General Manipulation Theory of Homosexuality

Jaroslav Flegr and Petr Tureček
Department of Philosophy and History of Science, Faculty of Science, Charles University, Prague, Czech Republic

Synonyms

Manipulation hypothesis

Definition

The *General Manipulation Theory of Homosexuality* proposes that male homosexuality is an adaptation or xenoadaptation that serves to increase the inclusive fitness of certain, or sometimes all, family members—including the homosexual individual—under conditions where reproductive success depends supralinearly on access to resources. In such contexts, it may be advantageous to concentrate resources on selected offspring while manipulating others to forgo reproduction or disperse, thereby increasing the inclusive fitness of the manipulator.

Evolutionary Puzzle of Homosexuality

The evolutionary persistence of homosexuality presents a long-standing puzzle. Individuals with exclusive same-sex orientation typically have lower direct reproductive success compared to their heterosexual counterparts (Apostolou 2022, Fořt et al. 2024a), yet homosexual orientation occurs with consistent frequency across cultures and persists over generations. This apparent paradox has led to the proposal of several evolutionary hypotheses that attempt to explain how such a trait could be maintained by natural selection.

Some hypotheses focus on indirect fitness benefits, such as the kin selection hypothesis (Wilson 1975), which suggests that homosexual individuals may enhance the reproductive success of close relatives by helping or providing resources. Others invoke pleiotropic effects, such as the sexually antagonistic selection hypothesis, which posits that genes predisposing to homosexuality may reduce male fertility while increasing female fecundity (Zietsch et al., 2021). The same-sex affiliation hypothesis proposes that homosexual behavior facilitates long-term social alliances, especially in male groups (Kirkpatrick, 2000), while the bisexuality by-product hypothesis (Dewar, 2003) interprets exclusive homosexuality as a nonadaptive side effect of genes promoting bisexuality, which may have reproductive advantages in certain contexts.

Although these theories offer partial explanations, none fully accounts for one of the most

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robust empirical findings in the field—the fraternal birth order effect (FBOE), i.e., the increased likelihood of homosexuality in individuals with older biological brothers. This phenomenon has been replicated across diverse populations and does not depend on postnatal upbringing or cultural environment. The *General Manipulation Theory of Homosexuality* (GMTH) (Tureček et al., 2025) seeks to integrate this pattern into a broader evolutionary framework by proposing that homosexual orientation in some individuals arises from manipulative processes—genetic or physiological—that most likely serve to enhance the inclusive fitness of other family members.

The Fraternal Birth Order Effect

The fraternal birth order effect (FBOE) is one of the most robust and consistently replicated findings in research on male homosexuality (Slater, 1962). It refers to the observation that the probability of a man being homosexual increases with the number of older biological brothers he has. Importantly, this effect is not influenced by postnatal environment or shared upbringing: It is observed regardless of whether the brothers were raised together (Blanchard & Bogaert, 1996).

Meta-analyses have confirmed that the FBOE is statistically significant and culturally widespread (Blanchard et al., 2021). Each additional older brother increases the odds of a man being homosexual by approximately 27% (Blanchard et al., 2021). Critically, the effect is specific to biological older brothers—it is not observed with stepbrothers, adoptive siblings, and older sisters (Bogaert, 2006). This specificity strongly suggests a prenatal mechanism, rather than social or psychological influences. The leading explanation involves a maternal immune response to male-specific proteins expressed during gestation, which may become more pronounced with each successive male pregnancy. This immune response, in turn, could influence the sexual differentiation of the brain in subsequent male fetuses (Blanchard & Klassen, 1997).

Although the FBOE has been most clearly established in men, some recent studies suggest that a parallel, though weaker, birth order effect may also exist among women (Ablaza et al., 2022; Fořt et al., 2024b). In these cases, the presence of older brothers may also be associated with non-heterosexual orientation in women, possibly due to shared developmental mechanisms such as maternal immune reactions to male-specific antigens that cross-react with female neurodevelopmental pathways.

Intriguingly, analogous birth order effects have also been observed in nonhuman animals. For example, a study on laboratory rats found that males born to multiparous mothers—those that had previously carried several male fetuses—exhibited increased levels of same-sex sexual behavior compared to males born to primiparous females (Hernández et al., 2024). These findings raise the possibility that the mechanisms underlying FBOE may have deep evolutionary roots and may operate across species.

Taken together, the consistency, biological specificity, and cross-cultural generalizability of the fraternal birth order effect provide a strong empirical foundation for theories that attribute at least some instances of homosexuality to prenatal influences. These include manipulation-based theories that posit an evolutionary role for such influences in shaping family-level reproductive strategies.

Manipulation-Based Hypotheses

The *General Manipulation Theory of Homosexuality* (GMTH) proposes that same-sex orientation may evolve or be maintained as a consequence of manipulative processes within the family that increase the inclusive fitness of the manipulator. These manipulations can be driven by parents, siblings, or, under certain conditions, the individual's own genes. Crucially, the theory is not limited to sons or to male homosexuality; it may also help explain some cases of female same-sex orientation, provided that the evolutionary logic holds. GMTH was first formally introduced and modeled in (Tureček et al., 2025).

Three main hypotheses fall under the GMTH framework: the *Parental Manipulation*

Hypothesis, the *Sibling Manipulation Hypothesis*, and the *Alternative Reproductive Strategy Hypothesis*.

Parental Manipulation Hypothesis

Parental Manipulation Hypothesis (PMH) (Ruse, 1988; Trivers, 1974) proposes that a mother may increase her inclusive fitness by influencing the development of some of her offspring—often laterborns—in ways that lower their reproductive motivation or ability, allowing her to concentrate resources on others with better reproductive prospects; see also entry "▶ Birth Order: Parental Manipulation Hypothesis" in this encyclopedia. This reduces intrafamily competition and may enhance the total number of grandchildren she produces.

Theoretical modeling shows, however, that such manipulation benefits the mother only if concentrating resources on one or a few children yields disproportionately high reproductive returns—i.e., when the relationship between resources and reproductive success shows increasing returns (e.g., when the first unit of resources allocated to an individual leads on average to producing 1 offspring, another equivalent resource unit must allow producing $x > 1$ offspring) (Tureček et al., 2025). In contrast, if returns diminish with added investment (second unit of resources produces $x < 1$ offspring), equal distribution of resources tends to maximize the mother's inclusive fitness. This constraint limits the scope of environments where parental manipulation is adaptive.

Sibling Manipulation Hypothesis

The Sibling Manipulation Hypothesis (SMH) (Flegr, 2022) proposes that the manipulation originates from the genome of an older sibling, who benefits by lowering the reproductive potential of a younger sibling; see also entry "▶ Sibling Manipulation Hypothesis of Male Homosexuality" in this encyclopedia. This helps the older sibling secure a larger share of rival family resources such as inheritance or parental and grandparental care.

Since full siblings share half of their alleles, modest losses in the manipulated sibling's fitness can be outweighed by larger gains to the manipulator, making such manipulation advantageous in inclusive fitness terms. Importantly, under some conditions, SMH remains adaptive even when reproductive returns slightly diminish with added resources—unlike parental manipulation, which requires increasing returns.

The manipulation may be executed via intermediaries—most plausibly the maternal body, either through immune mechanisms (Bogaert et al., 2018) or microchimerism (Haig, 2014), a process in which fetal cells from earlier pregnancies persist in the mother and then enter later embryos and influence their development, including potentially their brain development.

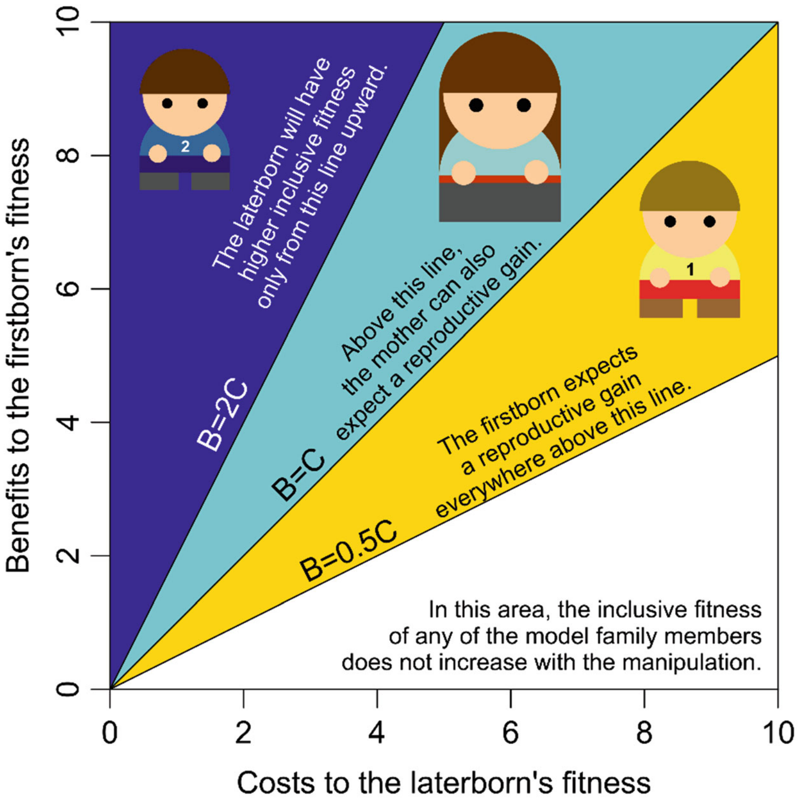
SMH also provides an evolutionary explanation for *primogeniture* and similar inheritance systems that favor firstborns. While often attributed to cultural evolution alone, such practices may also reflect evolved biological strategies that align with the inclusive fitness interests of older siblings.

Alternative Reproductive Strategy Hypothesis

This third hypothesis suggests that same-sex orientation may sometimes represent a *self-directed adaptive strategy* (Tureček et al., 2025). For example, in environments characterized by steep social stratification, where lower-status individuals have little realistic chance of reproducing, it may be more beneficial for these individuals to forgo reproduction and indirectly enhance their inclusive fitness by reallocating effort or resources toward kin.

Under this model, the shift in sexual orientation is not caused by manipulation from others but arises from the individual's own genome in response to environmental and familial cues. This aligns with conditional life-history theory, which posits that individuals flexibly adjust their reproductive strategies to optimize fitness under different ecological conditions.

It can be easily proven that the sets of external conditions under which homosexuality (or any other practice that discourages direct reproduction of the laterborn in favor of increasing the firstborn's direct fitness) can evolve are strictly nested (Fig. 1). There can be no situation in which the



General Manipulation Theory of Homosexuality, Fig. 1 Areas defined by the benefit to the firstborn (B) and the cost to the laterborn (C), in which it makes sense to establish reproductive specialization between brothers—where the firstborn becomes the heir and the one who primarily reproduces, and the laterborn focuses more on maximizing the prosperity of nieces and nephews rather than on his own reproduction

mother benefits from the laterborn's resignation on reproduction, but the firstborn does not. It all boils down to a simple application of Hamilton's rule.

If the direct fitness of the firstborn is f_1 and that of the laterborn is f_2, then the inclusive fitness of the firstborn can be expressed as $f_1 + f_2/2$, and the inclusive fitness of the laterborn as $f_1/2 + f_2$. The inclusive fitness of their mother (in the generation of her grandchildren) is then $f_1/2 + f_2/2$, since she shares 50% of her genetic alleles with each of her children.

If manipulation leads to increasing the direct fitness of the firstborn at the expense of the laterborn, we add B (benefits) to f_1 and subtract C (costs) from f_2. The inclusive fitness of the firstborn after accounting for these changes is $(f_1 + B) + (f_1 - C)/2$. A simple rearrangement shows that the average allele of the firstborn benefits from this manipulation if $B > C/2$, i.e., if benefits are greater than half the costs.

In a similar way, we can see that the average allele of the mother benefits from the manipulation if $B > C$. The benefits to the firstborn must outweigh the entire amount that is "withdrawn" from the reproductive account of the laterborn, because the mother is equally related to both sons. If the benefits are high enough to outweigh twice the cost—that is, if $B/2 > C$—then even the younger brother's alleles gain on average from the shift in reproduction toward the firstborn.

The Sibling manipulation hypothesis is, therefore, most likely to apply all else being equal. If it turns out that laterborn transition to non-reproductive strategies is directed (for instance) by alleles in mother's body irrespective of their presence in the laterborn, it must be because of developmental constraints that somehow prevent or mitigate direct genetic manipulation between siblings. Still, the firstborn's alleles gain more from this trade-off resolution than mother's alleles.

Theoretical Models: Crusaders and Monks

The nesting of hypothesis applicability is valuable on its own. However, the general terms B (benefits) and C (costs) can be defined more specifically using parameters that reflect key aspects of how humans live.

To formally compare the conditions under which manipulation-based strategies can evolve, Tureček et al. (2025) introduced two mathematical models grounded in inclusive fitness theory. These models—known as the *Crusader* and *Monk* models—differ in how severely the manipulated individual (typically a laterborn sibling) is affected, and they illustrate how the evolutionary payoffs of manipulation vary depending on resource structure and reproductive ecology.

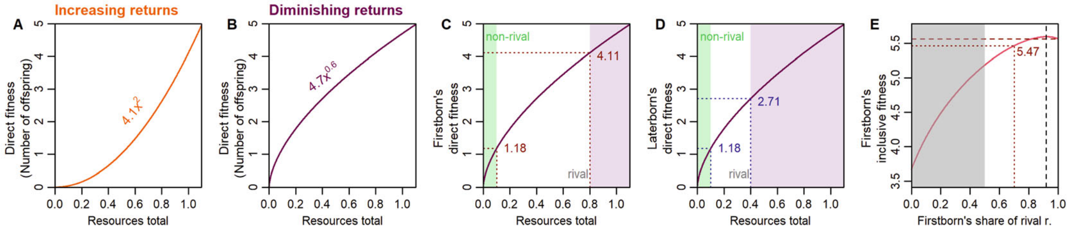
Rival Versus Nonrival Resources

A central concept in both models is the distinction between *rival* and *nonrival resources*. *Rival resources*—such as land, inheritance, or parental investment—are finite and consumable: Any portion allocated to one offspring reduces what remains for others. In contrast, *nonrival resources*—such as innate talents, social skills, or transmitted knowledge—can be used by one individual without diminishing their availability to others. One sibling's benefit from a nonrival resource does not reduce its potential benefit for the other.

In both models, two siblings (a firstborn and a laterborn) compete over a fixed pool of rival resources and independently acquire nonrival resources. The outcome of this competition, and the resulting fitness consequences for each actor (firstborn, laterborn, and mother), depends critically on two parameters—the relative importance of rival versus nonrival resources, and the shape of the relationship between total resources and direct fitness—whether returns are increasing (Fig. 2a), linear, or diminishing (Fig. 2b).

The Crusader Model

In the *Crusader model*, manipulation affects only rival resources. The manipulated sibling loses access to contested goods (e.g., inheritance or family investment) but retains full capacity to convert their nonrival resources into reproductive success. This mirrors



General Manipulation Theory of Homosexuality, Fig. 2 The function of direct fitness and its implications for inclusive fitness. The exponent of returns determines how acquired resources affect the expected number of offspring. For $a > 1$, we expect increasing returns (**a**); for $a < 1$, diminishing returns (**b**). The number by which x^a is multiplied (here 4.7) does not affect the model's predictions but allows the function to be scaled to realistic offspring counts (between 0 and 5). The function $x^{0.6}$ (**b**) serves as the basis for the following panels; two brothers—the firstborn (**c**) and the laterborn (**d**)—each receives, by definition, the same amount of nonrival resources n, here $n = 0.1$, which they convert into an average of 1.18 offspring. In addition, there is a budget of rival resources $r = 1$, which the brothers must divide. In this example, the firstborn secures $r_1 = 0.7$ of the rival resources, leaving 0.3 for the laterborn. The firstborn thus expects a total of 4.11 offspring, while the laterborn expects 2.71. The brothers share, on average, 50% of their genetic alleles; and the inclusive fitness of the firstborn is therefore $4.11 + 0.5 \times 2.71 = 5.47$ (**e**, dotted line). By varying the amount of rival resources claimed by the firstborn, we can observe how his inclusive fitness would change. We see that he would prefer a greater deviation from an equal split, up to $r_1 = 0.92$ (**e**, dashed black line), beyond which his inclusive fitness would start to decline again. The illustration uses the Crusader model, in which the laterborn's ability to convert nonrival resources into offspring is not affected by the manipulation that leads to unequal division of rival resources historical or cultural settings where disfavored offspring—such as younger sons in primogeniture systems—are excluded from inheritance but retain opportunities to reproduce via dispersal or self-sufficiency.

In this model, the laterborn may still achieve moderate reproductive success, albeit typically lower than that of the favored sibling. The manipulative strategy is most attractive to the firstborn, who benefits disproportionately by monopolizing rival resources. The mother, in contrast, prefers a fairer split unless reproductive returns rise steeply with investment.

Under conditions of diminishing returns and low importance of nonrival resources, the Crusader model predicts that the firstborn is the only actor consistently motivated to manipulate. The laterborn resists manipulation, and the mother typically acts as a stabilizing force favoring equity. However, as returns increase, alignment between mother and firstborn becomes more likely.

The Monk Model

The Monk model represents a more extreme form of manipulation. Here, if the manipulated sibling loses access to rival resources, he simultaneously exhibits reduced ability or motivation to convert nonrival resources into reproductive success (As a consequence, the manipulated sibling may be more likely to redirect transferable resources toward enhancing the reproductive success of the older sibling.) At extreme, this scenario corresponds to cases of exclusive homosexuality, celibacy, or deep social dependence within the natal family.

In this model, the direct reproductive success of the manipulated sibling can approach zero if manipulation is intense. The laterborn's inclusive fitness may still be nonzero if they contribute to the success of close kin, but this contribution, which was in fact observed in some traditional societies, such as fa'afafine in Samoa and muxes in southern Mexico (Vasey & VanderLaan, 2010; Gómez Jiménez & Vasey, 2022), is not assumed or required in the model. This is the main difference between present model and older kin selection model of male homosexuality (Wilson, 1975).

The Monk model still predicts alignment of interests between the firstborn and the mother when rival resources dominate and reproductive returns rise sharply with investment. In contrast, the laterborn consistently loses from manipulation unless the environment is so unfavorable that forgoing reproduction becomes the best available strategy from the perspective of their own inclusive fitness—a case that overlaps with the *Alternative Reproductive Strategy Hypothesis*.

The parameter space in the Monk model is richer: as shown by (Tureček et al., 2025), it allows for six distinct strategic regimes that can be all realized in a single actor (the firstborn) depending on relative importance of nonrival resources and profile of returns (characterized by "returns exponent" a, see Fig. 2 for $a = 2$ and $a = 0.6$). These regimes include scenarios in which manipulation is always beneficial, always detrimental, and detrimental/beneficial only up to some point. These convex/concave inclusive fitness profiles are then distinguished by whether maximal manipulation is in theory preferred to the fair split (like the inclusive fitness function in Fig. 2e) or the other way around. Only in this model can the inclusive fitness of the firstborn, the mother, and the laterborn each peak at different points along the manipulation gradient. In the Crusader model, mother is either perfectly aligned with the firstborn or laterborn.

Strategic Implications

Together, the Crusader and Monk models illustrate that the evolutionary logic of manipulation is sensitive to:

- The structure of the resource (rival vs. nonrival) dependence of the subsistence strategy
- The shape of reproductive return functions
- The nature and intensity of manipulation
- The kinship relationships and inclusive fitness stakes of the involved actors

In general:

- The firstborn benefits from manipulation under the broadest range of conditions, especially when rival resources are important.
- The mother benefits only when increasing returns make it advantageous to concentrate resources in one offspring.
- The laterborn resists manipulation in most scenarios unless it becomes the best way to salvage inclusive fitness in hopeless conditions.

The models thus formalize the logic behind the three major hypotheses of the General Manipulation Theory and clarify when and why different actors within a family might evolve manipulative or countermanipulative strategies.

From Crusaders to Monks: An Evolutionary Pathway Via Reproductive Blackmail

Crusader scenario would be primary and preferable for the firstborn, who indirectly transmits some of his genes through the offspring of the laterborn sibling. However, if the manipulated sibling responds by refusing to reproduce—becoming effectively celibate or homosexual—the inclusive fitness benefit for the firstborn decreases, thereby reducing the firstborn's incentive to manipulate. It has been hypothesized that this threat of transitioning to the Monk model—foregoing reproduction altogether—might serve as a form of evolutionary "blackmail," allowing laterborn siblings to defend against excessive manipulation aimed at monopolizing all resources (Tureček et al., 2025). While this intriguing possibility aligns with the theoretical logic of inclusive fitness conflicts, it has not yet been formally modeled and thus remains speculative.

Physiological Mechanisms

The most widely discussed physiological explanation of the fraternal birth order effect (FBOE) is the maternal immune hypothesis, which aligns with the Parental Manipulation Hypothesis. According to this view, after one or more male pregnancies, the mother's immune system may become sensitized to male-specific antigens. In subsequent pregnancies, maternal antibodies, particularly those targeting the Y-linked protein *NLGN4Y*, may cross the placenta and influence brain development in ways that affect sexual orientation (Bogaert et al., 2018).

However, the Sibling Manipulation Hypothesis proposes that the manipulative actor is not the mother but the older sibling. While he might still use maternal immunization as a tool, this route depends on the mother's immune response and is therefore constrained by her physiological cooperation—limiting its usefulness when her evolutionary interests conflict with his.

A more autonomous mechanism proposed under SMH is *microchimerism*. Fetal cells from earlier pregnancies can persist in the mother's body and later migrate into younger embryos (Yan et al., 2005; O'Donoghue, 2008; Schepanski et al., 2022). This allows the older sibling to potentially influence the development of the younger one directly, including neural development relevant to sexual orientation.

Unlike antibodies, which act in relatively nonspecific ways, microchimeric cells of sibling origin could exert complex and targeted effects on brain development. These cells can interact with developing tissues, influence gene expression, and integrate into functional circuits—offering a far more sophisticated mode of manipulation. Moreover, because this route bypasses maternal control, it enables the older sibling to pursue inclusive fitness benefits even at the mother's expense, consistent with model predictions (Tureček et al., 2025).

Although empirical data are still limited, the hypothesis that FBOE may result—at least in part—from inter-sibling cellular manipulation opens novel avenues for research into the developmental biology of sexual orientation.

Broader Implications and Limitations

The *General Manipulation Theory of Homosexuality* provides a versatile evolutionary framework for understanding how same-sex orientation may persist despite reducing direct reproductive success. By incorporating inclusive fitness logic, intrafamilial conflict, and nonlinear reproductive returns, the theory explains not only the fraternal birth order effect but also broader features of family structure, sibling dynamics, and cultural practices such as primogeniture.

A key insight of GMTH is that traits seemingly maladaptive at the individual level may persist when they benefit relatives, especially under conditions that favor asymmetric allocation of reproductive resources. This perspective helps integrate disparate findings across evolutionary biology, anthropology, and developmental psychology.

While originally developed to explain male homosexuality, GMTH may also help account for fraternal birth order effects observed in some samples of lesbian women. Although sons and daughters typically occupy somewhat distinct social niches and thus compete over different sets of resources, certain rival resources—such as parental attention or investment—may still be shared. In such cases, manipulative processes favoring one child at the expense of another could, under specific ecological and familial conditions, also contribute to the development of same-sex orientation in daughters.

At the same time, GMTH does not claim universality. It is unlikely that all cases of same-sex orientation arise through manipulative processes. Prior research suggests multiple etiological pathways, including genetic, hormonal, developmental, and social influences. The fraternal birth order effect, which GMTH seeks to explain, likely applies only to a subpopulation of homosexual individuals (Swift-Gallant et al., 2019).

Moreover, cultural norms may either amplify or mask underlying biological predispositions. For example, same-sex behavior may be shaped by institutional settings, gender systems, or social roles that mimic biological outcomes without reflecting them. These complexities make cross-cultural comparisons challenging and require caution in generalizing the theory.

Nevertheless, GMTH implies that sequencing only a younger brother's genome will not capture the full genetic basis of his sexual preference, because the causal allele may reside in a relative's genome (e.g., an older brother). Genetic sequences of all family members (within a hypothetical Family-Wide Genome-Wide Association Studies, FWGWAS) are to be considered when heritable shifts in sexual preferences toward homosexuality and/or asexuality are studied.

Similarly, in the context of cultural practices, it is important to consider who benefits when and why. For example, the tendency of siblings to support LGBT+ coming outs of their brothers and sisters, contrasted with the relatively lower tolerance observed among parents, may not simply reflect the notion that "older people are conservative by default," but rather differences in the average interests of their respective alleles.

Finally, GMTH assumes that manipulative mechanisms can evolve and persist even in the presence of counterselection by the manipulated individual or the mother. Although theoretical models suggest that older siblings often have the strongest incentive to manipulate and may do so even against maternal interests (Tureček et al., 2025), the empirical plausibility and limits of such conflicts remain to be thoroughly explored.

The principles underpinning GMTH can be seen as extending to an even more encompassing framework: a Manipulation Theory of Life History Strategies. This broader perspective would posit that an individual's life-history traits—ranging from reproductive decisions and developmental timing to behavioral dispositions like dispersal or philopatry with inclusive fitness specialization—can be adaptively shaped by the genes of any family member who stands to benefit from the focal individual exhibiting those specific traits. In essence, "an individual's life-history traits can be driven by the genes of whichever relative gains an evolutionary advantage from that individual behaving in that particular way." GMTH, with its focus on how same-sex orientation might be one such manipulated life-history outcome, would then represent a specific application of this overarching theory. This reinforces the necessity, already highlighted by GMTH, of considering the full web of intrafamilial genetic interests and opportunities when analyzing the evolution of any individual's traits or behaviors.

Conclusion

The *General Manipulation Theory of Homosexuality* offers a coherent evolutionary explanation for one of the most consistent findings in human homosexuality research—the fraternal birth order effect. By modeling manipulation as a fitness-maximizing strategy employed by family members—especially older siblings—the theory links physiological mechanisms (such as maternal immune responses and microchimerism) with patterns of family structure and kin competition.

GMTH unifies and extends earlier ideas by showing how same-sex orientation in some individuals may arise not despite evolutionary pressures, but because of them—as a result of inclusive fitness conflicts in environments where concentrating resources yields greater reproductive returns. While the theory is not intended to explain all forms of homosexuality, it provides a powerful framework for understanding how complex family interactions and evolutionary incentives can produce seemingly paradoxical outcomes.

By generating clear empirical predictions, GMTH invites further research in genetics, developmental biology, and anthropology. As new data emerge, the theory offers a roadmap for testing whether and how manipulative strategies have shaped one of the most enigmatic traits in human behavior.

Cross-References

- ▶ Birth Order: Parental Manipulation Hypothesis
- ▶ Sibling Manipulation Hypothesis of Male Homosexuality
- ▶ Xenoadaptations

Competing Interest Declaration The authors have no competing interests to declare that are relevant to the content of this manuscript.

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