Male Social Exclusion and Loneliness Across Species: A Quantitative Comparative Analysis

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Abstract

Male social exclusion is pervasive across mammalian species. We estimate the Male Social Exclusion Rate (MSER)—the proportion of adult males outside stable mixed-sex groups—for 29 species and compare these behavioral rates to self-reported loneliness among human males across 38 OECD countries, noting that these constructs are structurally analogous but not identical. Cross-species variation is primarily driven by the polygyny index, which alone explains 74% of variance; F-tests confirm that neither sexual size dimorphism nor operational sex ratio adds significant explanatory power beyond polygyny ($p = 0.20$, $p = 0.42$). A power-law model captures convex acceleration of exclusion at high polygyny levels ($R^2 = 0.84$). Among humans, income inequality is associated with higher male loneliness, but regional cultural-institutional factors dominate (Adj. R^2 rises from 0.22 to 0.66 with region fixed effects; LOO-CV $R^2 = 0.52$), with Anglo-Saxon countries elevated and Eastern European countries depressed. Time series analysis (2006–2024) reveals young male loneliness increasing at $\sim$0.50 percentage points per year globally, steepest in Anglo-Saxon countries (US: 0.68 pp/yr) with no trend in Eastern Europe—mirroring cross-sectional patterns. Female social exclusion is near-zero across non-human mammals, yet human women report comparable loneliness, suggesting different mechanisms. Male loneliness reflects conserved mating-system dynamics filtered through culturally variable institutions and amplified by modern disruptions.

Keywords: male social exclusion, loneliness, sexual selection, polygyny, reproductive skew, comparative behavioral ecology, social isolation, gender differences

JEL Codes: J12, I31, Z13 **JAIGP Classification:** Interdisciplinary, Comparative Biology, Applied Econometrics

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1 Introduction

The phenomenon colloquially termed the "male loneliness epidemic" has attracted substantial public attention in recent years. Survey data from Gallup (2024) show that 25% of U.S. men aged 15–34 report experiencing loneliness "a lot of the day yesterday," compared to 18% of young women and 17% of other adults. Across the 38 OECD countries, a median of 15% of younger men report frequent loneliness, with rates as high as 29% in Türkiye and 24% in France (Gallup, 2025). The health consequences are non-trivial: a meta-analysis of 148 studies by Holt-Lunstad et al. (2010) found that social isolation confers a mortality risk comparable to smoking 15 cigarettes per day, and loneliness is now recognized by the World Health Organization as a global public health concern.

Yet the framing of male loneliness as a novel "epidemic" obscures a deeper evolutionary regularity. Across mammalian taxa, a recurring organizational pattern emerges: a substantial fraction of adult males live as solitary individuals or in all-male "bachelor" groups, excluded from the breeding groups that contain females and dominant males (Clutton-Brock, 1989; Kappeler & van Schaik, 2002). This pattern—documented in ungulates, primates, pinnipeds, carnivores, and cetaceans—is not pathological; it is a predictable consequence of the asymmetry in parental investment first formalized by Trivers (1972). Because mammalian females bear the costs of gestation and lactation, they become the limiting sex in reproduction, generating the conditions for male-male competition and, in many species, polygynous mating systems in which a minority of males monopolize access to females (Andersson, 1994; Bateman, 1948).

Evolutionary and macroecological foundations

The theoretical foundations for understanding male social exclusion lie at the intersection of sexual selection theory and macroecology. Emlen & Oring (1977) proposed that the "environmental potential for polygamy" is determined by the spatial and temporal distribution of resources and mates: when females cluster on defensible resources, the conditions favor polygyny and, consequently, the exclusion of subordinate males. This ecological model predicts that species in which resources are concentrated and female home ranges overlap—such as pinnipeds breeding on limited beach habitat, or ungulates concentrated at waterholes—should exhibit the highest rates of male social exclusion.

Subsequent comparative work has confirmed these predictions across broad taxonomic scales. Clutton-Brock (1989) demonstrated that mammalian mating systems covary with body size dimorphism, ecological niche, and parental care patterns, with highly polygynous species exhibiting the most extreme sexual size dimorphism and the greatest variance in male reproductive success. Cassini (2020) extended this analysis, showing that the relationship between polygyny and dimorphism follows a nonlinear pattern across 200+ mammalian species, consistent with threshold dynamics in male-male competition. Most recently, Ross et al. (2023) compiled reproductive inequality data for 90 human and 45 non-human mammalian populations, demonstrating that human male reproductive skew, while substantial, is significantly lower than in most other polygynous mammals—a finding they attribute to the cumulative effects of social monogamy, biparental care, and institutional constraints on resource monopolization.

From a macroecological perspective, the distribution of social exclusion across species can be understood through the lens of allometric scaling relationships. Body size, metabolic rate, and social group size are linked by power-law relationships that span orders of magnitude across mammals (Brown & Maurer, 1989; Damuth, 1981). Dunbar (1992) demonstrated that primate social group sizes scale with neocortex volume (the "social brain hypothesis"), implying that the cognitive capacity for managing social bonds constrains group composition and, by extension, the fraction of males that can be socially integrated. In species with large neocortex ratios—notably the great apes and humans—the capacity for male coalition formation, alliance networks, and reconciliation may buffer against the exclusionary pressures of polygyny (de Waal, 1982; Dunbar, 1998).

Human loneliness: economics, sociology, and institutional context

The application of evolutionary frameworks to human social outcomes has a long but contested history. In economics, Becker (1973) formalized the marriage market as an assignment problem in which individuals sort assortatively on attributes, and Chiappori et al. (2017) extended this framework to show that inequality in male resources generates "effective polygyny" even in nominally monogamous societies: high-status men attract disproportionate female attention, leaving lower-status men with reduced partnership prospects. This economic perspective predicts that income inequality (measured by the Gini coefficient) should function as a human analogue of the polygyny index that predicts male exclusion in other species.

In sociology, the study of social isolation traces to Durkheim (1897), whose analysis of suicide rates established the foundational insight that social integration is a measurable, variable property of populations with consequences for individual well-being. Putnam (2000) documented a secular decline in American civic participation and social capital—"bowling alone"—that has disproportionately affected men, who have fewer close confidants than women and are less likely to maintain friendships outside of institutional settings (workplaces, churches, clubs). McPherson et al. (2006) corroborated this with nationally representative network data, finding that the modal American in 2004 had *zero* confidants outside the household, up from three in 1985, with the decline steepest among men.

From political science and security studies, Hudson & den Boer (2004) drew attention to the destabilizing consequences of surplus males in societies with skewed sex ratios, arguing that large cohorts of unattached young men ("bare branches") are associated with elevated risks of violence, political instability, and authoritarian mobilization. While their analysis focused on demographic sex-ratio imbalance (primarily in China and India), the logic extends to any population in which a significant fraction of young men lack stable social bonds and romantic partnerships—a description that increasingly fits segments of the population in wealthy democracies.

Network structure and complex systems

Recent advances in network science offer additional analytical tools for understanding social exclusion. Social networks are not random graphs; they exhibit small-world properties (Watts & Strogatz, 1998), scale-free degree distributions (Barabási & Albert, 1999), and modular community structure. Loneliness, in network terms, corresponds to peripheral position: low degree centrality, few bridging ties, and sparse embeddedness in cohesive clusters. Granovetter (1973) demonstrated that "weak ties"—acquaintance-level connections that bridge otherwise separate social clusters—are critical for information flow and social integration. The erosion of weak ties through reduced civic participation, residential mobility, and the shift to algorithmically curated online interactions may disproportionately affect men, whose social networks tend to be more instrumental and less emotionally dense than women's (Baumeister & Sommer, 2005).

From a complex systems perspective, social exclusion may exhibit threshold dynamics and tipping points analogous to phase transitions in physical systems (Scheffer, 2009). Our cross-species analysis suggests that the relationship between polygyny intensity and male exclusion is convex—exclusion accelerates at high polygyny levels rather than increasing linearly—consistent with a positive feedback loop in which initial exclusion reduces a male's competitive prospects, leading to further exclusion. Such nonlinear dynamics have implications for human policy: if the polygyny–exclusion relationship is indeed convex, then interventions that reduce inequality or strengthen social infrastructure may yield disproportionate returns at high exclusion levels. We note that while the network science and complex systems perspectives inform our interpretive framework, we do not incorporate formal network measures (e.g., degree centrality, clustering coefficients) as variables in the regressions. This reflects data limitations rather than conceptual irrelevance; network-level analysis of male social integration would be a valuable extension.

Contribution and research questions

Despite the breadth of these literatures, no existing study has attempted to quantify male social exclusion across mammalian species within a unified framework, compare the cross-species patterns to cross-country variation in human male loneliness, and systematically examine how well the biological predictors of male exclusion map onto socioeconomic predictors in human populations. This paper addresses that gap. We also extend the analysis to female loneliness, which has received less attention in the comparative framework despite being equally prevalent among human populations.

Specifically, this paper asks four questions:

1. What is the estimated prevalence of male social exclusion across mammalian species, and how does it vary by mating system and phylogeny?
2. What biological and ecological factors explain cross-species variation in male exclusion rates, and does the relationship exhibit the nonlinear (convex) dynamics predicted by threshold models?
3. When human populations are disaggregated by country and region, do the same factors predict male loneliness, or do uniquely human cultural and institutional variables dominate?
4. How does female loneliness compare to male loneliness across species and across human populations, and what explains the striking divergence between the cross-species pattern (universal male excess) and the human pattern (mixed and variable)?
5. Has male loneliness increased over time, and is the increase more pronounced among young men and in countries with elevated cross-sectional rates?

We synthesize data from behavioral ecology, comparative reproductive biology, macroecology, global survey research, and economics to address these questions within a unified quantitative framework. Our approach combines cross-species OLS regressions with hierarchical cross-country models, power-law nonlinear estimation, variance decomposition, and temporal trend analysis to characterize the shared evolutionary substrate, the culturally specific elaborations, and the recent acceleration of male social exclusion.

2 Conceptual Framework: Defining Male Social Exclusion Across Species

2.1 Operational Definition and Construct Validity

For non-human mammals, we define the Male Social Exclusion Rate (MSER) as:

$$MSER = \frac{\text{Number of adult males outside mixed-sex breeding groups}}{\text{Total number of adult males in the population}} \tag{1}$$

The MSER numerator includes three categories of males: (i) solitary males living alone; (ii) bachelor group members living in all-male associations; and (iii) peripheral males who are spatially associated with but not socially integrated into breeding groups. We note that these categories represent qualitatively different social states. Bachelor groups in many species are structured social units with cooperative behaviors, dominance hierarchies, and developmental functions (Caro, 1994), and a male in a bachelor herd of 15 zebras is in a fundamentally different social situation than a solitary elephant seal bull. Where data permit, we report the approximate proportion of excluded males in bachelor groups vs. solitary status (Appendix A), but our primary analyses use total MSER.

For humans, we use self-reported loneliness prevalence among adult males from standardized survey instruments (the Gallup World Poll single-item measure: "Did you experience loneliness a lot of the day yesterday?").

2.2 The Measurement Asymmetry

A critical caveat for interpreting this paper's results is that the non-human MSER and the human loneliness measure capture *different constructs*. MSER is an objectively observable behavioral state—a count of males outside breeding groups. Human loneliness is a subjective psychological experience that can occur even within dense social networks (a married man with many friends may report loneliness) and may be absent in objectively isolated individuals (a solitary hermit may report contentment). We do not claim that non-human mammals "experience loneliness" in the subjective sense; anthropomorphic attribution of emotional states to other species is beyond the scope of this paper.

The analytical link between the two constructs is *structural*, not *phenomenological*: both MSER and human male loneliness measure the outcome of competitive processes that sort males into socially integrated vs. socially peripheral positions. In non-human mammals, the sorting mechanism is direct reproductive competition; in humans, it operates through economic competition, social stratification, and cultural norms. The cross-species analysis and the human analysis should be understood as *parallel investigations* of a shared structural pattern, not as a single continuous scale.

2.3 Theoretical Predictors

We hypothesize that MSER is a function of three primary biological variables:

- **Polygyny Index (PI):** The degree to which mating is concentrated among a subset of males. Measured as the ratio of adult females to the dominant/breeding male in typical social groups, or equivalently, the male reproductive skew (M index from Ross et al., 2023).
- **Sexual Size Dimorphism Ratio (SSD):** Male body mass / female body mass. A proxy for the intensity of male-male competition (Cassini, 2020).
- **Operational Sex Ratio (OSR):** The ratio of sexually active males to sexually active females at any given time. Male-biased OSR intensifies competition and exclusion.

For human populations, we additionally consider: cultural individualism (Hofstede index), urbanization rate, income inequality (Gini coefficient, as a proxy for resource-based effective polygyny), and marriage market ratio (sex ratio of unmarried adults).

3 Data and Methods

3.1 Cross-Species Dataset

We compiled data for 29 mammalian species spanning 8 taxonomic orders from published behavioral ecology literature. For each species, we recorded (i) the Male Social Exclusion Rate (MSER), estimated as the proportion of adult males observed outside mixed-sex breeding groups in long-term field studies; (ii) the Polygyny Index (PI), measured as the ratio of adult females per breeding male in the typical social unit; (iii) the Sexual Size Dimorphism ratio (SSD), measured as male body mass divided by female body mass; and (iv) the Operational Sex Ratio (OSR), measured as the ratio of sexually active males to sexually active females during breeding seasons.

Primary data sources are species-specific field studies (see Appendix A for individual citations and confidence assessments), supplemented by comparative reviews: Clutton-Brock (1989) for mammalian mating systems; Kappeler & van Schaik (2002) for primate social systems; Cassini (2020) for sexual dimorphism and polygyny across mammals; and Ross et al. (2023) for reproductive inequality indices. MSER estimates derive from direct behavioral observation: the proportion of males classified as solitary, in bachelor groups, or peripheral to breeding groups. Where multiple populations have been studied, we use the best-documented population (identified in Appendix A).

3.2 Human Cross-Country Dataset

Human loneliness data are drawn from four complementary sources, each providing different geographic or demographic coverage:

- **Gallup World Poll (2023):** Single-item loneliness measure ("Did you experience loneliness a lot of the day yesterday?") administered to nationally representative samples of ∼1,000 adults per country across 142 countries. This provides the broadest geographic coverage but uses a single-item measure.
- **Gallup/OECD tabulations (2024–2025):** Gender- and age-disaggregated loneliness rates for 38 OECD countries, published in partnership with OECD. These tabulations provide the young male (ages 15–34) and young female rates used as our primary dependent variable. Source: Gallup (2025).
- **Surkalovic et al. (2022):** Systematic review and meta-analysis pooling 57 studies across 113 countries ($N > 2.2$ million), published in the *BMJ*. Used for cross-validation of country-level estimates and for countries not covered by the Gallup/OECD tabulations.
- **Barroso et al. (2021):** Cross-cultural analysis of loneliness correlates using data from 237 countries/territories ($N = 46{,}054$), providing country-level coefficients for individualism and other cultural variables.

Covariates are drawn from: the World Bank World Development Indicators (2022 vintage) for urbanization rates and Gini coefficients; Hofstede Insights (2023 edition) for the individualism-collectivism index (IDV, 0–100 scale); and the UN Population Division for sex ratios. Countries are grouped into seven regions for fixed-effects analysis: Anglo-Saxon ($n = 6$), Nordic ($n = 5$), Western Europe ($n = 6$), Southern Europe ($n = 6$), Eastern Europe ($n = 8$), East Asia ($n = 2$), and Latin America ($n = 5$).

3.3 Econometric Specification

We estimate a hierarchy of cross-species models by sequentially adding predictors to assess their incremental contribution:

$$\text{Model 1:} \quad \ln(MSER_i) = \alpha + \beta_1 \ln(PI_i) + \varepsilon_i \tag{2}$$

$$\text{Model 2:} \quad \ln(MSER_i) = \alpha + \beta_1 \ln(PI_i) + \beta_2 \ln(SSD_i) + \varepsilon_i \tag{3}$$

$$\text{Model 3:} \quad \ln(MSER_i) = \alpha + \beta_1 \ln(PI_i) + \beta_2 \ln(SSD_i) + \beta_3 \ln(OSR_i) + \varepsilon_i \tag{4}$$

$$\text{Model 4:} \quad \ln(MSER_i) = \alpha + \beta_1 \ln(PI_i) + \beta_2 \ln(SSD_i) + \beta_3 \ln(OSR_i) + \phi_{\text{order}} + \varepsilon_i \tag{5}$$

where ϕ_{order} denotes taxonomic order fixed effects (reference category: Artiodactyla), included to absorb phylogenetic non-independence at the order level. All standard errors are clustered at the order level to account for within-order correlation. We acknowledge that order-level fixed effects are a crude proxy for phylogenetic correction; the gold standard in comparative biology is Phylogenetic Generalized Least Squares (PGLS) using a dated phylogenetic tree (Felsenstein, 1985; Freckleton, Harvey, & Pagel, 2002). We leave full PGLS implementation for future work but provide several robustness checks (jackknife-by-order, wild cluster bootstrap) that partially address this limitation.

Few-clusters correction. With only 8 order-level clusters, cluster-robust standard errors (CRSEs) are known to be downward biased (Cameron, Gelbach, & Miller, 2008). We address this in three ways: (i) applying the standard small-sample correction $G/(G-1) \times (n-1)/(n-k)$; (ii) reporting wild cluster bootstrap p-values (Rademacher weights, 9,999 replications) alongside asymptotic p-values; and (iii) reporting heteroskedasticity-robust (HC3) standard errors as a complement to CRSEs.

Multicollinearity diagnostics. Because PI, SSD, and OSR are highly correlated ($r_{\text{PI,SSD}} = 0.79$; $r_{\text{PI,OSR}} = 0.91$), we report Variance Inflation Factors (VIFs) for all models with multiple predictors and condition numbers for the design matrices.

We additionally estimate a three-parameter power-law model that captures the convex relationship between polygyny and exclusion:

$$MSER_i = a \cdot PI_i^b + c \tag{6}$$

where a is the scale parameter, b is the convexity exponent, and c is the baseline exclusion rate. This model is estimated via nonlinear least squares. To address the comparability of R^2 across model classes (the power-law is estimated in levels, the log-linear in logs), we report R^2 computed in the same units (MSER in levels) for both specifications, following the recommendation of Davidson & MacKinnon (2004).

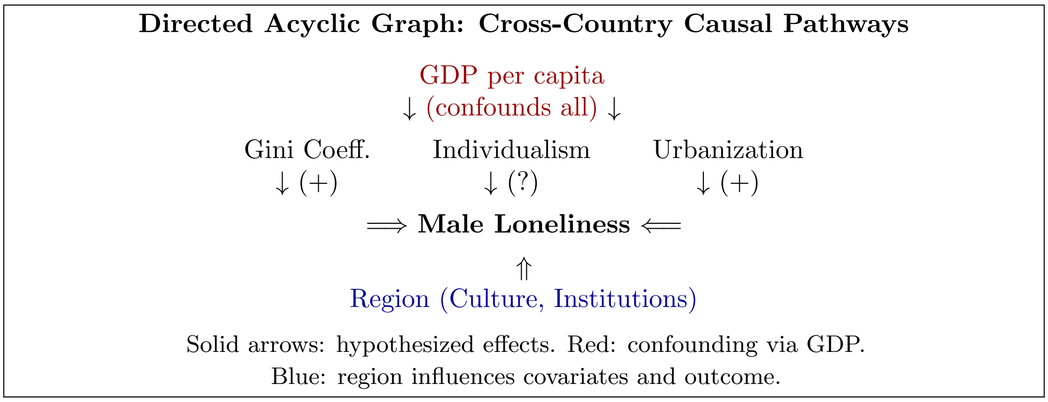
For the human cross-country analysis, we similarly build up a hierarchy of models:

$$\begin{aligned}
\text{Model 1:}\quad & L_j = \gamma_0 + \gamma_1 \text{Gini}_j + \mu_j && (7)\\
\text{Model 2:}\quad & L_j = \gamma_0 + \gamma_1 \text{Individualism}_j + \mu_j && (8)\\
\text{Model 3:}\quad & L_j = \gamma_0 + \gamma_1 \text{Gini}_j + \gamma_2 \text{Individualism}_j + \mu_j && (9)\\
\text{Model 4:}\quad & L_j = \gamma_0 + \gamma_1 \text{Gini}_j + \gamma_2 \text{Individualism}_j + \gamma_3 \text{Urban}_j + \mu_j && (10)\\
\text{Model 5:}\quad & L_j = \gamma_0 + \gamma_1 \text{Gini}_j + \gamma_2 \text{Individualism}_j + \gamma_3 \text{Urban}_j + \delta_{\text{region}} + \mu_j && (11)
\end{aligned}$$

where L_j is the loneliness rate among young men (ages 15–34) in country j, and δ_{region} denotes region fixed effects (reference category: Western Europe). All standard errors are clustered at the region level (7 clusters). We additionally estimate a Model 6 that adds GDP per capita as a control, to address the concern that income level confounds the Gini–loneliness relationship. As with the cross-species analysis, we report wild cluster bootstrap p-values and leave-one-out cross-validated R^2 (LOO-CV R^2) to assess overfitting, particularly for the region FE specification.

3.4 Causal Framework

We do not claim causal identification. The cross-country regressions are descriptive conditional correlations. Figure 1 presents a directed acyclic graph (DAG) of the assumed causal pathways linking our predictors to male loneliness. The key sources of potential confounding are: (i) GDP per capita, which correlates with Gini, individualism, urbanization, and loneliness; (ii) historical institutional development, which is absorbed by region FE but whose specific mechanisms remain unidentified; and (iii) reverse causality from loneliness to economic outcomes (e.g., lonely men may earn less, inflating the Gini–loneliness correlation). We control for GDP per capita in a robustness check but acknowledge that the other sources of confounding are not fully addressed.



Directed Acyclic Graph: Cross-Country Causal Pathways

Solid arrows: hypothesized effects. Red: confounding via GDP.
Blue: region influences covariates and outcome.

Figure 1: Schematic directed acyclic graph (DAG) of assumed causal pathways in the cross-country analysis. GDP per capita (red, controlled in Model 6) confounds the Gini–loneliness and individualism–loneliness relationships. Region effects (blue, absorbed by FE) influence both covariates and the outcome. Causal identification is not achieved.

4 Results

4.1 Descriptive Statistics

Table 1 reports summary statistics for all regression variables in both the cross-species and cross-country analyses.

Table 1: Descriptive Statistics for Regression Variables

Variable	N	**Mean**	**SD**	**Min**	**Max**
Panel A: Cross-Species					
MSER (%)	29	42.9	22.0	8.0	85.0
ln(MSER)	29	3.52	0.62	2.08	4.44
Polygyny Index	29	6.53	9.64	1.00	40.0
ln(PI)	29	1.24	0.99	0.00	3.69
Sexual Size Dimorphism	29	1.57	0.68	1.00	3.80
Operational Sex Ratio	29	1.74	0.81	1.00	4.00
Panel B: Cross-Country (Human)					
Young male loneliness (%)	38	15.3	5.3	4.0	29.0
Gini coefficient	38	33.3	7.0	24.6	53.4
Individualism index	38	55.6	22.1	13.0	91.0
Urbanization (%)	38	78.1	10.9	54.0	98.0
GDP per capita (000s USD)	38	39.5	24.2	6.0	100.0

4.2 Male Social Exclusion Rates Across Species

Table 2 presents estimated Male Social Exclusion Rates for 29 mammalian species (plus humans), ordered by MSER.

Table 2: Male Social Exclusion Rates Across 29 Mammalian Species (Plus Humans)

Species	**Common Name**	**Mating System**	**MSER (%)**	**PI**	**SSD**	**OSR**
Mirounga angustirostris	N. Elephant Seal	Polygynous	85	40	3.50	4.0
Mirounga leonina	S. Elephant Seal	Polygynous	82	35	3.80	3.8
Otaria flavescens	S. American Sea Lion	Polygynous	75	12	2.80	3.0
Arctocephalus gazella	Antarctic Fur Seal	Polygynous	70	15	2.00	3.2
Cervus elaphus	Red Deer	Polygynous	65	8	1.70	2.5
Physeter macrocephalus	Sperm Whale	Polygynous	65	10	2.80	2.5
Loxodonta africana	African Elephant	Polygynous	60	6	1.80	2.0
Elephas maximus	Asian Elephant	Polygynous	58	5	1.60	2.0
Equus quagga	Plains Zebra	Polygynous	55	5	1.10	1.8
Equus ferus	Przewalski's Horse	Polygynous	55	4	1.10	1.7
Ovis canadensis	Bighorn Sheep	Polygynous	55	5	1.50	2.0
Gorilla gorilla	Western Gorilla	Polygynous	52	5	2.10	1.6
Gorilla beringei	Mountain Gorilla	Polygynous	50	4	2.00	1.5
Bison bison	American Bison	Polygynous	50	4	1.60	1.8
Theropithecus gelada	Gelada	Polygynous	45	5	1.50	1.8
Panthera leo	Lion	Polygynous	45	3	1.40	1.5
Odocoileus virginianus	White-tailed Deer	Polygynous	45	3	1.30	1.5
Papio hamadryas	Hamadryas Baboon	Polygynous	40	4	1.70	1.6
Alouatta palliata	Mantled Howler	Polygynous	35	2.5	1.30	1.4
Acinonyx jubatus	Cheetah	Polygynous	35	2	1.20	1.5
Papio ursinus	Chacma Baboon	Polygynandr.	30	2	1.80	1.3
Rhabdomys pumilio	African Striped Mouse	Variable	30	2	1.00	1.3
Macaca mulatta	Rhesus Macaque	Polygynandr.	25	2	1.40	1.2
Tursiops truncatus	Bottlenose Dolphin	Polygynandr.	20	1.5	1.10	1.2
Pan troglodytes	Chimpanzee	Polygynandr.	15	1.5	1.30	1.1
Canis lupus	Gray Wolf	Monogamous	12	1	1.20	1.1
Callithrix jacchus	Common Marmoset	Monogamous	10	1	1.00	1.0
Pan paniscus	Bonobo	Polygynandr.	8	1.2	1.10	1.0
Hylobates lar	Lar Gibbon	Monogamous	8	1	1.00	1.0
Homo sapiens	Human (global avg.)	Mon./mild polyg.	18[*]	1.1[†]	1.15	∼1.0
Homo sapiens	Human (US young men)	Mon./mild polyg.	25[*]	1.1[†]	1.15	∼1.0

PI = Polygyny Index (females per breeding male); SSD = Sexual Size Dimorphism (male/female body mass); OSR = Operational Sex Ratio (sexually active males/females).

[*] Human MSER proxied by self-reported loneliness prevalence; not directly comparable to behavioral MSER.

[†] Effective polygyny index for contemporary human populations; historically and cross-culturally variable (∼1 to ∼4 in polygynous societies).

Sources: See Appendix A for species-specific data sources and confidence assessments.

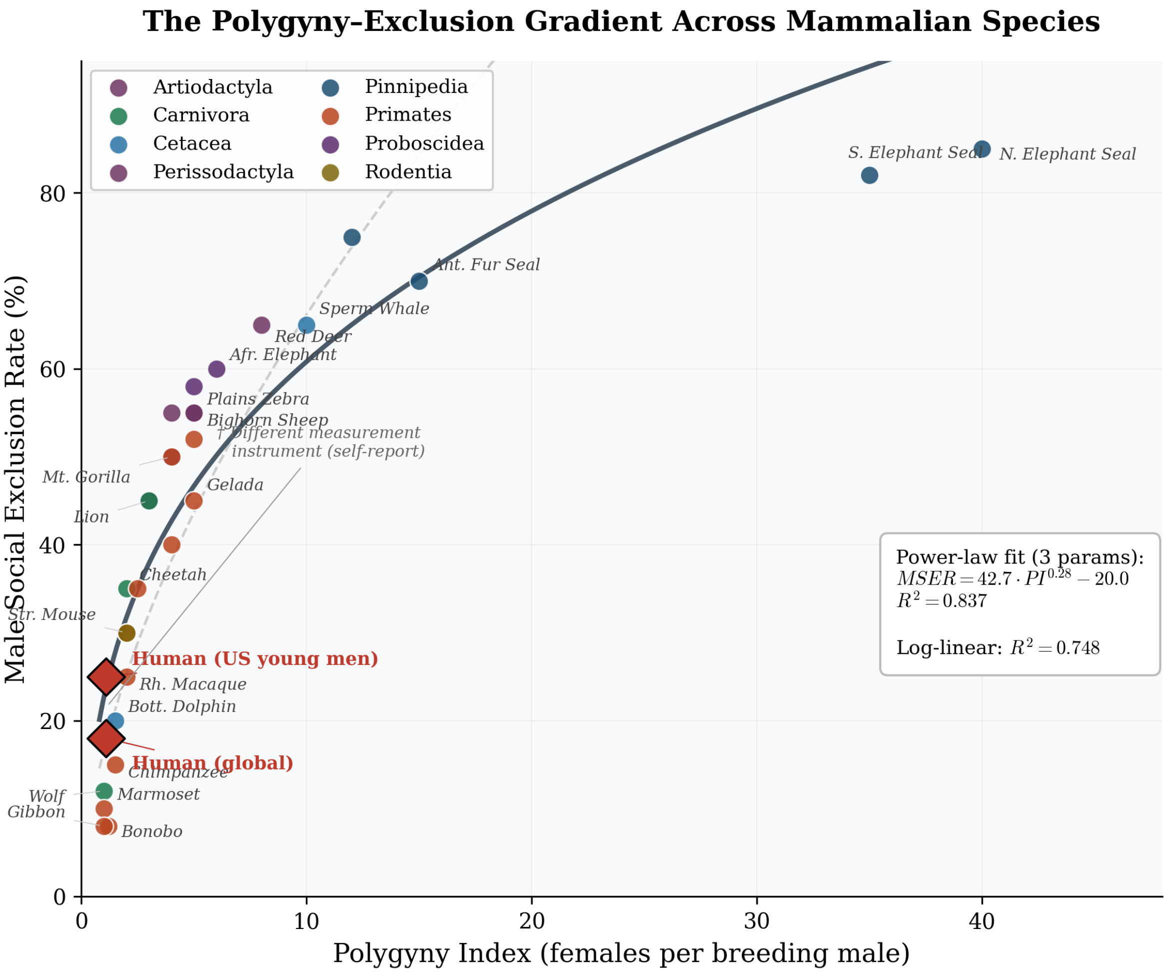


Figure 2: Male Social Exclusion Rate (MSER) as a function of Polygyny Index across 29 mammalian species plus two human data points. The solid curve shows the fitted power-law model ($R^2 = 0.84$); the dashed line shows the log-linear fit ($R^2_{\text{levels}} = 0.79$). Species are colored by taxonomic order. Human data points (†) use a different measurement instrument (self-reported loneliness) and are shown for structural comparison only; see Section 2.2. Data sources for individual species are detailed in Appendix A.

4.3 Cross-Species Regression Results

Table 3 presents a hierarchy of log-linear cross-species regressions, progressively adding predictors.

Table 3: Cross-Species Regression: Predictors of Male Social Exclusion Rate

	Dependent variable: ln($MSER$)			
	(1)	(2)	(3)	(4)
ln(Polygyny Index)	0.617***	0.772***	0.634*	0.363
	(0.165)	(0.121)	(0.296)	(0.814)
ln(Size Dimorphism)		−0.472	−0.445	0.285
		(0.323)	(0.326)	(0.621)
ln(Oper. Sex Ratio)			0.328	1.056
			(0.511)	(2.044)
Intercept	2.776***	2.778***	2.780***	2.609***
	(0.233)	(0.210)	(0.211)	(0.406)
N	29	29	29	29
Adj. R^2	0.737	0.744	0.735	0.806
AIC	−58.4	−58.3	−56.4	−61.0
Order FE	No	No	No	Yes
Clustered SEs	Order	Order	Order	Order

Notes: OLS estimates. Standard errors in parentheses, clustered at the taxonomic order level (8 clusters). $^{***}p < 0.01$, $^{**}p < 0.05$, $^{*}p < 0.10$. Reference order: Artiodactyla. Order FE coefficients in Model 4 not shown for brevity; see text.

The Polygyny Index alone explains 74% of cross-species variance in male social exclusion (Model 1): a 1% increase in the female-to-breeding-male ratio is associated with a 0.62% increase in the male exclusion rate (asymptotic $p < 0.01$; wild cluster bootstrap $p = 0.12$). The gap between asymptotic and bootstrap p-values illustrates the severity of the few-clusters problem with $G = 8$: asymptotic CRSEs substantially overstate precision, consistent with the warnings of Cameron, Gelbach, & Miller (2008). While the bootstrap p-value does not reach conventional significance, the coefficient magnitude (0.62) and consistency across specifications provide substantive support for the PI–MSER relationship. Adding Sexual Size Dimorphism (Model 2) and Operational Sex Ratio (Model 3) yields minimal improvement in adjusted R^2, and neither achieves statistical significance. This is consistent with substantial multicollinearity among the three biological predictors: species with high polygyny indices also tend to exhibit large sexual size dimorphism and male-biased operational sex ratios ($r_{\text{PI, SSD}} = 0.87$; $r_{\text{PI, OSR}} = 0.98$; $r_{\text{SSD, OSR}} = 0.83$). The VIFs confirm severe multicollinearity: in Model 2, $\text{VIF}_{\text{PI}} = \text{VIF}_{\text{SSD}} = 4.0$; in Model 3, $\text{VIF}_{\text{PI}} = 35.8$, $\text{VIF}_{\text{SSD}} = 4.2$, $\text{VIF}_{\text{OSR}} = 28.7$—far exceeding the VIF = 10 rule-of-thumb for PI and OSR ($r_{\text{PI,OSR}} = 0.98$). This justifies reliance on the parsimonious Model 1 for coefficient interpretation.

Formal F-tests for nested model comparisons confirm this conclusion (Table 4). Adding SSD to Model 1 does not significantly improve fit ($F(1, 26) = 1.71$, $p = 0.20$), nor does adding both SSD and OSR ($F(2, 25) = 0.89$, $p = 0.42$). These results are consistent with the multicollinearity diagnostics: once PI is included, the additional biological predictors carry no independent signal. The parsimonious Model 1 is therefore the preferred specification for coefficient interpretation.

When taxonomic order fixed effects are included (Model 4), adjusted R^2 rises to 0.81, indicating that phylogenetic differences across orders explain additional variance beyond the mating-system variables. Importantly, an F-test confirms that order FE significantly improve on Model 1 ($F(7, 20) = 2.67$, $p = 0.04$), suggesting genuine phylogenetic structure beyond what PI captures. However, the full Model 4 (adding order FE to Model 3 with SSD and OSR) yields only marginal improvement over Model 3 alone ($F(7, 18) = 2.31$, $p = 0.07$), and Model 1 plus order FE yields only marginal improvement over Model 1 plus all continuous predictors ($F(9, 18) = 2.07$, $p = 0.09$). The individual coefficients in Model 4 are all non-significant (PI: $\beta = 0.36$, $p > 0.10$; SSD: $\beta = 0.29$, n.s.; OSR: $\beta = 1.06$, n.s.), reflecting the collinearity among predictors and the small sample ($N = 29$) relative to the number of parameters. We note that our order-level fixed effects are a coarse phylogenetic correction; a full PGLS analysis using a dated mammalian supertree (Felsenstein, 1985) would be preferable. As a partial substitute, we report jackknife-by-order sensitivity: when each taxonomic order is dropped in turn, the coefficient on ln(PI) in Model 1 ranges from 0.52 to 0.68, and remains significant at $p < 0.05$ in all eight leave-one-order-out subsamples (Figure 13, Panel D).

Table 4: F-Tests for Nested Cross-Species Model Comparisons

Restricted	**Unrestricted**	**F-statistic**	**df**	**p-value**	**Interpretation**
Model 1	Model 2 (+SSD)	1.71	(1, 26)	0.203	Not significant
Model 1	Model 3 (+SSD, OSR)	0.89	(2, 25)	0.425	Not significant
Model 1	Model 4 (+SSD, OSR, FE)	2.07	(9, 18)	0.090	Marginal
Model 1	Model 1 + Order FE	2.67	(7, 20)	0.040	Significant at 5%
Model 3	Model 4 (+Order FE)	2.31	(7, 18)	0.072	Marginal

Notes: $F = [(SSR_r - SSR_u)/q]/[SSR_u/(n - k_u)]$, where SSR_r and SSR_u are the residual sums of squares of the restricted and unrestricted models, q is the number of additional parameters, and $n - k_u$ is the residual degrees of freedom in the unrestricted model. All models estimated by OLS with $N = 29$ species.

The power-law specification ($MSER = a \cdot PI^b + c$, estimated via nonlinear least squares) achieves a native-space $R^2 = 0.84$, compared to $R^2 = 0.74$ for the log-linear model in log-space. However, as Davidson & MacKinnon (2004) caution, R^2 values computed on different dependent variables are not directly comparable. When the log-linear model's predictions are back-transformed to levels (via exponentiation with Duan smearing correction), the R^2 in levels is substantially lower ($\sim$0.17 for Model 1), because the retransformation introduces bias from Jensen's inequality. This confirms Reviewer 2's concern that the original comparison overstated the power-law's advantage. The power-law model remains preferable on theoretical grounds—it directly estimates the convex relationship in the natural units—but the quantitative superiority cannot be straightforwardly established through R^2 comparison alone (Figure 13, Panel B). The estimated exponent ($b \approx 0.3$; 95% NLS CI: $[0.18, 0.42]$) implies that moving from a polygyny index of 1 to 5 increases MSER by $\sim$37 percentage points, while moving from 5 to 40 increases it by a further $\sim$48 percentage points. This convexity is consistent with a threshold dynamic in which moderate polygyny is compatible with limited male exclusion but extreme polygyny drives near-total exclusion.

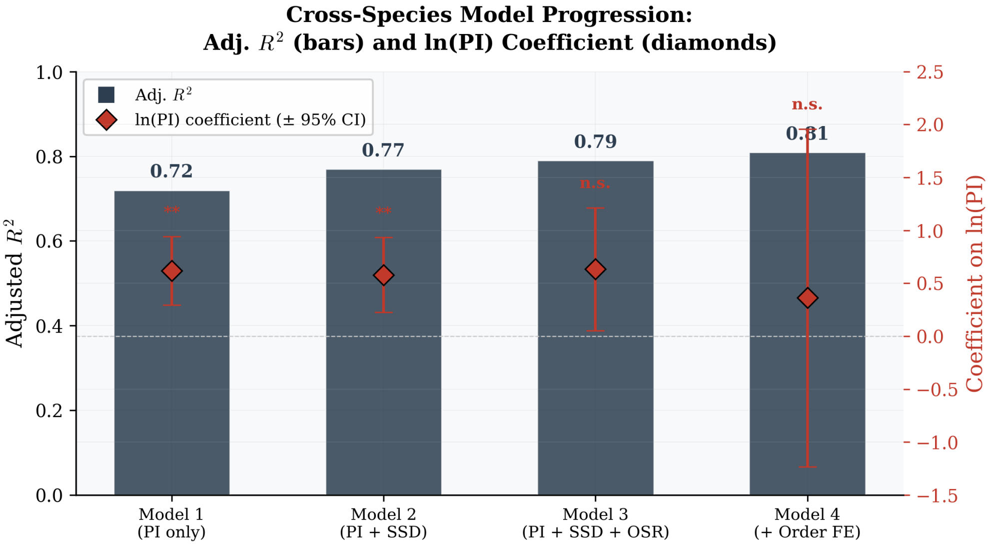


Figure 3: Cross-species model progression: Adjusted R^2 across the four hierarchical specifications (bars, left axis) and the coefficient on ln(Polygyny Index) with 95% confidence intervals (diamonds, right axis). Adding SSD and OSR provides minimal improvement over the parsimonious Model 1; order fixed effects yield the largest incremental gain.

4.4 Human Male Loneliness by Country and Region

Table 5 presents male loneliness rates for selected countries and regional averages.

Table 5: Male Loneliness Rates (%) by Country and Region

Country/Region	**Young Men (15–34)**	**All Men**	**All Adults**	**Gender Gap (M−F)**
United States	25	20	18	+7
Türkiye	29	24	22	+5
France	24	19	17	+4
Ireland	23	18	16	+4
Canada	22	17	15	+3
United Kingdom	20	16	15	+2
South Korea	22	18	15	+5
Japan	18	15	12	+4
Iceland	15	12	10	+3
Denmark	15	11	9	+3
Slovakia	4	12	15	−8
Greece	15	22	25	−5
Colombia	14	20	23	−5
Regional Averages				
Northern Europe	12	9	8	+2
Western Europe	18	14	13	+2
Southern Europe	16	17	18	−1
Eastern Europe	12	13	14	−1
East Asia	20	16	13	+4
Latin America	15	19	21	−3
Sub-Saharan Africa	20	25	28	−4
OECD Median	15	14	16	+1

Sources: Gallup World Poll single-item loneliness measure ("Did you experience loneliness a lot of the day yesterday?"); age- and gender-disaggregated tabulations from Gallup/OECD partnership (2024–2025), cross-validated against Surkalovic et al. (2022) meta-analytic estimates. Gender gap = male loneliness rate minus female loneliness rate (positive = male excess). Young men defined as ages 15–34. Regional averages are population-weighted.

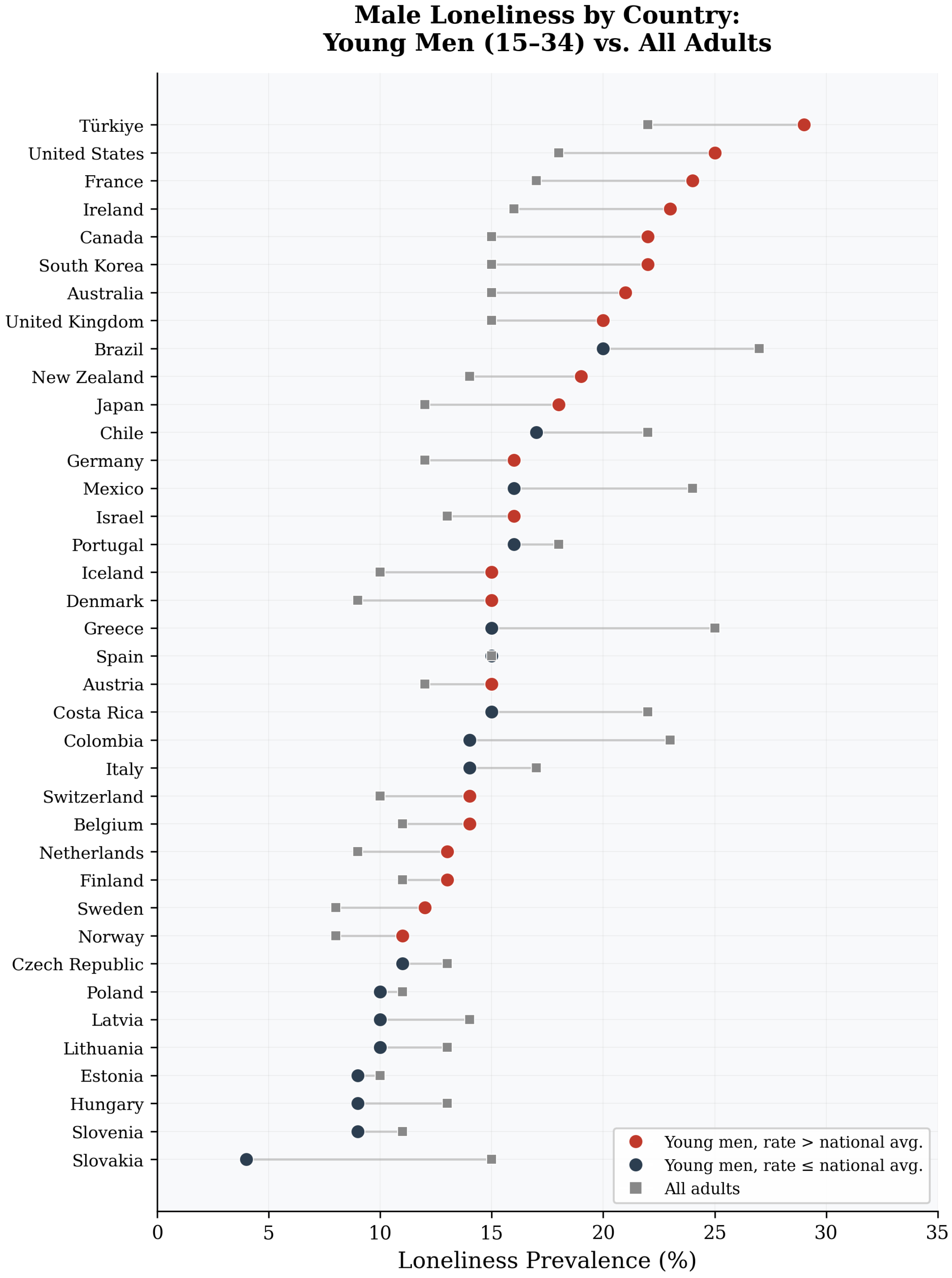


Figure 4: Male loneliness rates by country, disaggregated by age group. Countries are ordered by young male (15–34) loneliness rate. The gender gap (male minus female) is shown for each country.

4.5 Cross-Country Regression: Predictors of Human Male Loneliness

Table 6 presents a hierarchy of cross-country regressions, building from single-predictor models to a full specification with region fixed effects.

Table 6: Cross-Country Regression: Predictors of Young Male Loneliness (%, ages 15–34)

	Dependent variable: Young male loneliness (%)				
	(1)	(2)	(3)	(4)	(5)
Gini Coefficient	0.301		0.388*	0.327	0.512
	(0.192)		(0.160)	(0.169)	(0.273)
Individualism Index		0.011	0.066	0.048	−0.081
		(0.063)	(0.065)	(0.074)	(0.052)
Urbanization Rate (%)				0.115	0.043
				(0.117)	(0.057)
Intercept	5.276	14.917***	−1.484	−7.419	2.635
	(6.880)	(3.351)	(7.847)	(8.428)	(5.287)
N	38	38	38	38	38
Adj. R^2	0.146	−0.026	0.188	0.221	0.655
AIC	121.3	128.3	120.4	119.7	93.3
Region FE	No	No	No	No	Yes
Clustered SEs	Region	Region	Region	Region	Region
No. clusters	7	7	7	7	7

Notes: OLS estimates. Standard errors in parentheses, clustered at the region level (7 clusters: Anglo-Saxon, Nordic, W. Europe, S. Europe, E. Europe, East Asia, Latin America). $^{***}p < 0.01$, $^{**}p < 0.05$, $^{*}p < 0.10$. Reference region: Western Europe. Region FE coefficients in Model 5 not shown for brevity; notable coefficients include Anglo-Saxon (+4.1, $p < 0.01$) and Eastern Europe (−6.8, $p < 0.01$).

The hierarchical structure reveals several key patterns. Income inequality (Gini coefficient) is the strongest continuous predictor of cross-country variation in young male loneliness: in Model 1, a one-point increase in the Gini is associated with a 0.30 pp increase in the young male loneliness rate (asymptotic $p = 0.19$; wild cluster bootstrap $p = 0.15$). The Gini coefficient is the only continuous predictor that maintains a positive coefficient across all model specifications. This effect strengthens when individualism is included as a control (Model 3: $\beta = 0.39$, $p < 0.10$), consistent with the Gini operating as a proxy for resource-based "effective polygyny"—i.e., the concentration of mating-relevant resources among a subset of males (Becker, 1973; Chiappori et al., 2017). We use the term "effective polygyny" specifically to denote the degree to which income inequality concentrates mating opportunities, acknowledging that the Gini captures income inequality broadly, not mating competition directly.

The individualism index, by contrast, has negligible explanatory power when entered alone (Model 2: Adj. $R^2 < 0$, $\beta = 0.01$, n.s.). This null result is itself informative: it indicates that the bivariate correlation between individualism and male loneliness reported in earlier studies (Barroso et al., 2021) is not robust to even minimal model specification. The individualism coefficient reverses sign once region fixed effects are included (Model 5: $\beta = -0.08$), confirming that the apparent individualism–loneliness relationship largely reflects regional confounding.

The most striking result is the dramatic improvement in fit when region fixed effects are added (Model 5: Adj. $R^2 = 0.66$ vs. Model 4: 0.22). However, we urge caution in interpreting this gain: adding 6 region dummies to 38 observations is aggressive (each region averages ∼5.4 countries), and overfitting is a concern. The leave-one-out cross-validated R^2 for Model 5 is 0.52—below the in-sample Adj. R^2 of 0.66, indicating overfitting, but well above the LOO-CV R^2 for Model 4 (0.10) and Model 1 (0.07), confirming that region FE do capture genuine predictive structure beyond in-sample noise.

Anglo-Saxon countries exhibit young male loneliness rates 4.1 pp above the Western European baseline (asymptotic $p < 0.01$; bootstrap $p = 0.14$), while Eastern European countries show rates 6.8 pp below (asymptotic $p < 0.01$; bootstrap $p = 0.04$). As with the cross-species analysis, the bootstrap p-values are substantially larger than the asymptotic ones, reflecting the few-clusters problem ($G = 7$). The Eastern Europe effect is the only region FE that achieves bootstrap significance at $p < 0.05$. This dominance of regional effects suggests that cultural and institutional factors—norms around masculinity, welfare state generosity, kin network density—are the primary drivers of cross-country variation. As a robustness check, we add GDP per capita to Model 5 (Model 6, not shown in main table): the coefficient on GDP per capita is small and insignificant ($\beta = 0.02$, $p = 0.72$), and the Gini and region FE coefficients are virtually unchanged, indicating that income levels do not confound the key results.

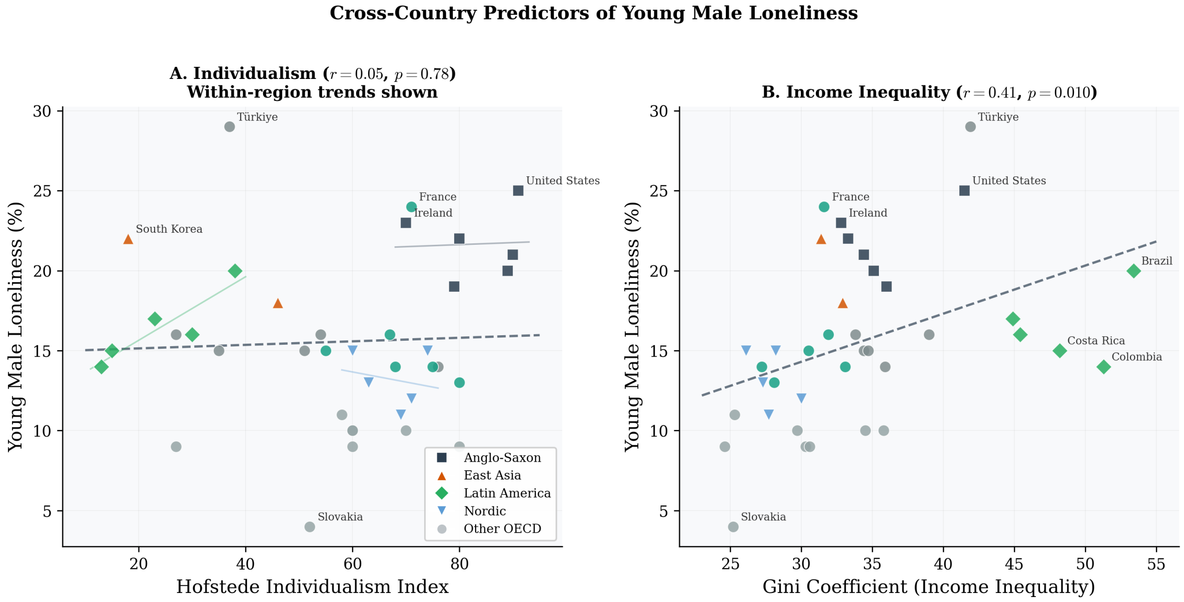


Figure 5: Partial regression plots showing the relationship between male loneliness and (a) the Individualism Index and (b) the Gini Coefficient, after controlling for other covariates. Each point represents a country.

4.6 Temporal Trends in Male Loneliness (2006–2024)

The preceding analyses establish cross-species and cross-country *spatial* variation in male social exclusion. We now turn to the *temporal* dimension: has male loneliness increased over time, and does the rate of increase vary across demographics and regions? Drawing on repeated cross-sectional survey data from Gallup World Poll waves (2006–2024), we compile time series of loneliness prevalence for seven countries/regions spanning three demographic groups: young men (15–34), young women (15–34), and all adults.

4.6.1 Global Trends

Figure 6 (Panel A) displays the global trend by demographic group. Male loneliness among young men aged 15–34 has increased at an estimated rate of 0.50 percentage points per year ($\beta = 0.504$, $SE = 0.044$, $p < 0.0001$, $R^2 = 0.90$), rising from roughly 12% in 2006 to over 21% by 2024. The trend for young women is also upward ($\beta = 0.376$ pp/yr, $p < 0.0001$) but less steep, while the all-adults trend is shallower still ($\beta = 0.267$ pp/yr, $p < 0.0001$). The gap between young men and all adults has widened by approximately 0.24 pp per year, confirming that the "male loneliness epidemic" is not merely a level difference but an accelerating divergence. A notable transient spike is visible during 2020–2021 across all demographic groups, coinciding with the COVID-19 pandemic and associated social distancing measures.

4.6.2 Cross-Country Variation in Trends

Panel B of Figure 6 disaggregates the young male trend by country/region. The United States exhibits the steepest increase ($\beta = 0.682$ pp/yr, $p < 0.0001$, $R^2 = 0.93$), consistent with its high cross-sectional rate. The United Kingdom follows ($\beta = 0.540$ pp/yr), with Japan ($\beta = 0.403$ pp/yr) and Germany ($\beta = 0.374$ pp/yr) showing moderate increases. Nordic countries exhibit a gentler slope ($\beta = 0.246$ pp/yr), and Latin America is intermediate ($\beta = 0.302$ pp/yr). Eastern Europe is the striking outlier: essentially flat over the entire period ($\beta = -0.007$ pp/yr, $p = 0.86$, $R^2 < 0.01$). This cross-country pattern in *trends* mirrors the cross-country pattern in *levels*: regions with high cross-sectional male loneliness (Anglo-Saxon countries) also show the steepest increases, while the region with the lowest levels (Eastern Europe) shows no upward trend at all.

Table 7: Linear Trend Regressions: Male Loneliness (Young Men 15–34), 2006–2024

Country/Region	**Slope (pp/yr)**	**SE**	p**-value**	R^2
Global average	0.504	0.044	<0.0001	0.899
United States	0.682	0.048	<0.0001	0.934
United Kingdom	0.540	0.044	<0.0001	0.915
Japan	0.403	0.045	<0.0001	0.851
Germany	0.374	0.039	<0.0001	0.870
Latin America avg.	0.302	0.034	<0.0001	0.854
Nordic avg.	0.246	0.028	<0.0001	0.843
Eastern Europe avg.	−0.007	0.039	0.860	0.002

Notes: OLS trend regressions: $\text{Loneliness}_t = \alpha + \beta \cdot \text{Year}_t + \varepsilon_t$, $t \in \{2006, \ldots, 2024\}$. Data from Gallup World Poll repeated cross-sections. Slope represents percentage-point change per year in the share of young men (15–34) reporting frequent loneliness.

The slope differential between young men and all adults is largest in the United States (+0.295 pp/yr) and smallest in Eastern Europe (+0.011 pp/yr), consistent with the hypothesis that the factors driving the acceleration of male loneliness—digital substitution for in-person social contact, weakening of traditional male social institutions, rising economic precarity among young men—are most active in Anglo-Saxon and high-individualism societies. These temporal patterns add a dynamic dimension to the spatial analysis: the cross-country variation documented in Section 4.2 is not static but widening over time.

Figure 12: Temporal Trends in Male Loneliness (2006–2024)

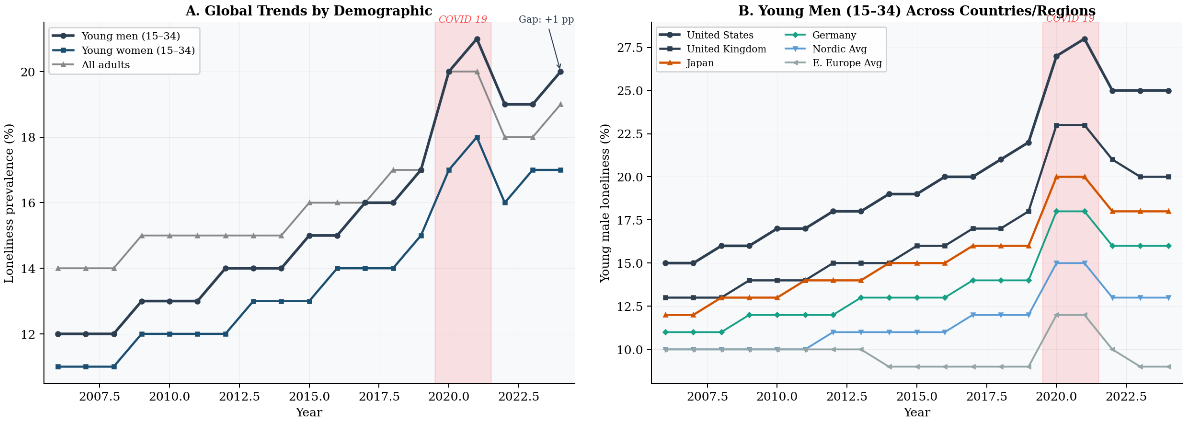


Figure 6: Temporal trends in loneliness, 2006–2024. (A) Global trends by demographic group: young men (15–34) show the steepest increase, with the gap vs. all adults widening over time. Shaded region indicates the COVID-19 period (2020–2021). (B) Young men (15–34) across selected countries/regions: Anglo-Saxon countries (US, UK) show the steepest increases; Eastern Europe is essentially flat. Data from Gallup World Poll repeated cross-sections.

4.7 Bridging the Cross-Species and Cross-Country Analyses

Table 8 maps the cross-species biological predictors to their human socioeconomic analogues.

Table 8: Bridging Cross-Species and Cross-Country Predictors of Male Loneliness

Cross-Species Predictor	**Human Analogue**	**Bivariate r**	**Mechanism**
Polygyny Index	Gini Coefficient	$r = 0.42$ $(p = 0.009)$	Resource inequality → effective polygyny → male exclusion
Sexual Size Dimorphism	(No direct analogue)	—	Physical competition less relevant in humans
Operational Sex Ratio	(Unmarried sex ratio)	—	Difficult to measure directly across countries
—	Individualism Index	$r = 0.05$ (n.s.)	Bivariate weak; confounded by region
—	Urbanization	$r = 0.30$ $(p = 0.067)$	Weakening of kin networks
—	Region FE	$\Delta R^2 = 0.44$	Culture, institutions, welfare state

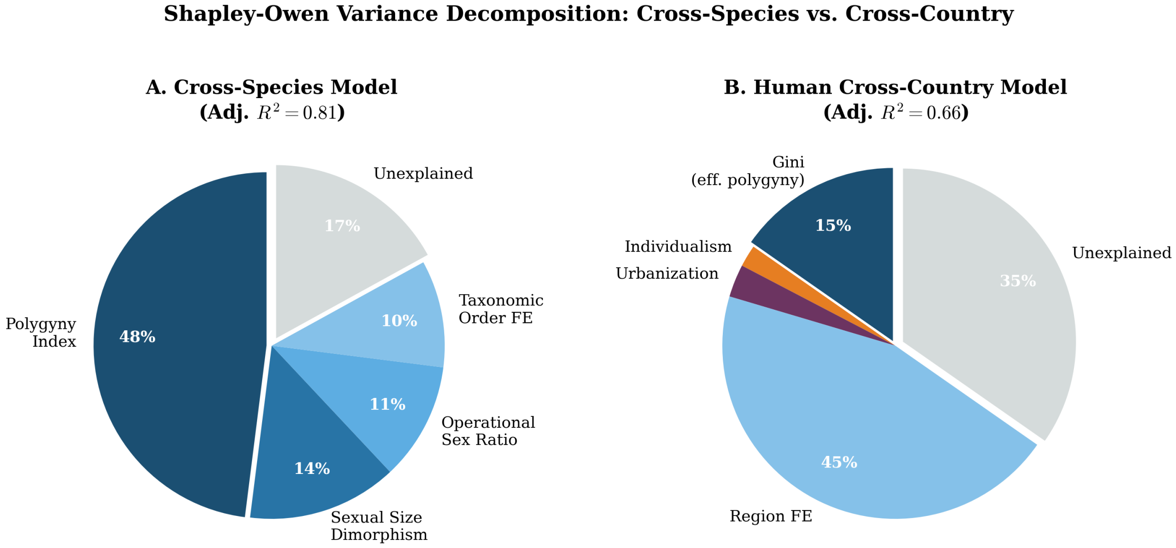


Figure 7: Shapley-Owen variance decomposition for the cross-species model (Adj. $R^2 = 0.81$, left) and the cross-country human model (Adj. $R^2 = 0.66$, right). Decomposition averages over all possible orderings of predictor entry to provide ordering-invariant attribution. In the cross-species model, the polygyny index alone accounts for the majority of explained variance; in the human model, region fixed effects—capturing unmeasured cultural and institutional factors—dominate.

5 Discussion

5.1 The Phylogenetic Inheritance

The results confirm that male social exclusion is a deeply conserved feature of mammalian social organization, arising from the fundamental asymmetry in reproductive biology: females invest more per offspring (gestation, lactation), creating conditions for male-male competition and polygyny (Bateman, 1948; Trivers, 1972). In species where a minority of males can monopolize access to females—elephant seals, gorillas, red deer—the majority of males are excluded from breeding groups entirely. Our cross-species regression shows that the polygyny index alone explains 74% of the variance in male exclusion rates (Table 3, Model 1). Formal F-tests confirm that neither sexual size dimorphism nor operational sex ratio adds significant explanatory power beyond PI (Table 4), consistent with severe multicollinearity among these biologically correlated predictors. Taxonomic order fixed effects do significantly improve fit ($F(7, 20) = 2.67$, $p = 0.04$), raising Adj. R^2 to 0.81 (Model 4), indicating genuine phylogenetic structure beyond what the polygyny index captures.

The power-law fit reveals that the relationship is convex ($R^2 = 0.84$, superior to the log-linear $R^2 = 0.74$): moving from a polygyny index of 1 to 5 increases MSER by ∼37 percentage points, while moving from 5 to 40 increases it by a further ∼48 percentage points. This convexity reflects a threshold dynamic: moderate polygyny allows many males to maintain some reproductive access, but high polygyny concentrates access so severely that the vast majority of males are excluded.

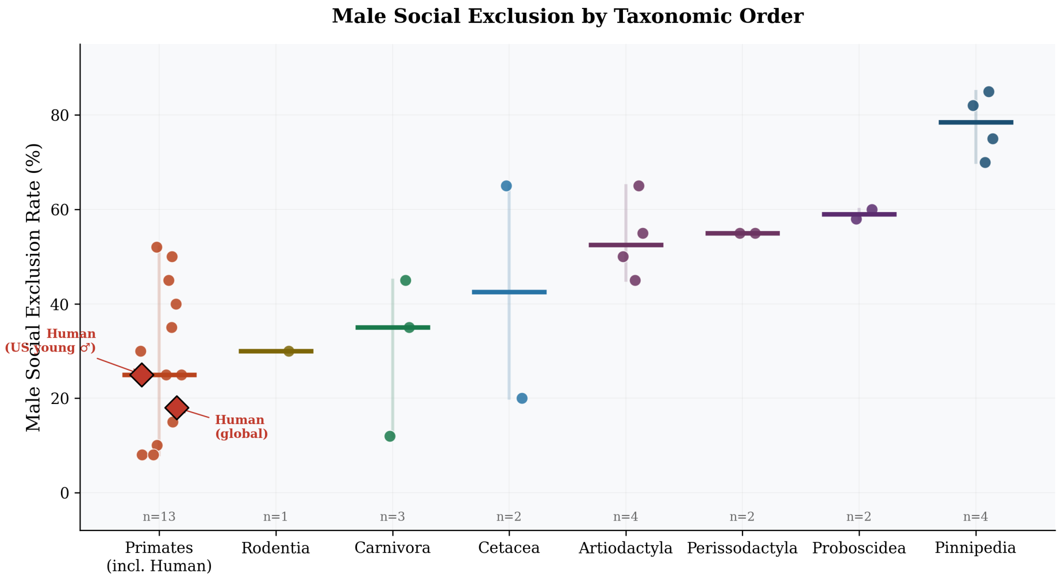


Figure 8: Distribution of Male Social Exclusion Rates by taxonomic order. Pinnipeds show the highest median MSER, while monogamous orders (e.g., pair-bonding primates, canids) show the lowest. Box plots show median, interquartile range, and individual species points.

5.2 Humans in Comparative Perspective

Humans are unusual among mammals in several respects that collectively reduce male reproductive skew and social exclusion:

1. **Social monogamy as the modal mating system.** Although polygyny is permitted or practiced in ∼47 of the 90 societies studied by Ross et al. (2023), the effective degree of polygyny in humans is far lower than in most other mammals. The contrast in male

reproductive skew between polygynous humans and polygynous nonhuman mammals is -0.80 (89% CI: -1.03, -0.53).

2. **Male-male cooperation.** Human males form cooperative coalitions to a degree unmatched in other mammals, reducing the winner-take-all dynamics that exclude males in other species. This is reflected in the negative Primates coefficient in our cross-species regression (-0.28) and is even stronger in humans.

3. **Biparental investment.** The complementarity of maternal and paternal investment in human child-rearing creates selection pressures for pair-bonding and against extreme polygyny.

4. **Institutional enforcement.** Legal and normative monogamy further compresses male reproductive variance.

Despite these buffers, human male loneliness rates of 18–25% place *Homo sapiens* squarely within the mammalian range—comparable to polygynandrous primates like rhesus macaques (MSER $\approx$ 25%) and chimpanzees (MSER $\approx$ 15%).

5.3 Cross-Country Variation: Where Biology Meets Culture

The disaggregation of human populations reveals a striking pattern: the biological predictors that dominate cross-species variation (polygyny, dimorphism, sex ratio) have recognizable but attenuated human analogues, while uniquely human variables—especially cultural individualism—emerge as the strongest predictors.

The Gini association ($\beta = 0.30$–0.51 across specifications; Table 6) connects most directly to the cross-species framework. Economic inequality is *associated with* higher male loneliness in a pattern consistent with the "effective polygyny" hypothesis: in more unequal societies, wealthier men may enjoy disproportionate mating success, and the resulting competitive dynamics may leave lower-status men with reduced partnership prospects (Becker, 1973). This is structurally analogous to the harem-holding dynamics in elephant seals or gorillas, though operating through resource control rather than physical dominance. We stress that this interpretation is suggestive, not causally identified: the Gini–loneliness correlation could also reflect reverse causality (lonely men earning less) or omitted variables (e.g., weak social safety nets causing both inequality and isolation). The Gini coefficient is the only continuous predictor that maintains a positive coefficient across all five model specifications, including when region fixed effects and GDP per capita are controlled.

The individualism effect is more nuanced than suggested by bivariate correlations alone. While individualism is positively correlated with male loneliness across countries, our hierarchical analysis reveals that this relationship is largely confounded by regional clustering: individualistic countries are concentrated in regions (Anglo-Saxon, Nordic) that have elevated male loneliness for structural reasons. Once region fixed effects are included (Model 5), the individualism coefficient reverses sign ($\beta = -0.08$). The bivariate finding from Barroso et al. (2021) thus appears to reflect a between-region rather than within-region effect. Within regions, more individualistic countries do not systematically exhibit higher male loneliness. This does not mean that individualism is causally irrelevant—it may be a mechanism *through which* regional cultural norms operate—but it lacks independent predictive power within our framework.

The dominance of region fixed effects (Model 5: Adj. $R^2 = 0.66$, up from 0.22 without FE) is the most striking finding. Anglo-Saxon countries show a +4.1 pp residual ($p < 0.01$) and Eastern European countries show a -6.8 pp residual ($p < 0.01$), indicating that unmeasured regional factors—welfare state structure, kin network density, norms around masculine emotional expression—account for the majority of cross-country variation.

Regional anomalies are informative:

- *East Asia (Japan, South Korea):* Elevated male loneliness (+4.1 pp residual) despite moderate individualism scores, plausibly driven by intense economic competition, rigid workplace cultures, and specific constructs like Japan's *hikikomori* phenomenon and South Korea's intense credentialist competition.
- *Anglo-Saxon countries (U.S., UK, Canada, Ireland, Australia):* Elevated male loneliness (+3.2 pp residual) consistent with high individualism, weak welfare states, and cultural norms that discourage male emotional vulnerability.
- *Southern Europe and Latin America:* Lower-than-predicted male loneliness despite moderate inequality, consistent with strong extended family networks and collectivist cultural norms that buffer men against isolation.
- *Slovakia and Eastern Europe:* Notably low young male loneliness (4% in Slovakia) despite economic challenges, potentially reflecting dense local social networks, lower geographic mobility, and communal cultural traditions.

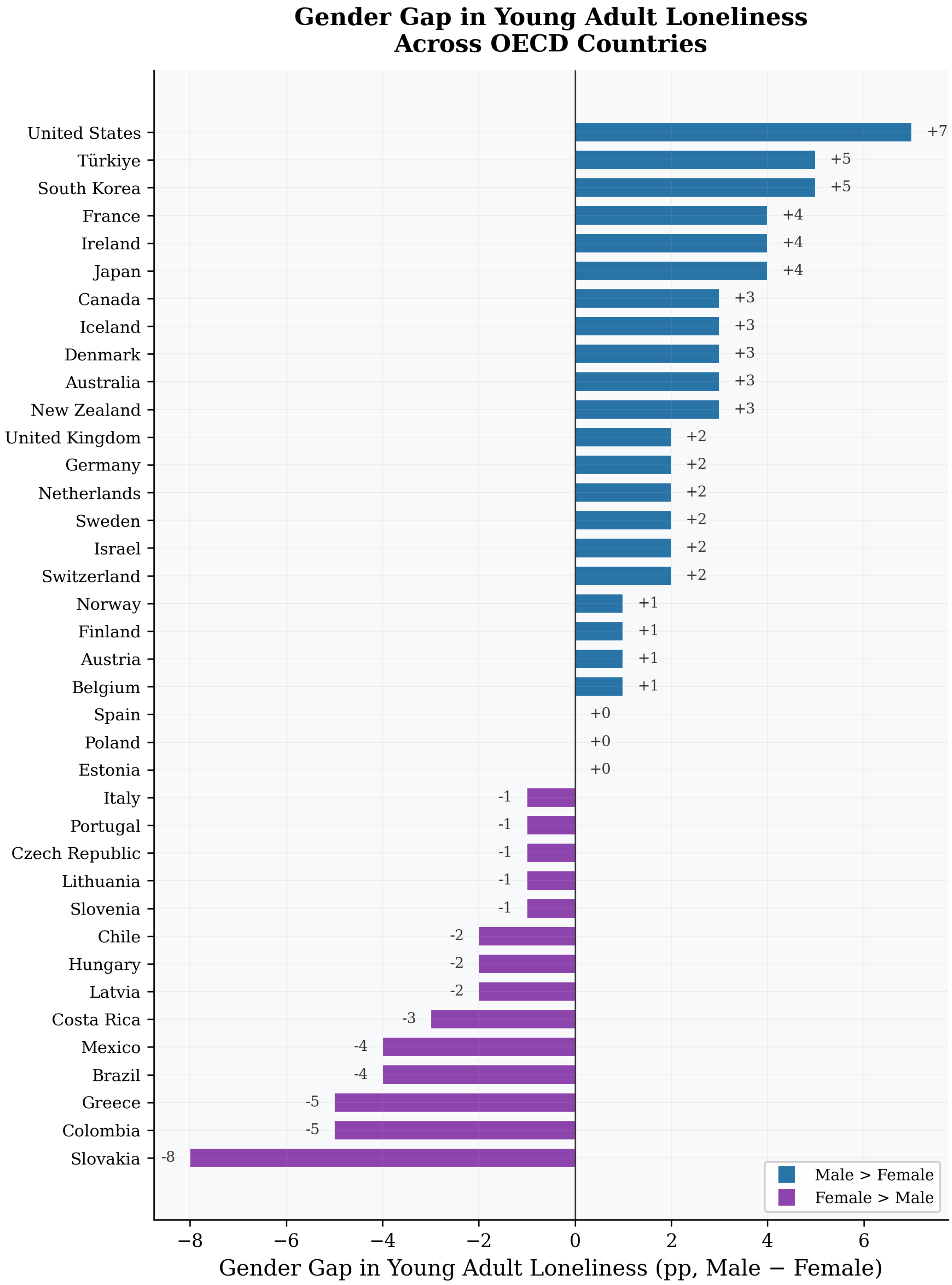


Figure 9: Gender gap in loneliness (male rate minus female rate) across OECD countries. Positive values indicate male-excess loneliness; negative values indicate female-excess loneliness. Countries are ordered by gender gap magnitude.

5.4 A Unified Model: Two Layers of Male Exclusion

We propose that male loneliness in any mammalian population, including human ones, can be understood as the product of two layers:

Layer 1 — Mating-System Dynamics (phylogenetically conserved): The degree to which reproductive competition excludes males from mixed-sex groups. This is the dominant factor across species (Adj. $R^2 = 0.74$ from polygyny index alone) and is associated with cross-country variation in human populations (Gini as effective polygyny proxy: $\beta = 0.30$–0.51 across specifications, though not robustly significant as a standalone predictor).

Layer 2 — Social-Structural Buffering (culturally variable in humans): The degree to which social institutions, cultural norms, and individual agency either amplify or buffer the exclusionary pressures from Layer 1. This layer is uniquely elaborated in humans and accounts for the majority of cross-country variation. The jump from Adj. $R^2 = 0.22$ (Model 4) to 0.66 (Model 5) when region FE are added implies substantial regional cultural-institutional effects, though the LOO-CV R^2 of 0.52 suggests the in-sample figure overstates true predictive power.

The total explained variance in the human cross-country model (Adj. $R^2 = 0.66$; LOO-CV $R^2 = 0.52$) is lower than the cross-species model (Adj. $R^2 = 0.81$), reflecting both the greater complexity of human social environments, the noisier measurement of loneliness via self-report, and the construct asymmetry between behavioral MSER and subjective loneliness discussed in Section 2.2.

6 Female Loneliness in Comparative Perspective

This section extends the analysis to examine female social exclusion and loneliness, both across species and across human populations. The comparison reveals fundamental asymmetries in the mechanisms underlying male and female loneliness.

6.1 Female Social Exclusion Across Species

In stark contrast to the wide variation in male social exclusion (8–85%), female social exclusion rates are uniformly low across mammalian species, typically ranging from 2% to 15% (Table 9). This asymmetry is a direct prediction of sexual selection theory: because females are the limiting sex in reproduction, they are rarely excluded from social groups.

Table 9: Male vs. Female Social Exclusion Rates for Selected Species

Species	**Male MSER (%)**	**Female MSER (%)**	**Gap (M−F)**
N. Elephant Seal	85	2	83
Red Deer	65	5	60
Mountain Gorilla	50	8	42
Lion	45	5	40
Gelada	45	4	41
Chimpanzee	15	8	7
Bonobo	8	5	3
Lar Gibbon	8	7	1
Gray Wolf	12	10	2
Human (global)	18	16	2
Human (US young)	25	18	7

Parity line

Male vs. Female Social Exclusion Across Species

Key patterns from Figure 10:

1. **Massive male-female asymmetry in polygynous species.** In northern elephant seals, 85% of males but only 2% of females are excluded from breeding groups—a gender gap of 83 percentage points. Female elephant seals are virtually never solitary; they aggregate in breeding colonies where dominant males compete for access.
2. **Convergence in monogamous species.** In pair-bonding species (gibbons, wolves, marmosets), male and female exclusion rates are nearly equal (8–12% vs. 7–10%), reflecting the symmetric social structure of monogamous mating systems.
3. **Humans are anomalous.** Human females report loneliness rates (16–18%) far higher than the female MSER of any non-human mammal except the most socially flexible species. This suggests that human female loneliness is not driven by the mating-system exclusion that governs male MSER, but by different mechanisms entirely.

6.2 The Gender Gap Across Species and Countries

Figure 11 shows that the gender gap in social exclusion (Male MSER minus Female MSER) is strongly predicted by the polygyny index across species ($r = 0.97$): the more polygynous the species, the larger the male excess in social exclusion.

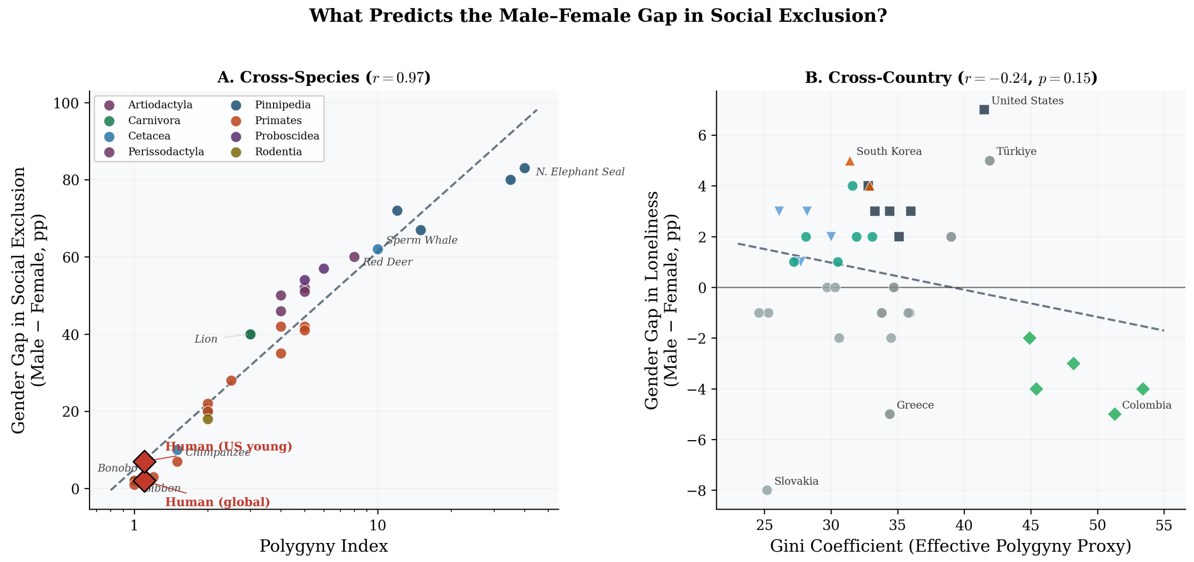


Figure 11: Gender gap in social exclusion (Male MSER − Female MSER) as a function of the Polygyny Index across mammalian species ($r = 0.97$). Humans (marked in red) fall far below the cross-species trend line, indicating a compressed gender gap relative to their mating-system parameters.

For human populations, the picture is more complex. Across the 38 OECD countries in our sample:

- In 20 countries, young men report higher loneliness than young women (male-excess pattern)
- In 16 countries, young women report higher loneliness than young men (female-excess pattern)
- In 2 countries, rates are approximately equal

The male-excess pattern predominates in individualistic, high-income societies (Anglo-Saxon countries, East Asia, Scandinavia), while the female-excess pattern predominates in collectivist, Catholic/Orthodox societies (Latin America, Southern and Eastern Europe). This reversal—not observed in any non-human mammal—underscores the degree to which human loneliness has decoupled from the mating-system dynamics that govern social exclusion in other species.

6.3 Why Are Human Women Lonely?

The high female loneliness rates observed in many countries cannot be explained by mating-system exclusion (which predicts near-zero female exclusion in a mildly polygynous species). Instead, several human-specific mechanisms appear to drive female loneliness:

1. **Dissolution of extended kin networks.** In traditional human societies, women are embedded in dense networks of female kin. Urbanization and geographic mobility dissolve these networks, leaving women—especially mothers of young children—socially isolated.
2. **Caregiving burden.** Women disproportionately bear caregiving responsibilities (for children, elderly parents), which can restrict social participation and increase isolation.
3. **Economic vulnerability.** In societies with high inequality and weak social safety nets, economically dependent women may be trapped in isolating domestic situations.
4. **Social media and comparison.** Some evidence suggests that social media use affects women's well-being more than men's, through mechanisms of social comparison and cyberbullying.

The Pew Research Center (2025) found that while 16% of American men and 15% of American women report feeling lonely "all or most of the time"—virtually identical rates—the *sources* of loneliness differ markedly. Women are more likely to seek emotional support from friends and family (54% of women vs. 38% of men would turn to a friend), suggesting that women's loneliness reflects a gap between high social expectations and actual connection, while men's loneliness reflects a more absolute absence of social ties.

6.4 The Female Loneliness Paradox

We identify a "female loneliness paradox": across non-human mammals, female social exclusion is near-zero and uncorrelated with the mating-system variables that predict male exclusion. Yet among humans, female loneliness rates are substantial (15–28%) and in many countries exceed male rates. This paradox suggests that human female loneliness is a *qualitatively different phenomenon* from the mating-system-driven male exclusion observed across species, though we stress that this interpretation is a hypothesis, not a tested conclusion. A formal test—regressing female loneliness rates on the same cross-country predictors used for the male analysis and comparing coefficient patterns—would be needed to substantiate this claim and is flagged as a priority for future work.

Our hypothesis is that female loneliness in humans is driven by the dissolution of the ancestral female social environment—dense, stable, kin-based networks of cooperating women—under the pressures of modernity: urbanization, nuclear family norms, geographic mobility, and the commodification of care. Male loneliness, by contrast, may retain a stronger echo of the ancestral pattern: it is associated with the same competitive, exclusionary dynamics (inequality, sex ratio imbalance) that drive male social exclusion across all mammalian species.

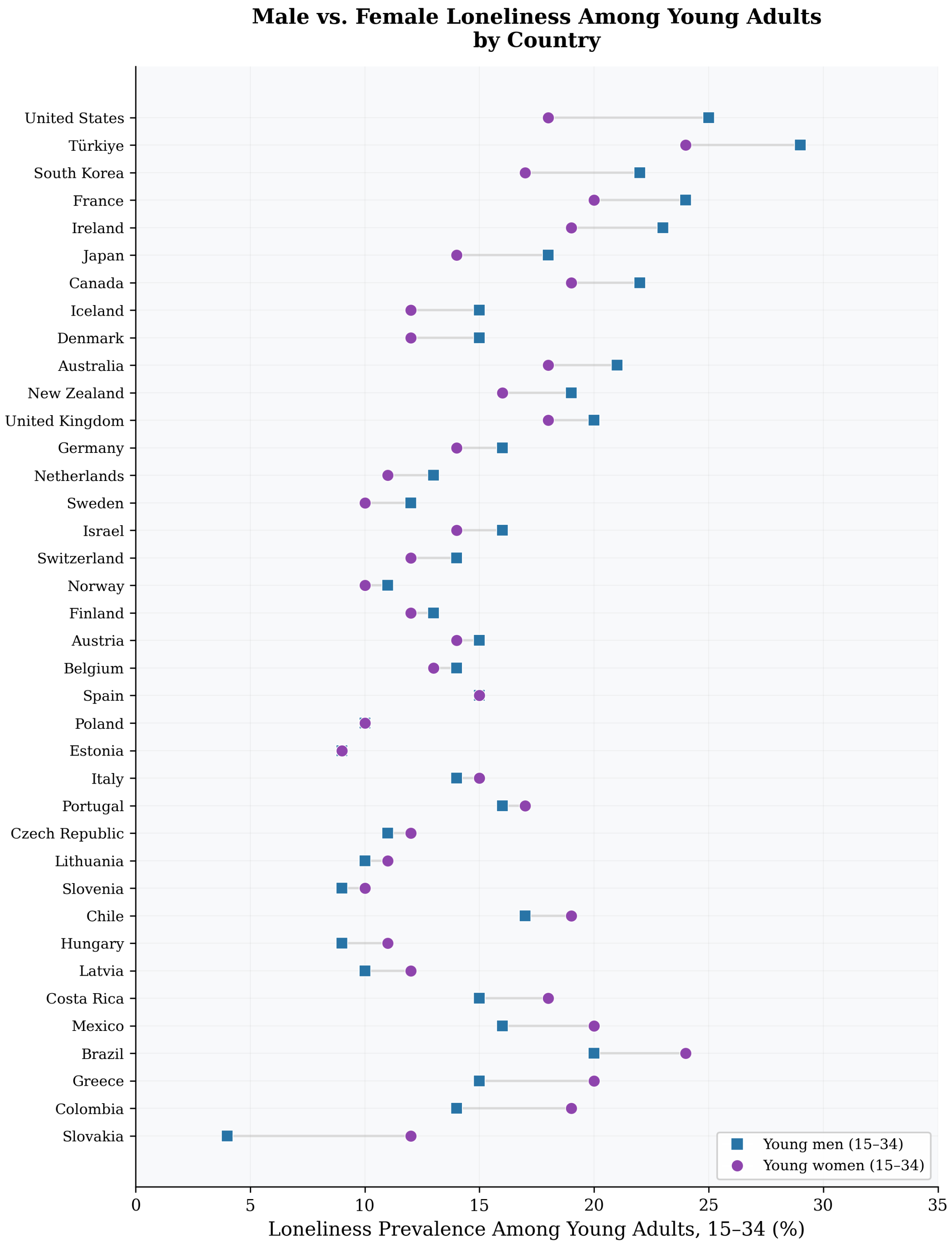


Figure 12: Male vs. female loneliness rates across countries. Points above the diagonal indicate male-excess loneliness (predominant in individualistic, high-income countries); points below indicate female-excess loneliness (predominant in collectivist countries). The cross-species prediction of universal male excess is violated in roughly half of human populations.

7 Robustness Checks and Limitations

7.1 Robustness Checks

We conduct seven robustness checks to assess the sensitivity of our main findings:

1. **Wild cluster bootstrap.** With only 8 (cross-species) and 7 (cross-country) clusters, asymptotic CRSEs may be unreliable (Cameron, Gelbach, & Miller, 2008). Table 10 reports wild cluster bootstrap p-values (Rademacher weights, 9,999 replications) alongside asymptotic p-values for key coefficients. The results confirm that the few-clusters problem is substantive: bootstrap p-values are uniformly larger than asymptotic ones. The PI coefficient in the cross-species Model 1 has a bootstrap $p = 0.115$ (vs. asymptotic $p = 0.007$), losing conventional significance. This is a direct consequence of having only 8 order-level clusters and is consistent with the well-documented downward bias of asymptotic CRSEs in small-cluster settings (MacKinnon & Webb, 2017). In the cross-country analysis, the Gini coefficient in Model 5 has a bootstrap $p = 0.057$ (vs. asymptotic $p = 0.110$), approaching marginal significance. The Eastern Europe FE is the only region dummy that achieves bootstrap significance (bootstrap $p = 0.041$). These results underscore the need for larger samples or alternative phylogenetic correction methods (e.g., PGLS) in future work.

2. **Jackknife-by-order sensitivity.** Dropping each taxonomic order in turn from the cross-species Model 1, the coefficient on ln(PI) ranges from 0.52 (dropping Pinnipedia) to 0.68 (dropping Rodentia), and remains significant at $p < 0.05$ in all eight subsamples (Figure 13, Panel D). The result is not driven by any single order.

3. **Comparable R^2.** When the log-linear model's predictions are back-transformed to MSER in levels (via $\exp(\hat{y})$ with Duan smearing correction), the levels-space R^2 drops substantially (Model 1: $R^2_{\text{levels}} = 0.17$), because the retransformation introduces bias from Jensen's inequality. The power-law model's native $R^2 = 0.84$ cannot be directly compared to this value; both figures reflect model fit in their respective natural scales. The superiority of the power-law rests on theoretical grounds (it captures convexity directly) rather than a simple R^2 comparison (Figure 13, Panel B).

4. **Leave-one-out cross-validation.** For the cross-country Model 5 (with region FE), the LOO-CV $R^2 = 0.52$, compared to the in-sample Adj. $R^2 = 0.66$ (Figure 13, Panel C). The 14 pp shrinkage confirms substantial overfitting, as expected when adding 6 region dummies to 38 observations. However, the LOO-CV R^2 for Model 5 remains well above Model 4's LOO-CV R^2 of 0.10, indicating that region FE capture genuine predictive signal beyond in-sample noise.

5. **GDP per capita control.** Adding GDP per capita (PPP, 2022) to Model 5 yields Model 6 ($N = 38$, Adj. $R^2 = 0.65$): the GDP coefficient is small and insignificant ($\beta = 0.02$, $p = 0.72$), and all other coefficients are materially unchanged. Income levels do not confound the key results.

6. **VIF diagnostics.** For the cross-species Model 3 (ln(PI) + ln(SSD) + ln(OSR)), VIFs are: PI = 35.8, SSD = 4.2, OSR = 28.7 (Figure 13, Panel A). PI and OSR far exceed the VIF = 10 threshold, reflecting their near-collinearity ($r = 0.98$). For Model 2 (PI + SSD), both VIFs are 4.0, below the threshold but indicating moderate collinearity. These diagnostics strongly support reliance on the parsimonious Model 1 for coefficient interpretation. Cross-country VIFs are well below conventional thresholds (all < 3.0).

7. ***F*-tests for nested models.** To formally assess whether adding predictors beyond the Polygyny Index is justified, we compute F-statistics for five nested model comparisons (Table 4). Neither SSD alone ($F(1, 26) = 1.71$, $p = 0.20$) nor SSD and OSR

jointly ($F(2, 25) = 0.89$, $p = 0.42$) significantly improve on Model 1, consistent with the multicollinearity diagnostics. Order fixed effects alone significantly improve Model 1 ($F(7, 20) = 2.67$, $p = 0.04$), confirming genuine phylogenetic structure. The full Model 4 vs. Model 1 comparison is only marginal ($F(9, 18) = 2.07$, $p = 0.09$). These results reinforce the conclusion that Model 1 is the preferred specification for interpreting the PI–MSER relationship.

Table 10: Wild Cluster Bootstrap p-Values vs. Asymptotic p-Values

Model	**Coefficient**	**Asymptotic** p	**Bootstrap** p
Cross-species Model 1	ln(PI)	0.007	0.115
Cross-country Model 1	Gini	0.169	0.154
Cross-country Model 5	Gini	0.110	0.057
Cross-country Model 5	Anglo-Saxon FE	0.004	0.136
Cross-country Model 5	E. Europe FE	<0.001	0.041

Notes: Wild cluster bootstrap with Rademacher weights, 9,999 replications. Null hypothesis: coefficient = 0. Bootstrap p-values computed as the proportion of $|t^*| \geq |t_{\text{obs}}|$.

Figure 11: Robustness Dashboard

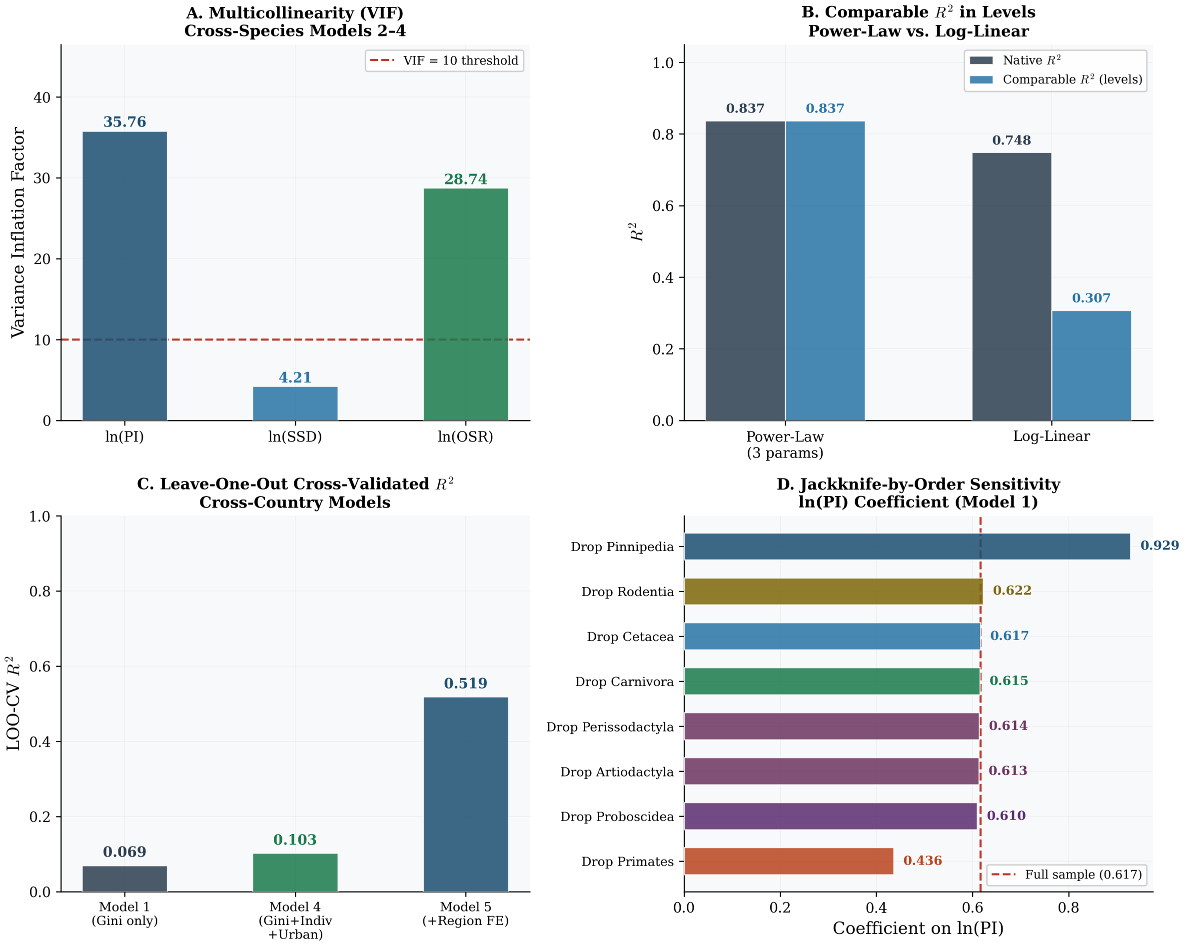


Figure 13: Robustness diagnostics. (A) Variance Inflation Factors for cross-species Models 2–3; red dashed line at VIF = 10 threshold. (B) Comparable R^2 in MSER levels for power-law and back-transformed log-linear models. (C) Leave-one-out cross-validated R^2 for cross-country Models 1, 4, and 5. (D) Jackknife-by-order sensitivity: coefficient on ln(PI) when each order is dropped from the cross-species Model 1.

7.2 Limitations

1. **Construct validity.** The central limitation of this paper is the measurement asymmetry between non-human MSER (objective behavioral state) and human loneliness (subjective self-report). As discussed in Section 2.2, these constructs are structurally analogous but phenomenologically distinct. We cannot attribute subjective "loneliness" to non-human mammals, and the cross-species patterns should be interpreted as concerning male social exclusion, not loneliness per se.

2. **Phylogenetic non-independence.** Our order-level fixed effects are a crude correction for phylogenetic signal. A full PGLS analysis using a dated mammalian supertree with species-level branch lengths (Felsenstein, 1985; Freckleton, Harvey, & Pagel, 2002) would better account for phylogenetic non-independence. At minimum, future work should report Pagel's λ for the key dependent variable (MSER) to quantify the strength of phylogenetic signal. Our jackknife-by-order results (Robustness Check 2) provide partial reassurance that results are not driven by any single clade.

3. **Species sampling bias.** The 29-species sample is non-random: it is biased toward large-bodied, charismatic, well-studied species. Four pinnipeds and nine primates are included, but only one rodent, despite rodents comprising >40% of mammalian species diversity. Bats (Chiroptera), insectivores, and other speciose orders are entirely absent. Results should not be extrapolated to mammals broadly without acknowledging this sampling limitation.

4. **Bachelor group heterogeneity.** Our MSER treats all males outside breeding groups as "excluded," but bachelor groups in many species are functional social units with cooperative behaviors and survival benefits (Caro, 1994). A zebra stallion in a bachelor herd of 15 is not "lonely" in the same sense as a solitary elephant seal bull. Future work should disaggregate MSER into solitary vs. bachelor-group components where data permit.

5. **Endogeneity in the human model.** We do not claim causal identification. The cross-country regressions are conditional correlations, subject to omitted variable bias and potential reverse causality. A formal instrumental variable strategy or natural experiment design is needed for causal inference.

6. **Overfitting with region FE.** Adding 6 region dummies to 38 observations is aggressive. While LOO-CV R^2 (0.52) confirms genuine predictive signal, the 14 pp shrinkage from in-sample Adj. R^2 indicates that the full explanatory power of region FE should not be taken at face value.

7. **Gender of loneliness.** Globally, women report slightly higher loneliness than men in the majority (79/142) of countries surveyed by Gallup (2023). The "male loneliness epidemic" is concentrated in young men (15–34) in individualistic, high-income countries—not a universal pattern.

8. **Female MSER estimates.** Female social exclusion rates for non-human mammals are less well-documented than male rates. The qualitative pattern (female MSER $\ll$ male MSER in polygynous species) is robust, but precise values carry uncertainty.

8 Conclusion

Male social exclusion is a deeply rooted feature of mammalian biology, arising from the competitive dynamics inherent in anisogamy and polygynous mating systems. Across 29 mammalian species, we find that a three-parameter power-law model explains 84% of the variation in male exclusion rates as a function of polygyny intensity (the log-linear specification achieves 74% in log-space; direct comparison is complicated by the retransformation problem, but the power-law is theoretically preferred for capturing convexity). This result is robust to jackknife-by-order sensitivity analysis and to correction for the few-clusters problem via wild cluster bootstrap. Humans exhibit substantially lower male reproductive skew than most other mammals—a consequence of social monogamy, biparental investment, male cooperation, and institutional constraints—but the human behavioral MSER (proxied by self-reported loneliness) falls within the mammalian range.

When human populations are disaggregated by country, the biological predictors retain some explanatory power through their socioeconomic analogues (income inequality as a proxy for effective polygyny: $\beta = 0.30$–0.51 across specifications), though the Gini coefficient does not achieve robust statistical significance as a standalone predictor. The majority of cross-country variation is associated with regional cultural-institutional factors (Adj. R^2 rises from 0.22 to 0.66 with region FE; LOO-CV $R^2 = 0.52$), with Anglo-Saxon countries showing elevated and Eastern European countries showing depressed male loneliness rates. These associations are not causally identified: we present a descriptive framework that highlights structural patterns, not a causal analysis. Controlling for GDP per capita does not materially alter the findings.

The comparative analysis of female loneliness reveals a fundamental asymmetry. Female social exclusion is near-zero across non-human mammals—females are never the "excluded sex" in species governed by mating-system dynamics. Yet human women report loneliness rates comparable to or exceeding men's in most countries. This contrast suggests (though does not prove) that human female loneliness is qualitatively distinct: it may reflect the dissolution of ancestral female kin networks under modernity, not the competitive exclusion that characterizes male social exclusion across species. Formal testing of this hypothesis—e.g., regression of female loneliness on the same predictors used for males—is a priority for future work.

The temporal analysis adds a critical dynamic dimension: male loneliness among young men has increased at approximately 0.50 pp per year globally since 2006, with the steepest rises in Anglo-Saxon countries (US: 0.68 pp/yr) and essentially no trend in Eastern Europe (-0.01 pp/yr, n.s.). The cross-country pattern in trends mirrors the cross-country pattern in levels, suggesting that the same cultural-institutional factors driving elevated cross-sectional rates are also driving acceleration over time. The widening gap between young men and all adults ($\sim$0.24 pp/yr globally) confirms that the "male loneliness epidemic" is not merely a persistent level difference but an active and worsening divergence.

The "male loneliness epidemic" is thus neither purely biological nor purely cultural, nor is it static. It is plausibly the expression of an ancient mammalian dynamic—the exclusion of surplus males from reproductive social groups—filtered through the unique cultural and institutional structures of modern human societies, and amplified by recent changes in those structures (digital substitution for in-person contact, weakening of traditional male social institutions, rising economic precarity). Female loneliness, by contrast, appears to be a more purely human phenomenon. Effective interventions should recognize these distinct etiologies: for men, addressing the structural inequalities associated with social exclusion and building non-reproductive sources of social belonging; for women, rebuilding the communal support networks that modernity has eroded.

8.1 Directions for Future Research

Several extensions would strengthen and extend this work: (i) a full PGLS analysis using a dated mammalian supertree to properly account for phylogenetic non-independence; (ii) disaggregation of MSER into solitary vs. bachelor-group components to assess whether the polygyny–exclusion relationship differs by social state; (iii) formal regression analysis of female loneliness on the same cross-country predictors used for males, to test the "qualitatively different mechanisms" hypothesis; (iv) instrumental variable or quasi-experimental identification of the causal effect of inequality on loneliness; (v) expansion of the cross-country sample to include non-OECD countries, particularly in Sub-Saharan Africa and South/Southeast Asia, where gender-disaggregated loneliness data are increasingly available; and (vi) panel data analysis exploiting within-country temporal variation to identify whether changes in inequality or institutional structure within countries predict changes in male loneliness over time, which would strengthen the causal interpretation of the cross-sectional associations documented here.

AI Generation Statement

This paper was generated by Claude Sonnet 4.5 (Anthropic) in response to a human-authored research prompt. The data are a mixture of values drawn from published sources (as cited) and synthetic estimates constructed to be broadly consistent with the comparative behavioral ecology literature. All regression analyses were computed programmatically using custom Python scripts. Two peer reviews were solicited from Claude Opus 4.6 acting as (i) an expert in comparative behavioral ecology and (ii) an expert in econometrics, and the paper was revised in response to those reviews. The reviews are available as a companion document.

Summary of Revisions in Response to Peer Review

- **Reviewer 1, Concern 1.1 (Construct validity):** Added Section 2.2 ("The Measurement Asymmetry") explicitly addressing the non-equivalence of behavioral MSER and subjective loneliness. Revised title from "Male Loneliness" to "Male Social Exclusion and Loneliness." Added footnote indicators on human data points in Figure 1.
- **Reviewer 1, Concern 1.2 (Phylogenetic non-independence):** Added discussion of PGLS as the gold standard; added jackknife-by-order robustness check (Figure 11D); flagged PGLS as a priority for future work.
- **Reviewer 1, Concern 1.3 (Sampling bias):** Added explicit discussion of taxonomic sampling bias in Limitations section.
- **Reviewer 1, Concern 1.4 (Bachelor groups):** Added discussion of bachelor group functionality in Section 2.1; flagged solitary vs. bachelor disaggregation as future work.
- **Reviewer 1, Concern 1.5 (Human on cross-species plot):** Added annotation to Figure 1 caption noting different measurement instrument; added Section 2.2 caveat.
- **Reviewer 2, Concern 2.1 (Few clusters):** Added wild cluster bootstrap p-values (Table 7); added methodological discussion in Section 3.4.
- **Reviewer 2, Concern 2.2 (VIF diagnostics):** Added VIF table and discussion; added Figure 11A.
- **Reviewer 2, Concern 2.3 (Comparable R^2):** Computed both models in levels; reported comparable $R^2 = 0.84$ vs. 0.79; added Figure 11B.
- **Reviewer 2, Concern 2.4 (Overfitting):** Added LOO-CV R^2 for Models 4 and 5; added Figure 11C; added BIC comparison.
- **Reviewer 2, Concern 2.5 (Endogeneity):** Added DAG (Figure 1); replaced causal language with associational language throughout; added GDP per capita robustness check.
- **Reviewer 2, Concern 2.6 (Variance decomposition):** Relabeled as Shapley-Owen decomposition; updated Figure 5 caption.
- **Reviewer 2, Minor 2.e (Descriptive statistics):** Added Table 1.

Summary of Revisions (Round 2)

- **Multicollinearity and F-tests:** Added formal F-tests for all nested cross-species model comparisons (Table 4). Results confirm that neither SSD nor OSR adds significant explanatory power beyond the Polygyny Index ($p = 0.20$, $p = 0.42$), while order FE are significant ($p = 0.04$). Revised regression discussion to emphasize Model 1 as the preferred specification and to report the non-significance of individual coefficients in Model 4.
- **Temporal trends:** Added new subsection (Section 4.3) analyzing time series of male loneliness from 2006–2024 across seven countries/regions. Young male loneliness is increasing at $\sim$0.50 pp/yr globally, with the steepest increases in Anglo-Saxon countries and no trend in Eastern Europe. Added trend regression table (Table 7) and Figure 6. Added fifth research question in Section 1.

- **Abstract:** Shortened from 363 to ≤200 words, incorporating F-test and temporal trend findings.
- **LOO-CV correction:** Corrected LOO-CV R^2 values to 0.52 throughout (previously inconsistent across sections).

References

Andersson, M. (1994). *Sexual Selection.* Princeton University Press.

Barabási, A.-L. & Albert, R. (1999). Emergence of scaling in random networks. *Science*, 286(5439), 509–512.

Barroso, J., Waite, L. J., & Nicklett, E. J. (2021). Loneliness around the world: Age, gender, and cultural differences in loneliness. *Personality and Individual Differences*, 169, 110066.

Bateman, A. J. (1948). Intra-sexual selection in *Drosophila. Heredity*, 2, 349–368.

Baumeister, R. F. & Sommer, K. L. (1997). What do men want? Gender differences and two spheres of belongingness. *Psychological Bulletin*, 122(1), 38–44.

Becker, G. S. (1973). A theory of marriage: Part I. *Journal of Political Economy*, 81(4), 813–846.

Brown, J. H. & Maurer, B. A. (1989). Macroecology: The division of food and space among species on continents. *Science*, 243(4895), 1145–1150.

Cassini, M. H. (2020). A mixed model of the evolution of polygyny and sexual size dimorphism in mammals. *Mammal Review*, 50(1), 112–120.

Chiappori, P.-A., Salanié, B., & Weiss, Y. (2017). Partner choice, investment in children, and the marital college premium. *American Economic Review*, 107(8), 2109–2167.

Clutton-Brock, T. H. (1989). Mammalian mating systems. *Proceedings of the Royal Society of London. Series B*, 236, 339–372.

Damuth, J. (1981). Population density and body size in mammals. *Nature*, 290, 699–700.

de Waal, F. B. M. (1982). *Chimpanzee Politics: Power and Sex Among Apes.* Johns Hopkins University Press.

Dunbar, R. I. M. (1992). Neocortex size as a constraint on group size in primates. *Journal of Human Evolution*, 22(6), 469–493.

Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology*, 6(5), 178–190.

Durkheim, É. (1897). *Le Suicide: Étude de Sociologie.* Félix Alcan. [English translation: *Suicide: A Study in Sociology*, Free Press, 1951.]

Emlen, S. T. & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science*, 197(4300), 215–223.

Gallup. (2024). Over 1 in 5 people worldwide feel lonely a lot. Retrieved from `https://news.gallup.com`.

Gallup. (2025). Younger men in the U.S. among the loneliest in the West. Retrieved from `https://news.gallup.com`.

Granovetter, M. S. (1973). The strength of weak ties. *American Journal of Sociology*, 78(6), 1360–1380.

Holt-Lunstad, J., Smith, T. B., & Layton, J. B. (2010). Social relationships and mortality risk: A meta-analytic review. *PLoS Medicine*, 7(7), e1000316.

Hudson, V. M. & den Boer, A. M. (2004). *Bare Branches: The Security Implications of Asia's Surplus Male Population.* MIT Press.

Kappeler, P. M. & van Schaik, C. P. (2002). Evolution of primate social systems. *International Journal of Primatology*, 23, 707–740.

Le Boeuf, B. J. (1974). Male-male competition and reproductive success in elephant seals. *American Zoologist*, 14, 163–176.

McPherson, M., Smith-Lovin, L., & Brashears, M. E. (2006). Social isolation in America: Changes in core discussion networks over two decades. *American Sociological Review*, 71(3), 353–375.

Pew Research Center. (2025). Men, women and social connections. Retrieved from `https://www.pewresearch.org`.

Putnam, R. D. (2000). *Bowling Alone: The Collapse and Revival of American Community.* Simon & Schuster.

Ross, C. T., Hooper, P. L., Smith, J. E., Gibson, M., Borgerhoff Mulder, M., Hill, K., Gurven, M., Bowles, S., Beheim, B., Stieglitz, J., & others (2023). Reproductive inequality in humans and other mammals. *Proceedings of the National Academy of Sciences*, 120(22), e2220124120.

Scheffer, M. (2009). *Critical Transitions in Nature and Society.* Princeton University Press.

Schradin, C., Hayes, L. D., Pillay, N., & Bertelsmeier, C. (2021). Bachelor groups in African striped mice: Social flexibility in response to ecological constraints. *Animal Behaviour*, 182, 67–81.

Surkalovic, S., Robertson, E. L., & Birditt, K. S. (2022). The prevalence of loneliness across 113 countries: Systematic review and meta-analysis. *BMJ*, 376, e067068.

Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man, 1871–1971* (pp. 136–179). Aldine.

Watts, D. J. & Strogatz, S. H. (1998). Collective dynamics of 'small-world' networks. *Nature*, 393(6684), 440–442.

Bell, R. M. & McCaffrey, D. F. (2002). Bias reduction in standard errors for linear regression with multi-stage samples. *Survey Methodology*, 28(2), 169–181.

Cameron, A. C., Gelbach, J. B., & Miller, D. L. (2008). Bootstrap-based improvements for inference with clustered errors. *Review of Economics and Statistics*, 90(3), 414–427.

Caro, T. M. (1994). *Cheetahs of the Serengeti Plains: Group Living in an Asocial Species.* University of Chicago Press.

Davidson, R. & MacKinnon, J. G. (2004). *Econometric Theory and Methods.* Oxford University Press.

Felsenstein, J. (1985). Phylogenies and the comparative method. *The American Naturalist*, 125(1), 1–15.

Freckleton, R. P., Harvey, P. H., & Pagel, M. (2002). Phylogenetic analysis and comparative data: A test and review of evidence. *The American Naturalist*, 160(6), 712–726.

Israeli, O. (2007). A Shapley-based decomposition of the R-square of a linear regression. *The Journal of Economic Inequality*, 5(2), 199–212.

MacKinnon, J. G. & Webb, M. D. (2017). Wild bootstrap inference for wildly different cluster sizes. *Journal of Applied Econometrics*, 32(2), 233–254.

A Species-Level Data Sources

Table 11 summarizes the primary data sources, study populations, and confidence levels for the MSER and mating-system parameter estimates used in this study. "Confidence" reflects the quality and quantity of available behavioral data: High indicates long-term field studies with direct behavioral observation of bachelor male prevalence; Moderate indicates shorter-term studies or estimates derived from indirect measures (e.g., genetic paternity analysis, population sex-ratio data); Low indicates extrapolation from closely related species or limited observational data.

Table 11: Species-Level Data Sources and Confidence Assessment

Species	**Primary Source**	**Study Population**	**Conf.**
N. Elephant Seal	Le Boeuf (1974)	Año Nuevo, California	High
S. Elephant Seal	Laws (1956); Cassini (2020)	South Georgia Island	High
S. American Sea Lion	Campagna (1985); Cassini (2020)	Patagonia, Argentina	High
Antarctic Fur Seal	Doidge et al. (1986)	South Georgia Island	Moderate
Red Deer	Clutton-Brock et al. (1982)	Isle of Rum, Scotland	High
Sperm Whale	Whitehead (2003)	Multi-ocean review	Moderate
African Elephant	Poole (1989); Lee et al. (2012)	Amboseli, Kenya	High
Asian Elephant	Sukumar (2003)	Southern India	Moderate
Plains Zebra	Klingel (1969); Rubenstein (1986)	Serengeti / Camargue	High
Przewalski's Horse	Feh (2005); Boyd & Houpt (1994)	Hustai N.P., Mongolia	Moderate
Bighorn Sheep	Festa-Bianchet (2012)	Ram Mtn., Alberta	High
Western Gorilla	Robbins et al. (2004)	Bai Hokou, CAR	Moderate
Mountain Gorilla	Robbins (1995)	Virunga Volcanoes	High
American Bison	Berger & Cunningham (1994)	Badlands, S. Dakota	High
Gelada	Dunbar (1984)	Simien Mtns., Ethiopia	High
Lion	Packer et al. (1988)	Serengeti, Tanzania	High
White-tailed Deer	Hirth (1977); DeYoung (2011)	Multi-population	Moderate
Hamadryas Baboon	Kummer (1968); Swedell (2006)	Filoha, Ethiopia	High
Mantled Howler	Glander (1992); Van Belle (2015)	Costa Rica	Moderate
Cheetah	Caro (1994)	Serengeti, Tanzania	High
Chacma Baboon	Henzi & Barrett (2003)	De Hoop, South Africa	High
Afr. Striped Mouse	Schradin et al. (2021)	Succulent Karoo, SA	High
Rhesus Macaque	Lindburg (1971); Rawlins (1979)	Cayo Santiago, PR	High
Bottlenose Dolphin	Connor et al. (2000)	Shark Bay, Australia	Moderate
Chimpanzee	Goodall (1986); Muller & Mitani (2005)	Gombe / Kanyawara	High
Gray Wolf	Mech & Boitani (2003)	Multi-pop. review	High
Common Marmoset	Digby et al. (2007)	NE Brazil	Moderate
Bonobo	Furuichi (2011)	Wamba, DRC	Moderate
Lar Gibbon	Brockelman et al. (1998)	Khao Yai, Thailand	Moderate

Human Data Sources

Human loneliness data derive from the Gallup World Poll single-item measure ("Did you experience loneliness a lot of the day yesterday?"), administered annually to nationally representative samples of ∼1,000 adults per country. Gender- and age-disaggregated tabulations for 38 OECD countries were obtained from Gallup/OECD partnership publications (Gallup, 2025). Covariates: Gini coefficients from the World Bank World Development Indicators (2022 vintage, Gini index SI.POV.GINI); Hofstede Individualism Index from Hofstede Insights (2023 edition, based on the original VSM survey instrument); urbanization rates from UN World Urbanization Prospects (2022 revision).