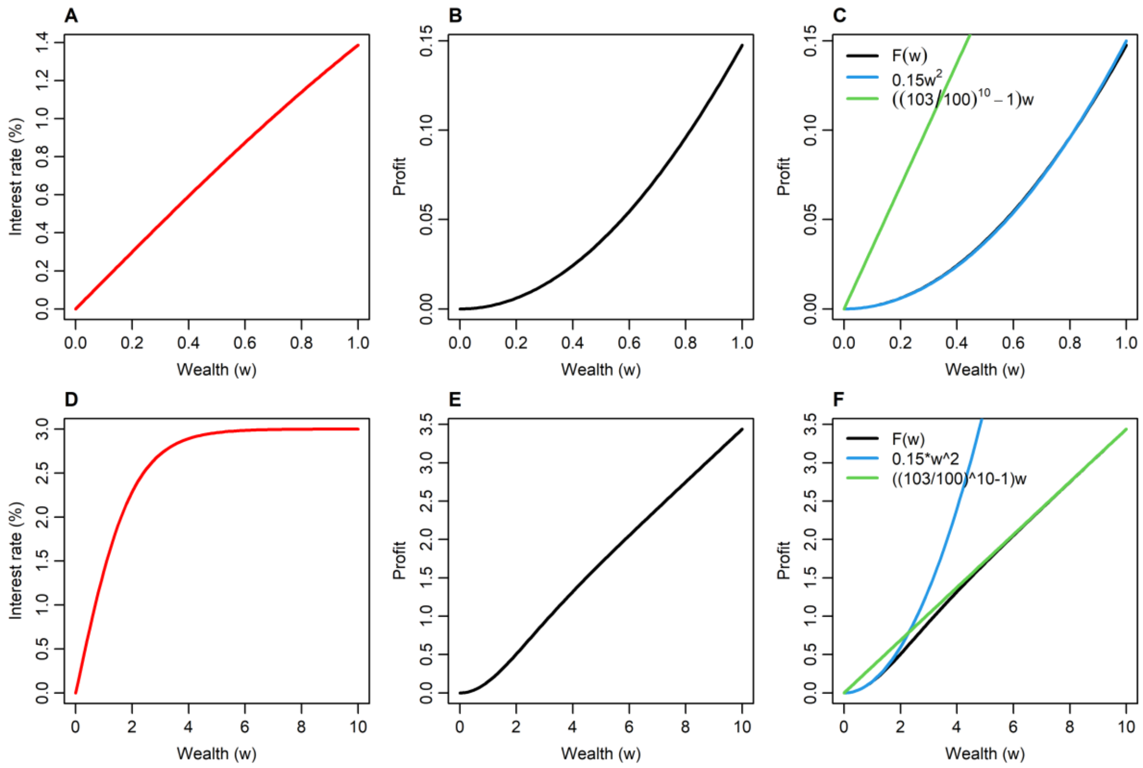


Fig. S6. Simple investment example with an increasing returns part that culminates in a linear relationship between wealth and returns that can be converted to offspring. Quadratic (blue) and linear (green) functions in the right column approximate the fitness function's behavior for small (quadratic) and large (linear) values of w. The top and bottom rows contain the same functions on different scales: top, $w \in [0,1]$; bottom, $w \in [0,10]$.

3.2 Agriculture

An example of an ecologically valid increasing returns strategy is horticulture or agriculture, so we will focus on a hypothetical society that has undergone the Neolithic Revolution. In agriculture, maintaining and harvesting an additional acre of land requires diminishing costs (e.g., it can be managed with the same equipment) but provides a constant yield.

If the function of managing a land of size s is

$$c = qs^{a}, \tag{53}$$

where $a < 1$, and the yield is $b = ps$, the returns are

$$R = ps - qs^{a}, \tag{54}$$

which simplifies to

$$R = s(p - qs^{a-1}). \tag{55}$$

As shown in Fig. S7C, the resulting function starts as a decreasing returns function but then transitions into an increasing returns function that eventually becomes indistinguishable from a linear function. We have a situation similar with the investment. As s approaches infinity, s^{a-1} with $a < 1$ approaches zero, and the returns become linear.

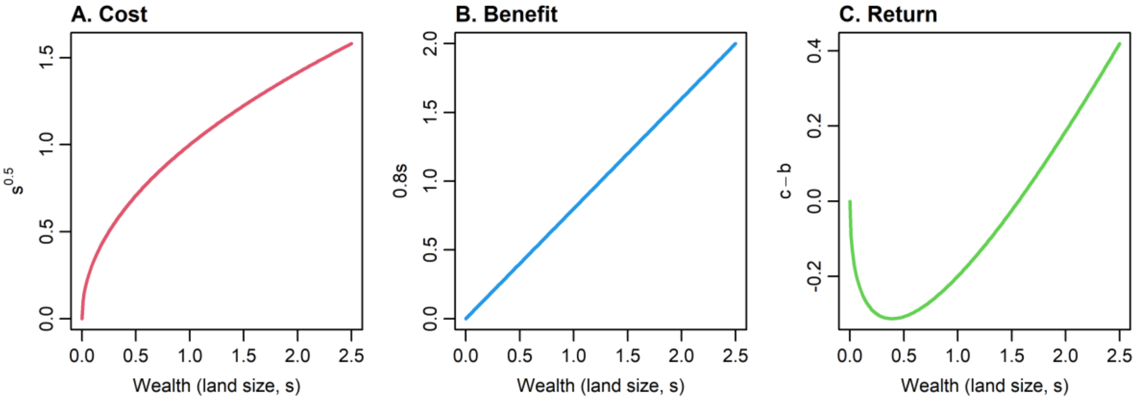


Fig. S7. Simple agricultural example with an increasing returns part that culminates in a linear relationship between wealth and returns.

The agricultural example may not be ideal when we aim to find a function that can be easily approximated by a power function with $a > 1$ over the whole definition domain—at least in this simplified parametrization. The reason why agricultural families choose not to split inheritance and keep the land together may not be because of increasing returns. It may be caused by the fact that because below a certain threshold, it does not pay to farm the land at all. (Other possibilities would emerge if benefits did increase with wealth – perhaps because larger fields offer greater security and resilience against unpredictable events.)

Our model allows to formulate viable predictions for agricultural societies even if the relationship between wealth and benefit is linear. Exclusive primogeniture (where the laterborn can expect to get nothing) and homosexuality should be present in poorer societies (small amount of land per individual) or in lower strata of a society, where the $-\frac{1}{s^{1-a}}$ term is relatively high. This causes a more pronounced increase in returns as described by the function (Fig. S7C). In rich societies (where all s are high) or in the high social strata (family-wise s high), where the relationship between wealth and wealth revenues is close to linear, the division of inherited wealth (probably still unequal with respect to the birth order) should be more common.

Note that the mother is indifferent to the allocation of resources if returns increase linearly, but the firstborn still prefers the exclusive allocation of rival resources if it does not limit the laterborn's capacity to convert non-rival resources to offspring (Crusader model). Therefore, primogeniture—as a result of sibling rather than parental manipulation—can still be prevalent in rich agricultural societies. Homosexuality (Monk model) should be less common, especially if non-rival resources play an important role or if the overall relationship between wealth and direct fitness is sublinear for reasons such as socially regulated maximum number of wives, or steeply diminishing fitness returns to additional wives [1].

3.3 Pastoralism

One might think that pastoral societies are good candidates for the presence of an increasing returns function due to the power function occurring in their subsistence strategy. Suppose the growth rate of a herd is 10% per year. The herd size after 10 years increases to $1.1^{10} \approx 2.6$ of the original size. Potential returns that can be converted to offspring are then $1.1^{10} - 1 \approx 1.6$, because the original herd size is preserved and can still be used to generate revenue.

However, notice that if such a herd is split between two sons, the growth rate of the herd is not halved, so the returns are not halved either:

$$\frac{1}{2} \cdot 1.1^{10} - \frac{1}{2} + \frac{1}{2} \cdot 1.1^{10} - \frac{1}{2} = 1.1^{10}\left(\frac{1}{2} + \frac{1}{2}\right) - 1 = 1.1^{10} - 1 = 1.6. \tag{56}$$

The original herd size does not occur under the exponent in this function, which makes the returns grow linearly with resources.

To ensure that the rich not only get richer, but that they get richer disproportionately (which would make splitting the herd between the sons unprofitable), the model would need to contain another term (perhaps one describing that larger herds exhibit higher average growth rates, which would make it equivalent to the Investment model in 3.1). This is perhaps true but not necessarily across all scales. Again, delving into details is not the focus of this paper.

If we considered protection of the herd from wolves, building of the fences around pastures (while circumference grows linearly with the diameter, the enclosed area grows quadratically), or herd management in general, we would arrive at a situation that copies the Agriculture model (3.2). Such measures show diminishing costs per animal.

Without too many restrictions, we can say that in pastoral societies, we expect linear rather than increasing returns in the conversion of wealth to offspring. Therefore, the parental manipulation hypothesis does not apply here, and primogeniture is only in the interest of the firstborn. The same can be said about manipulation of the laterborn towards homosexuality. If other effects tilt the linear relationship between wealth and offspring to sublinear (such as a socially reinforced ceiling on the number of wives), there is either a manipulation optimum between the fair split and maximal manipulation (if non-rival resources are unimportant), or all actors including the firstborn align on the fair split (if non-rival resources are important).

3.4 Social Stratification

A prime example of a situation where the conversion of resources to offspring promises increasing returns is a highly wealth-stratified society, where only a fraction of males get to reproduce. (These are assumed to be typically the wealthy ones. The onset of demographic transition—when wealthier families start to limit their reproduction to preserve and enhance their children’s living standards and prestige—has been more an exception than the norm in our evolutionary history. Recent research has shown that in densely populated urban areas, where competition for space is intense, wealthier individuals have currently more offspring than poorer ones [2].)

Consider an example, where typically $100p\%$ of males get to reproduce and each of them sires $2/p$ offspring (half male, half female) to keep the population constant. This is already an increasing returns function (Fig. S8A), but not a smooth one. We will now show how this step function can be turned into a smooth, differentiable increasing returns function, which can be approximated by a power function central to our main models.

The only other parameter needed is the amount of randomness in reproduction, σ. For deterministic reproduction ($\sigma = 0$), the function is step-like, which makes difficult to predict the behavior of actors whose rival wealth is below the reproduction-sufficient threshold. Note that the chance parameter σ should not be confused with non-rival resources n. Non-rival resources are as much a "deterministic" part of wealth as rival resources are. When we speak about a fitness function—even in parts of the article that do not explicitly include any stochastic term—we always assume an expected (or, in other words, average) fitness. Adding a parameter for the system's randomness does not prohibit treating the expected fitness function as a line.

If we have the probability of reproduction p and treat individual wealth relative to the population as percentile $w \in [0,1]$, the propensity for reproduction is $P = w + N(0, \sigma)$, where $N(\mu, \sigma)$ stands for a normal distribution with mean μ and standard deviation σ. The cumulative distribution function of this distribution is

$$\mathrm{CDF}_N(x) = \frac{1}{2}\left(1 + \mathrm{erf}\left(\frac{x-\mu}{\sigma\sqrt{2}}\right)\right), \tag{57}$$

where erf(z) stands for the error function

$$\mathrm{erf}(z) = \frac{2}{\sqrt{\pi}}\int_0^z e^{-t^2}\, dt. \tag{58}$$

Now, the fitness of an individual is $2/p$ if the propensity is above p and 0 otherwise. Based on the cumulative distribution function above, we can define the expected fitness function of an individual with wealth w as

$$F(w) = \frac{2}{p}\left(1 - \frac{1}{2}\left(1 + \mathrm{erf}\left(\frac{1-p-w}{\sigma\sqrt{2}}\right)\right)\right), \tag{59}$$

which can be simplified to

$$F(w) = \frac{1}{p}\left(1 - \mathrm{erf}\left(\frac{1-p-w}{\sigma\sqrt{2}}\right)\right). \tag{60}$$

We can ignore the fact that the stochastic term increases the range of propensity beyond the interval $[0,1]$, because the only thing that matters is the probability that two individuals with wealth percentiles w_1 and w_2 will effectively “swap places” in the “queue” for reproduction. The normal distribution kernel, which directs the swapping is symmetric with respect to μ and independent of w so, on average, proportion p of individuals are still above the threshold $1 - p$.

The advantage of this relatively simple fitness function is that it appeals to intuitive imagination by the two defining parameters of “what proportion of individuals gets to reproduce” (p) and “how much the differences in reproduction are due to chance” (σ). Yet, it can be easily approximated by a power function locally (Fig. S8C) or globally (Fig. S8B).

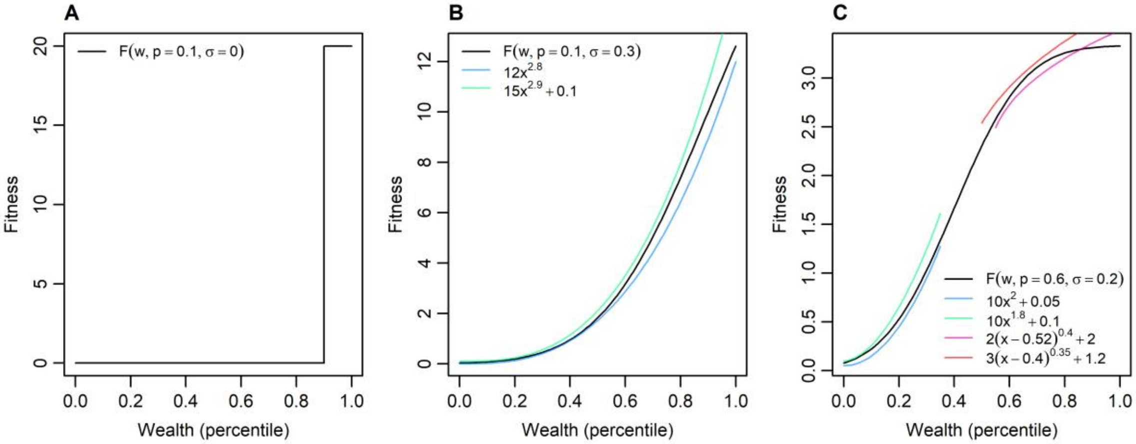


Fig. S8. Fitness function based on the proportion of the male population that gets to reproduce (p) and randomness in reproduction (σ). If $\sigma = 0$ the reproduction is deterministic (A). The function with $\sigma > 0$ can be approximated by a power function globally (B) or locally (C).

In principle, it would be possible to neglect the distinction between rival and non-rival resources and conduct all model analyses within the parameter space of p and σ. However, the results would frequently be conditional on the relative position of each family in the population (Figure S8C). Our original models allow us to make these predictions nevertheless, even if the fitness functions assume more complicated shapes.

Which parametrization is more insightful and useful is a separate question. We believe that the simple model with two types of resources (parameter n) and a single parameter describing the relationship between resources and reproductive outcomes (a) is more useful for predicting real-life phenomena. In nomadic pastoralists, for instance, there is rarely an established cultural institution of homosexual inclusive-fitness specialists (celibate monks, fa’afafines), yet they tend to exhibit a pronounce wealth inequality. It is the profile of fitness returns, not the stratification, that cannot be ignored. The resources-offspring relationship may be close to linear (see section 3.3) or diminishing because of a culturally transmitted ceiling on the number of wives.

3.4.1 It May Be the Other Way Around

Increasing returns functions cause wealth inequality and social stratification, regardless of whether they are linked to fitness. Independently of that, as our models have shown, the direct influence of increasing returns on reproduction may be why primogeniture and/or homosexuality evolves (in the latter case, through both biological and cultural evolution). This is why practices encouraging the exclusive allocation of resources to a single offspring and social stratification may go hand in hand (Fig. S9). Since they also reinforce each other, as we have demonstrated above, it might be difficult to determine precise causality as we discuss further elsewhere.

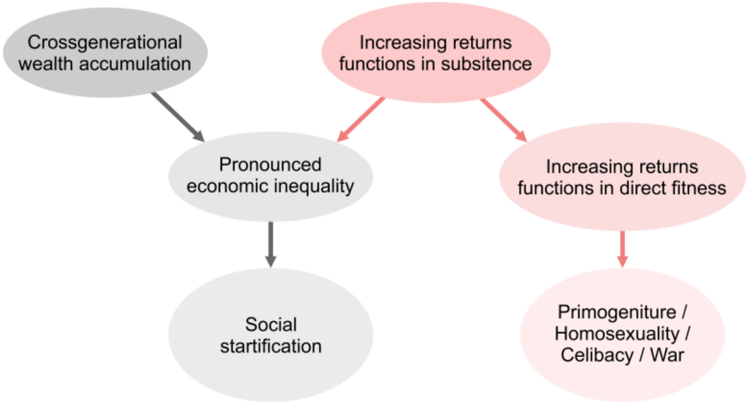


Fig. S9. Potential relationships that give rise to a common link between social stratification and practices like primogeniture and related phenomena without a direct causal link between the two

3.5 Combinatorial Subsistence Strategies

It has been pointed out that the nature of human culture and its associated success is combinatorial [3,4]. Combinatorial systems are excellent candidates for increasing returns direct fitness function.

Imagine that revenues convertible to offspring in a system are created through combinations. These can be combinations of two skills (non-rival resources) that can be put in sequence to create a complex hunting strategy, two professionals employed by the same individual (two rival resources) that can learn how to cooperate, or a piece of land (rival resource) and knowledge about a promising crop (non-rival resource) that are perfect for each other.

Even if we neglect combinations of higher order, the number of possible pairs of controlled resources grows quadratically with the number of resources. The exact relationship is $x(x-1)$ if we do not allow the combination of a resource with itself, and simply x^2 if we do allow that, because, for instance, the sequential reapplication of a skill (non-rival) can craft a qualitatively different product, or the same unique tool (rival) can be used in two different ways during a single procedure.

Even if a tiny fraction of all possible combinations is profitable, the argument holds, because, as we have shown in chapter 1.1.3 of this document, all functions $bx^a + c$ behave identically. Therefore, the evolution of primogeniture and homosexuality in a “cultural animal” such as humans can be fairly straightforward.

4 Supplementary References

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