Article Title: Indirect genetic effects increase the heritable variation available to selection and are largest for behaviours: a meta-analysis

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Abstract

The rate of trait evolution is governed by the amount of heritable variation available to selection. While this is typically quantified based on genetic variation in a focal individual for its own traits (direct genetic effects, DGEs), when social interactions occur, genetic variation in interacting partners can influence a focal individual's traits (indirect genetic effects, IGEs). Theory and studies on domesticated species have suggested IGEs can greatly impact evolutionary trajectories, but whether this is true more broadly remains unclear. Here we perform a systematic review and meta-analysis to quantify the amount of trait variance explained by IGEs and the contribution of IGEs to predictions of evolutionary change. We identified 180 effect sizes from 47 studies across 21 species and found that, on average, IGEs account for a small but statistically significant amount of phenotypic variation (0.03). As IGEs affect the trait values of each interacting group member and due to a typically positive – although statistically nonsignificant – correlation with DGEs ($r_{\text{DGE-IGE}}$ = 0.26, IGEs ultimately increase trait heritability substantially from 0.27 (narrow-sense heritability) to 0.45 (total heritable variance). This 66% average increase in heritability suggests IGEs have a great potential to enhance the rate of evolution. Furthermore, IGEs were most prominent for behavioural traits, and to a lesser extent for reproduction and survival, in contrast to morphological, metabolic, physiological, and development traits. Our meta-analysis therefore shows that IGEs tend to enhance the rate of evolution, especially for traits tightly related to interactions with other individuals such as behaviour and reproduction.

Lay Summary

Predicting evolutionary change is important for breeding better livestock and crops, for understanding how biodiversity arises and how populations respond to environmental change. Normally, these predictions are based on how the genetic variants in an organism influence its own traits (characteristics). However, when organisms socially interact, for instance by fighting or cooperating, then the genes in one individual can influence the traits of others, therefore affecting the potential for evolutionary change. We compared 47 studies across 21 animal species and found that the effect of the genes of others is small but important for evolutionary change. These effects are particularly important for the evolution of animals' behaviours and reproductive traits, but less so for other traits such as body size and physiology. We also found that, because an individual can interact with many others and influence them all, social interactions can substantially increase the

potential for a population to evolve from generation to generation. Our results show how social interactions can dramatically alter the evolution of those traits known to respond to social interactions in comparison to standard expectations.

Introduction

Traits can evolve when they are underpinned by heritable genetic variation and subject to selection. The (narrow-sense) heritability of a trait is defined as the ratio of the additive genetic variance to the total phenotypic variance within a population, with a higher ratio indicating greater potential for evolutionary change in response to selection (Falconer & Mackay, 1996; Fisher, 1930; Lynch & Walsch, 1998). Environmental variation generally makes up the majority of the remainder of the total phenotypic variation and is thought not to contribute to evolved changes. However, the environment of an individual can also include its conspecifics and their traits, such as the phenotype of the breeding partner, a neighbouring individual, or a competitor. Most organisms live at least part of their lives socially, interacting when they mate, fight, cooperate, and compete for access to resources (Frank, 2007; Székely et al., 2010; Westneat & Fox, 2010). Through these social interactions, individuals can influence the phenotypic expression of traits in conspecifics. If an individual's effect on others has a heritable component, then genes in one individual influence the phenotype of others, known as indirect genetic effects (hereafter IGEs; Fig. 1; Dickerson, 1947; Griffing, 1967; Moore et al., 1997; Scott & Fuller, 1965; Wolf et al., 1998). These IGEs can contribute to phenotypic evolution alongside the additive genetic variance stemming from an organism's own genes (direct genetic effects; hereafter DGEs; Fig. 1). However, when measuring the evolutionary potential of traits, researchers typically only quantify DGEs. Only considering DGEs neglects the total genetic variance in trait values stemming from other sources, such as IGEs, and can lead to inaccurate evolutionary predictions (Wolf et al., 1998).

Although the extra genetic variance generated by IGEs can speed up evolutionary change, IGEs can also reduce, remove, or even reverse the response to selection if DGEs and IGEs are negatively correlated (Griffing, 1967; Moore et al., 1997). A positive DGE-IGE correlation indicates that individuals with genes for high trait values elicit higher trait values in their partners (e.g. aggressive individuals instigating higher aggression in others, Alemu et al., 2014; Wilson et al., 2009). In contrast, a negative correlation indicates individuals with high trait values are associated with low trait values in partners (e.g. individuals good at acquiring limited resources cause others to acquire fewer resources, Wilson, 2014). IGEs have long been appreciated in livestock breeding, where they can be exploited to increase productivity and improve welfare (see Ellen et al., 2014 for a qualitative review). IGEs have also been studied in the context of maternal genetic effects (the heritable effect a mother has on the traits of her offspring beyond the direct effect of the genes they inherit from her;

Dickerson, 1947; McAdam et al., 2014; Mousseau & Fox, 1998), as well as implicitly within social and sexual runaway dynamics (Bailey & Kölliker, 2019). Recently, however, we have begun to appreciate that IGEs are applicable to a much broader array of traits and contexts (McAdam et al., 2014). Examples include the influence of a male bird on the lay date of his mate (Brommer & Rattiste, 2008; Evans et al., 2020), the elicitation of aggression from an opponent during a contest (Santostefano et al., 2017; Wilson et al., 2009), and the growth rate and infection status of neighbours (Costa E Silva et al., 2013). IGEs therefore are *expected* to alter the evolution of a wide range of traits, but whether they do is still unclear. In the wild, trait evolution frequently does not match expectations based on the ratio of direct genetic variance to phenotypic variance and the strength of selection observed in wild populations (Merilä et al., 2001; Pujol et al., 2018). Under artificial selection, the observed response may also not match the expectations based on calculations including only DGEs and the strength of imposed selection (Ellen et al., 2014; Falconer, 1981; Muir, 2005). Studying the role of IGEs in trait evolution more broadly is therefore essential to increase the predictability of evolutionary change and explain these apparent patterns of "evolutionary stasis", both in the wild and under artificial conditions.

The recent increase in the number of studies providing estimates of IGEs across taxa presents us a timely opportunity to quantitatively assess the role that IGEs play in trait evolution and their importance relative to DGEs. Further, by comparing standardised estimates across contexts and among different trait types, we can assess when IGEs are particularly prevalent, and when trait evolution will diverge most from that predicted by DGEs alone. For example, behavioural traits are a key element of any social interaction and are typically considered to be highly plastic. Behavioural traits may therefore show large IGE variance (Bailey et al., 2018; see Hunt et al., 2019 for a review of IGEs on behaviours). However, behavioural traits may also vary more in response to the non-social environment, in which case the proportion of variance in phenotypes due to IGEs may not be so high. IGEs could also impact traits related to competition such as growth, resource-dependent life-history traits, or fitness components that are not social traits *per se* (Fisher & McAdam, 2019; Wilson, 2014), but still depend on the phenotypes of conspecifics. Many studies on IGEs have taken place on captive populations housed at relatively high densities where individuals cannot avoid social interactions (reviewed in Ellen et al., 2014). In contrast, organisms in the wild typically live at lower densities and may have the option of avoiding social interactions when beneficial. There is therefore the untested possibility that IGEs in the wild are weaker than in captive populations, and so may not contribute as much to evolutionary change.

We performed a systematic review and meta-analysis to quantitatively assess the overall magnitude and generality, and several patterns of variation, in IGEs across the published literature.

We did not however consider maternal effects, as they have recently been reviewed elsewhere (see Moore et al., 2019). Further, we only analysed effect sizes stemming from the "variance-partitioning" approach used to estimate IGEs (see Methods for further details) since Bailey and Desjonquères (2022) recently reviewed IGEs estimates using the "trait-based" approach.

Our aims were as follows:

1. Quantify the proportion of variance explained by IGEs across studies (*social* h^2 = variance in IGEs [V_{IGE}] / total phenotypic variance [V_P]). We had no clear prediction about its magnitude, but based on our understanding of the literature we expected social h^2 to be relatively low.
2. Test whether IGEs differ among (a) types of traits, (b) ages, (c) sexes, and (d) wild and captive populations. Our predictions for (a) were that, because traits closely linked to fitness such as life-history traits typically have low heritabilities, but high evolvabilities (see Hansen et al., 2011; Houle, 1992; Postma 2014, for detailed metric interpretations), the pattern for IGEs variance would be similar. Instead, we expected that behavioural traits would be highly plastic and therefore may show larger IGE variances, but also high environmental variances, giving low heritabilities, but high evolvabilities (Bailey et al., 2018). We also predicted for (d) higher effects in captive populations compared to wild populations given the difficulty of avoiding interactions in captivity. We had no specific predictions for the remaining sub-aims.
3. Quantify the magnitude of IGEs in comparison to DGEs. Specifically, we compared: (a) direct additive genetic variance (V_A) vs. V_{IGE}, (b) heritability (h^2) vs. *social* h^2, and (c) I_{DGE} vs. I_{IGE} (where $I_{DGE} = V_A/\bar{x}^2$ and $I_{IGE} = V_{IGE}/\bar{x}^2$; Bailey et al., 2018). The latter relates variances to the trait mean to assess evolvability (i.e. a trait's evolutionary potential in response to selection, Hansen et al., 2011; Houle, 1992). IGEs are mediated by social interactions, giving a less direct relationship with trait expression than DGEs, and thus we expected them to be smaller than DGEs.
4. Test whether IGEs alter evolutionary trajectories, which we evaluated in two ways: (a) by assessing the overall size and direction of the DGE-IGE correlation ($r_{DGE\text{-}IGE}$) to understand whether IGEs are expected to increase (positive correlations) or decrease (negative correlations) the rate of evolutionary change, and (b) by comparing narrow-sense heritability (h^2) with total heritable variance (τ^2). Since h^2 only considers DGEs, while τ^2 considers DGEs, IGEs, and their covariance, larger τ^2 compared to h^2 values would indicate that IGE speed up evolution, while smaller τ^2 values would indicate IGEs slow down evolution.

Materials and methods

Systematic review

We performed our systematic literature search on the 8th of August 2019 in both *Web of Science Core Collection* (databases: SCI-EXPANDED 1900-present, SSCI 1956-present, A&HCI 1975-present, ESCI 2015-present) and *Scopus*, and consisted of three different steps. First, we searched for studies on IGEs published across all years using the string: (("indirect genetic effect*") OR ("social genetic effect*") OR ("associative genetic effect*") OR ("interacting phenotype*")). Second, we performed a backward search to identify references cited in two key recent reviews on the topic: Ellen et al. (2014) and Bailey et al. (2018). Third, we performed a forward search to identify references citing at least one of three seminal theoretical papers on the topic: Bijma & Wade (2008), Moore et al. (1997), and Wolf et al. (1998). We downloaded all the references and found and removed duplicates using the R package 'revtools' v.0.3.0 (Westgate, 2019). We screened the titles and abstracts of 1058 unique references using Rayyan (Ouzzani et al., 2016), of which 199 references were selected for full-text screening. Full-text screening identified 111 studies, of which 63 applied an 'animal model' approach to analyse their data and were then subjected to data extraction for our meta-analysis. All authors equally performed both the title-and-abstract and the full-text screening using predefined decision trees detailing the inclusion and exclusion criteria (Figures S1 and S2). To reduce any potential observer biases, the title and abstract of 27% of the references (N = 284), and the full text of 22% of the references (N = 44) were screened by more than one observer. Conflicting decisions (title-and-abstract: 7% [N = 20]; full-text: 16% [N = 7]) were collectively discussed and resolved. For more detailed information see our PRISMA diagram (Figure S3; Moher et al., 2009) and the provided data (https://github.com/ASanchez-Tojar/meta-analysis_IGEs).

Data extraction

Data were extracted from the text and tables in the main text and supplementary materials of the studies identified by our search. All authors equally performed data extraction and the data extraction of all the papers was double-checked by another author. The original and second observer discussed and resolved unclear decisions to ensure reliability. To ensure this process was uniform, all authors extracted data from four selected papers as a pilot at the beginning of this step.

From each included study, we extracted information about the article (year of publication, journal, author information), study subjects (species, population and years studied, population type [captive, semi-captive {defined as a population kept in captivity for no more than five generations}, wild], sex [males, females, both] and age [juveniles, adults, both] of included subjects) and type of trait(s) studied (behaviour, development, metabolism and physiology, morphology, reproduction,

survival). In addition, we extracted the information needed to interpret the statistical estimates of each animal model, namely whether response variables were mean- or variance-standardized, the error distribution and any transformations used, mean group size used to estimate IGEs, mean and standard deviation (SD) of the trait(s) studied (i.e. the response variables), and whether fixed effects pertaining to focal or partner individual traits were included in the models. Lastly, we extracted sample sizes (e.g. number of individuals studied, number of observations), pedigree-related information, and the estimates from the animal models (e.g. direct [V_A] and indirect genetic effect variances [V_{IGE}], narrow-sense [h^2] and total heritability [τ^2], direct-indirect genetic correlation [$r_{DGE\text{-}IGE}$], and direct-indirect genetic covariance [$CoV_{A\text{-}IGE}$]).

After data extraction, we excluded 16 studies: (i) 8 studies (k = 13 effect sizes) that did not contain usable data (i.e. because of being a conference abstract, reporting the same data as other studies, not estimating IGEs using the animal model approach, or solely reporting estimates from existing literature), (ii) 1 study (k = 1 effect size) on humans, (iii) 2 studies (k = 7 effect sizes) on *Eucalyptus globulus* because we did not find data for any other plant species, and (iv) 5 studies (k = 10 effect sizes) that exclusively analysed non-Gaussian traits. Notably, several wild studies fell into this latter exclusion category, reducing the sample size for that category (see below). Requests for missing or partially reported data were sent to the corresponding authors of 38 studies using a standardized email template (provided in Supplementary Materials), from which we obtained additional data for 25 studies. Finally, note that our meta-analytic dataset included 13 out of the 21 studies included in the qualitative literature review by Ellen et al. (2014; see Table 4 therein), with the difference being explained by the inclusion/exclusion criteria explained above. For a complete list of studies and extracted variables see Table 1 and the provided data (https://github.com/ASanchez-Tojar/meta-analysis_IGEs).

Effect size calculation

Our effect sizes of interest were: (i) proportion of variance explained by DGEs (narrow-sense heritability or h^2) and IGEs (*social* h^2; aims 1, 3 and 4), (ii) unstandardized variances associated with DGEs (V_A) and IGEs (V_{IGE}), which we log-transformed prior to the analyses to better match model assumptions (aim 3), (iii) DGE and IGE evolvability (I_{DGE} and I_{IGE}; aim 3), (iv) DGE-IGE correlation ($r_{DGE\text{-}IGE}$; aim 4), which when not reported, was calculated as $COV_{A\text{-}IGE}$ divided by the square root of the product of V_A and V_{IGE}, and (v) total heritable variance, τ^2 (i.e. total proportion of variance explained by DGEs, IGEs, and their covariance, aim 4), which was calculated as $[V_A + Cov_{A\text{-}IGE}*2*(n-1) + V_{IGE}*(n-1)^2] / V_P$ (Bijma, 2010; Bijma et al., 2007). For effect sizes extracted as (intra-class) correlation coefficients (i.e. variance-standardised variances), we applied Fisher's Z transformation (*Zr*) prior to

230 the analyses and so our meta-analytic estimates correspond to *Zr* instead of *r* throughout; however,
231 we present back-transformed values (i.e. *r*) in the figures to aid biological interpretation. The
232 variance in *Zr* (i.e. sampling variance) was calculated as: *VZr* = 1 / (n-3), where n represents the
233 number of unique individuals phenotyped. If *social* h^2 was not directly reported in the corresponding
234 study, we calculated it ourselves as V_{IGE} / V_P. If V_P was not reported, we calculated it ourselves as V_A /
235 h^2 when these variables were reported, and then calculated *social* h^2. These calculations allowed us
236 to add 13 additional effect sizes to our dataset. Additionally, there were nine estimates of V_{IGE}
237 reported as "0" in the primary literature. To avoid removing those values (as zeros cannot be log-
238 transformed), for the comparison of V_A and V_{IGE} only (aim 3) we converted the reported V_{IGE} values
239 to the minimum possible rounded value based on how the "0" was reported (e.g. reported 0.00
240 transformed to 0.001).
241

242 **Meta-analyses and meta-regressions**

243 We first ran an intercept-only meta-analytic model to estimate the overall effect size (i.e. meta-
244 analytic mean) for *social* h^2. We then ran a meta-regression for each of our hypotheses, giving eight
245 meta-regressions, each containing a single moderator at a time. All meta-regressions were
246 complete-case meta-regressions (i.e. effect sizes with unreported moderator data were discarded).
247 In addition, we also ran an intercept-only meta-analysis to estimate the overall effect size for $r_{DGE\text{-}IGE}$.
248 All models included the following six random effects: (i) phylogeny, which consisted of a
249 phylogenetic relatedness correlation matrix (Cinar et al., 2022), (ii) species ID, encompassing effect
250 sizes obtained from the same species and accounts for among-species differences not explained by
251 phylogeny, (iii) population ID, encompassing effect sizes obtained from the same population, (iv)
252 study ID, encompassing effect sizes extracted from the same study, (v) group ID, encompassing
253 effect sizes derived from the same group of animals and allowing us to model different experimental
254 groups within the same study, and (vi) record ID (unit-level effect), which represents residual and/or
255 within-study variance in meta-analytic models. The phylogeny was built by searching for the species
256 in the Open Tree Taxonomy (Rees & Cranston, 2017) and retrieving their phylogenetic relationships
257 from the Open Tree of Life (Hinchliff et al., 2015) using the R package 'rotl' v.3.0.11 (Michonneau et
258 al., 2016). We estimated branch lengths following (Grafen, 1989) as implemented in the function
259 'compute.brlen()' of the R package 'ape' v.5.4-1 (Paradis & Schliep, 2019) and included the
260 phylogenetic variance–covariance matrix as a random effect in all models. For the meta-regressions
261 used to compare the (relative) contribution of DGEs and IGEs as well as to compare narrow-sense
262 heritability (h^2) to total heritable variance (τ^2; hypotheses 3a, 3b, 3c and 4b), since each pair of
263 estimates (e.g. V_{IGE} and V_A) was obtained from the same model, we included an additional random

effect (vii; model ID) that encompassed effect sizes obtained from the same animal model to account for that extra level of nonindependence.

To evaluate the importance of each potential source of variation, for all meta-analytic (intercept-only) models, we calculated four heterogeneity metrics (σ^2, I^2, CV, M) to understand total and random effect-specific heterogeneities following the pluralistic approach suggested by Yang et al. (2023). For all meta-regressions, we estimated the percentage of heterogeneity explained by the moderator as $R^2_{marginal}$ (Nakagawa & Schielzeth, 2013).

We used the R programming language R v.4.0.4 (R Core Team, 2021) throughout. All meta-analytic and meta-regression models were fitted in the R package 'metafor' v.2.5-82 (Viechtbauer, 2010). Results were graphically represented as orchard plots using the R package 'orchaRd' v.2.0 (Nakagawa et al., 2023).

Testing for sources of bias, including publication bias

We confirmed the robustness of our results by running several sensitivity analyses that tested: a) the effect of including fixed effects pertaining to social partners in the original animal models, b) whether conclusions remained when only usingoriginally reported estimates (i.e. excluding our own calculations of some effect sizes; see above), and c) evidence for publication bias both small-study and decline effects (following Nakagawa et al., 2022; Sánchez-Tójar et al., 2018). None of these factors proved to be significant sources of bias, see the Supplementary Materials for further details on our approach and the results.

Results

Our full dataset contained 180 effect sizes from 47 studies published between 1997 and 2019 and involving 21 species. The median and mean number of studies per species was 1 and 2.2, respectively, with *Sus scrofa* (N = 15 studies) and *Gallus gallus* (N = 8 studies) being the most commonly studied species. Note that since we performed complete-case analyses throughout, sample sizes differ slightly across models and research questions.

Aim 1: What is the proportion of trait variance explained by IGEs (social h^2)?

The intercept-only model revealed a small, but statistically significant estimate for social h^2 (Zr = 0.031, 95% confidence intervals, CI, [0.012, 0.051], 95% prediction intervals, PI, [-0.061, 0.124], p = 0.002; k = 146 effect sizes, N = 40 studies, 19 species; Figure 2), but heterogeneity was high (I^2_{total} = 93.2%; CV_{total} = 1.46; M_{total} = 0.70). I^2_{total} and CV_{total} indicated that heterogeneity in our dataset is, on average, around 14 times larger than statistical noise and around 1.5 times larger than the meta-

297 analytic mean. Random effect-specific I^2 estimates showed that 62.8% of heterogeneity was
298 attributed to study ID, 20.1% to species ID not linked to the phylogenetic tree, and 10.3% to record
299 ID. Negligible or zero relative heterogeneity was attributable to the phylogenetic tree, group ID, and
300 population ID.

301 **Aim 2: Does the magnitude of IGEs vary with intrinsic or extrinsic factors?**

302 **2a: Trait category**

303 Social h^2 differed among trait categories (Figure 3a) with the moderator explaining 32.1% of the
304 heterogeneity ($R^2_{marginal}$ = 0.321). The only trait categories with a mean estimate statistically
305 significantly different from zero were behaviour (*Zr* = 0.061, 95% CI [0.031, 0.091]) and reproduction
306 (*Zr* = 0.053, 95% CI [0.014, 0.093]; Figure 3a). Behavioural traits had statistically significantly higher
307 social h^2 values than all other trait categories except for reproduction and survival (see Table S1 for
308 p-values from all pair-wise tests). The post-hoc Wald tests showed that most of the differences
309 between the remaining trait categories were not statistically significant, with only reproduction
310 either being significantly higher than both development and morphology, or showing a trend in that
311 direction when compared to metabolism and physiology (Table S1).

312 **2b: Age**

313 Social h^2 differed among age categories and was statistically significantly larger for effect sizes
314 combining both age classes (*Zr* = 0.091, 95% CI [0.022, 0.160]) compared to those from juveniles-
315 only (*Zr* = 0.013, 95% CI [-0.029, 0.055], p = 0.049) and adults-only (*Zr* = 0.028, 95% CI [-0.05, 0.062],
316 p = 0.027; Table S1, Figure 3b). Estimates for juveniles-only and adults-only were not statistically
317 significantly different from each other (p = 0.400; Table S1, Figure 3b). Overall, the moderator age
318 explained 6.8% of the heterogeneity ($R^2_{marginal}$ = 0.068). Note that there were only four effect sizes
319 for the category combining both age classes, and therefore caution should be applied when drawing
320 conclusions from those differences.

321 **2c: Sex**

322 Social h^2 differed among sex categories, with social h^2 for females-only effect sizes being larger (*Zr* =
323 0.063, 95% CI [0.041, 0.084]) than when including both sexes (*Zr* = 0.006, 95% CI [-0.011, 0.023], p <
324 0.001) or for only males (though not statistically significantly so; *Zr* = 0.038, 95% CI [-0.036, 0.112], p
325 = 0.526; Table S1, Figure 3c). Sex as a moderator explained a large amount of heterogeneity (31.1%;
326 $R^2_{marginal}$ = 0.311); however, there were only seven effect sizes for male-only data, and, out of the 40

327 female-only effect sizes, 28 were from chickens in a production setting, which limits our ability to
328 generalise these results.

329 **2d: Population type**

330 Social h^2 did not differ among population types (Table S1, Figure 3d) with the moderator explaining
331 1.5% of the heterogeneity ($R^2_{marginal}$ = 0.015). Social h^2 was statistically significantly different from
332 zero in captive populations (*Zr* = 0.030, 95% CI [0.006, 0.053]), however, the estimate did not
333 statistically differ from zero in semicaptive populations (*Zr* = 0.020, 95% CI [−0.037, 0.076]) and only
334 marginally so for wild populations (*Zr* = 0.048, 95% CI [−0.000, 0.097]: Table S1, Figure 3d). The pair-
335 wise comparisons revealed no statistically significant differences between all three levels (p > 0.448
336 in all cases; Table S1, Figure 3d). Note, however, that there were only six studies (k = 6 effect sizes)
337 from wild populations and four (k = 29 effect sizes) from semicaptive populations.

338 **Aim 3: What is the relative magnitude of IGEs compared to DGEs?**

339 We ran three meta-regressions to test for the difference in magnitude between V_{IGE} and V_A (aim 3a);
340 social h^2 and h^2 (aim 3b); and I_{IGE} and I_{DGE} (aim 3c). We found that regardless of whether IGEs were
341 estimated as raw variance (log(V_{IGE}): *Zr* = -3.775, 95% CI [-6.562, -0.988] vs. log(V_A) = -0.019, 95% CI [-
342 2.806, 2.767], p < 0.001), variance-standardized variance (*social* h^2: *Zr* = 0.042, 95% CI [-0.027, 0.111]
343 vs. h^2: *Zr* = 0.263, 95% CI [0.194, 0.331], p < 0.001), or mean-standardized variance (I_{IGE}: *Zr* = 0.045,
344 95% CI [-0.134, 0.223] vs. I_{DGE}: *Zr* = 0.224, 95% CI [0.045, 0.402], p = 0.003), IGEs were smaller than
345 DGEs (Figure 4). The moderator explained a considerable amount of variance in each meta-
346 regression (13.5%, 26.8%, and 4.0%, respectively).

347 **Aim 4: Do IGEs alter evolutionary trajectories?**

348 The intercept-only model revealed an overall positive but statistically non-significant correlation
349 between DGEs and IGEs ($r_{DGE\text{-}IGE}$; Z*r* = 0.270, 95% CI [-0.081, 0.621]; Figure 5b), but heterogeneity was
350 high (I^2_{total} = 99.98; CV_{total} = 3.25; M_{total} = 0.85). This high heterogeneity explains the large 95%
351 prediction intervals observed (95% PI [-1.497, 2.036]), which shows that, although positive on
352 average, $r_{DGE\text{-}IGE}$ should be expected to range from very negative to very positive depending on the
353 particular context investigated.

354 Total heritable variance (τ^2) was stastistically significantly larger (r = 0.449, 95% CI [0.241,
355 0.656]) than narrow-sense heritability (h^2; r = 0.270, 95% CI [0.062, 0.478], p < 0.001) and the
356 moderator explained 6.7% of the heterogeneity ($R^2_{marginal}$ = 0.067; Figure 5a).

To better understand whether the increase in τ^2 compared to h^2 was driven by the IGEs variance being amplified through the presence of many interacting partners (n) or due to the seemingly positive $r_{DGE\text{-}IGE}$ detected, as a post-hoc investigation we calculated the two components of τ^2 that stem from V_{IGE}, following Bijma et al., 2007 (*eq. 6*) and qualitatively compared their overall magnitude. These are the "covariance component" ($Cov_{A\text{-}IGE}*2*[n\text{-}1]$) and the "IGE variance component" ($V_{IGE}*[n\text{-}1]^2$). This additional analysis showed that the IGEs variance component was seemingly larger (mean = 693.14) than the covariance component (mean = 241.75), suggesting that it is the IGEs variance component that drives the increase in τ^2.

In addition, τ^2 represents how much genetic variation is available to *all* types of selection (including group-level selection). To test how much difference IGEs make to potential responses to direct, individual-level only selection, we calculated the difference between the predicted response to direct selection on unrelated individuals in the presence and absence of IGEs, following eq. 15 in Bijma and Wade (2008), and assuming a direct selection gradient of 1. This post-hoc analysis showed that the response to direct, individual-level only selection among unrelated individuals was not different in the presence of IGEs (Zr = 0.183, 95% CI [0.048, 0.319]) and in their absence (Zr = 0.225, 95% CI [0.089, 0.360], p = 0.470, $R^2_{marginal}$ = 0.002).

Discussion

We performed a meta-analysis to assess the overall strength and patterns of variation in indirect genetic effects across the published literature. IGEs are small but important, with the genotypes of social partners accounting for, on average, around 3% of phenotypic variation (social h^2). A recent meta-analysis concluded that genetic and non-genetic maternal effects together explained 11% of the phenotypic variance (Moore et al., 2019). Maternal *genetic* effects alone (a type of IGEs excluded from our own meta-analysis) must be smaller than 11% and, therefore, likely comparable to our IGEs estimate. The high levels of heterogeneity among effects that we found show that, as expected, the importance of IGEs varies across contexts, with the 95% prediction intervals suggesting that once estimate precision is accounted for, *social* h^2 is expected to range from 0 to 0.12 in most cases. Indeed, we found that factors such as trait type as well as age and sex of individuals explain substantial heterogeneity in *social* h^2 estimates across studies. Notably, IGEs were more prominent for behaviours (0.06) and traits related to reproduction (0.05), supporting the hypothesis that labile traits are most strongly affected by social interactions. Furthermeore, as expected, IGEs were smaller in magnitude compared to DGEs, with estimates of direct narrow-sense heritability (h^2 = 0.27) being, on average, 6 to 8 times (depending on the statistical model) larger than *social* h^2. However, despite this large difference, accounting for IGEs and their correlations with DGEs (i.e.

391 total heritable variance, τ^2) leads to a 66% increase in the total amount of genetic variation available
392 to selection (τ^2 = 0.45) when compared to narrow-sense h^2. This difference is mostly driven by the
393 impact of IGEs on many interacting partners who experience them, but also due to the overall
394 positive correlation bewtween DGEs and IGEs ($r_{DGE\text{-}IGE}$ = 0.26; although not statistically different from
395 zero). We detected no evidence of publication bias, and our results were robust to data imputations
396 and several aspects of model structure in the original studies (see Supplementary Materials).
397 Overall, our results show the general importance of IGEs for animal populations, the consequences
398 of which we outline below.

399

400 *IGEs can enhance the evolutionary potential of traits*

401 The most impactful consequence of IGEs on traits evolution to emerge from our meta-analysis is that
402 IGEs enhance evolutionary potential by increasing the amount of genetic variation available to
403 selection. In their review, Ellen et al., (2014) suggested that total heritable variance (τ^2) seems to be
404 larger than narrow-sense heritability (h^2) in most domesticated populations; we here confirm this
405 quantitatively and statistically. Two separate but not mutually exclusive mechanisms appear to
406 facilitate this increase in adaptive potential: (1) the influence of IGEs on many interaction partners,
407 and (2) a positive DGEs-IGEs correlation ($r_{DGE\text{-}IGE}$).

408 With a post-hoc analysis, we showed that the increase in τ^2 compared to h^2 is mainly driven
409 by the IGEs variance component ($V_{IGE}[n\text{-}1]^2$) rather than covariance component ($Cov_{A\text{-}IGE}*2*[n\text{-}1]$).
410 This result suggests that there is much greater evolutionary potential when organisms interact in
411 larger groups, as then the impact of V_{IGE} is considerably magnified; however, V_{IGE} may also decrease,
412 if the influence of any two random individuals on each other is diluted as n increases (see Arango et
413 al., 2005; Hadfield & Wilson, 2007; Wade et al., 2010). The suggested importance of group size
414 supports results from previous modelling approaches revealing that both DGEs and IGEs can depend
415 largely on both group size and interaction strength (Liu & Tang, 2016; Trubenová & Hager, 2012). In
416 most captive studies, experimenters enforce one group size across the experiment. Therefore,
417 caution should be exercised when trying to extrapolate estimates of IGEs to situations where group
418 sizes are outside the range of those used to estimate the IGEs in the first place (see also attempts to
419 weight interaction strengths with, for example, social- or spatial-based neighbour networks, and
420 determine effective group size: Bijma, 2010; Costa E Silva et al., 2013; Fisher et al., 2019;
421 Santostefano et al., 2021). Furthermore, differences among individuals in their effect on group
422 mates (e.g. "keystone" individuals: Modlmeier et al., 2014; or among individual variation in "social
423 impact": Araya-Ajoy et al., 2020; de Groot et al., 2023) could also become important and modulate
424 the magnitude of the effect of IGEs in a group.

The overall positive (though uncertain) correlation between DGEs and IGEs ($r_{DGE\text{-}IGE}$ = 0.26) also indicates that heritable social effects tend to facilitate trait evolution rather than impede it. This suggests that IGEs may not be a general explanation for phenotypic stasis in the face of directional selection (Kruuk et al., 2008; Merilä et al., 2001; Pujol et al., 2018; Wilson, 2014). Our result aligns with a review of the interacting phenotypes coefficient Ψ (Bailey & Desjonquères, 2022), which quantifies the effect of a trait on the expression of the same or a different trait in social partners. The sign of Ψ was generally positive, indicating positive feedback between the trait expression in interacting partners, and suggesting a predicted response to selection that is *greater* than in traits where Ψ is zero or without IGEs (Wolf et al., 1998). We then estimated the potential response to selection as an additional comparison for narrow-sense h^2 and τ^2, which revealed an important caveat. The response to individual-level direct selection in the presence of IGEs (in the absence of relatedness and multilevel selection) was not statistically different from that predicted in their absence. This lack of statistical difference, in contrast to the results for narrow-sense h^2 and τ^2, appears because it is multilevel selection and non-zero relatedness that magnify the influence of V_{IGE} on the response to selection. That IGEs do not enhance the response to selection when only individual-level selection occurs may partially explain the surprising lack of response to artificial selection for improvement of socially-affected traits (Craig & Muir, 1996; Ellen et al., 2014; Wade, 1976, 1977), and suggests that multilevel selection is necessary to "unlock" the evolutionary potential of IGEs (Bijma & Wade, 2008; Muir et al., 2013). However, multilevel selection is still controversial and typically not quantified in studies of selection in wild populations, nor always applied in breeding designs. We therefore do not yet know the general prevalence of multilevel selection and how that impacts the evolutionary potential of populations, and call researchers in the field to consider quantifying its influence in future studies.

IGEs are smaller than DGEs

As expected, DGEs were larger than IGEs (e.g. narrow-sense h^2 [0.27] was more than 6 times larger than *social* h^2 [0.03]) across metrics. Our estimates of h^2 are in accordance with other estimates of additive genetic variance derived from animal-model based studies (e.g. 30%: Postma, 2014; 10–30%: Wood et al., 2016; 22%: Moore et al., 2019). Overall, this result confirms our prediction that the effect of an individual's own genes on their own phenotype should be larger than the effect of the genotypes of interacting individuals, even for traits that are often considered highly plastic in response to conspecifics, such as behaviours (Bailey et al., 2018; West-Eberhard, 2003).

IGEs are largest for behaviours and reproductive traits

IGEs are larger for behaviours and reproductive traits (*social* h^2 = 0.06 and 0.05, respectively), compared to other traits categories such as morphology, development, survival, metabolism and

459 physiology (*social* h^2 = 0 to 0.02). This higher susceptibility may occur as behavioural and
460 reproductive traits likely involve feedback loops between interacting partners, such as mutual
461 escalation of aggression in contests (McGlothlin et al., 2010; Trubenová et al., 2015). Similarly,
462 reproductive traits such as lay date or offspring production should heavily depend on the influence
463 of the mating partner as the reproductive outcome is in part a joint phenotype, contributed to by
464 both parents. Further, behavioural traits often have relatively low estimates of h^2 (Dochtermann et
465 al., 2015; Moore et al., 2019; van Oers & Sinn, 2014) and so our analyses shows that traits with
466 higher *social* h^2 are those that often have low direct h^2. Therefore, while behaviours may show
467 limited response to direct selection, due to the prominence of IGEs they may respond more to social,
468 group-level, and other types of selection. Altogether, these findings suggest that behaviours and
469 reproductive traits might follow a substantially different evolutionary pathway (including indirect
470 effects), and that evolution for these traits is expected to diverge most from that predicted by DGEs
471 alone.

472 *Other sources of heterogeneity in IGEs*

473 The additional moderators that we tested to try to explain the high heterogeneity observed
474 showed varying levels of importance. Although life stage explained a non-negligible amount of
475 heteregenity across effect sizes, the magnitude of IGEs did not clearly differ between early and late
476 life stages, which could be because our meta-analysis did not include maternal genetic effects, a
477 type of IGE expected to be strong for juvenile traits (Moore et al., 2019). The sex of the studied
478 individuals explained a high amount of heterogeneity across effect sizes, with IGEs being most
479 important in female only estimates rather than in those including both sexes. However, we note that
480 we did not have enough male-only estimates for a meaningful comparison (7 effect sizes from only 2
481 studies) and that 30 out of the 40 female-only estimates corresponded to captive chickens, hence
482 more diversity in study systems is needed to directly compare sexes and confirm this trend. Indeed,
483 considering sex differences in the magnitude of IGEs in future studies will be useful as the sexes
484 often differ in their patterns of social interaction and competition, which is associated with sexually
485 dimorphic traits (Fairbairn et al., 2007; Shine, 1989).

486 The scarcity of wild studies hampered our assessment of whether IGEs estimates differ
487 compared to studies on captive animals. Fortunately, logistical challenges such as capturing
488 individuals and monitoring their social interactions, along with large sample sizes required by
489 quantitative genetics models (Charmantier et al., 2014), are gradually being met in recent years. The
490 development of large collaborative datasets (e.g. Culina et al. 2021), refined tools for spatial and
491 social network analyses (e.g. Fisher et al. 2019; Radersma 2021), tracking technology (e.g. Nathan et
492 al. 2022), as well as the ability to estimate genetic variances from genomic rather than pedigree data

(e.g. Gienapp et al. 2017, Johnston et al. 2022), are expected to lead to more studies estimating IGEs in the wild. These findings mirror results of a meta-analysis estimating DGEs, where there was no support for heritabilities differing between laboratory and field conditions, nor among wild, domestic, or semi-domestic species (Dochtermann et al., 2019), although previous studies show that behaviours measured in the field tended to exhibit higher heritabilities (Mousseau & Roff, 1987; van Oers & Sinn, 2014; Stirling et al., 2002).

Conclusions

Our meta-analysis across 21 animal species highlights the small yet important contribution of IGEs to evolutionary change. IGEs were most prominent for behaviour-related traits, including reproduction, suggesting a fundamentally different evolutionary route for these traits. Not accounting for IGEs underestimates the amount of genetic variance available to selection. IGEs can instead enhance the evolutionary potential of traits and speed up evolutionary rates by facilitating a response to selection, possibly promoting the adaptation of populations to rapidly changing environmental conditions. The increase in adaptive potential was mostly due to IGEs' impact on multiple interacting conspecifics, but also due to the correlation between IGEs and DGEs tending to be, on average, positive across studies. However, it may take the action of multilevel selection to realise a population's full potential to respond to selection in the presence of IGEs, and therefore understanding the interplay between IGEs, multilevel selection, and relatedness will be key for accurately predicting evolutionary change. Additionally, future studies should expand our knowledge to underrepresented taxonomic groups, particularly focusing on wild populations, which still remain severely understudied.

References

Adams, M. J., Robinson, M. R., Mannarelli, M., & Hatchwell, B. J. (2015). Social genetic and social environment effects on parental and helper care in a cooperatively breeding bird. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1810), 20150689. https://doi.org/10.1098/rspb.2015.0689

Alemu, S. W., Berg, P., Janss, L., & Bijma, P. (2016). Estimation of indirect genetic effects in group-housed mink (Neovison vison) should account for systematic interactions either due to kin or sex. *Journal of Animal Breeding and Genetics*, *133*(1), 43–50. https://doi.org/10.1111/jbg.12163

Alemu, S. W., Bijma, P., Møller, S. H., Janss, L., & Berg, P. (2014). Indirect genetic effects contribute substantially to heritable variation in aggression-related traits in group-housed mink (Neovison vison). *Genetics Selection Evolution*, *46*, 30. https://doi.org/10.1186/1297-9686-46-30

Arango, J., Misztal, I., Tsuruta, S., Culbertson, M., & Herring, W. (2005a). Estimation of variance components including competitive effects of Large White growing gilts. *Journal of Animal Science*, *83*(6). https://doi.org/10.2527/2005.8361241x

Arango, J., Misztal, I., Tsuruta, S., Culbertson, M., & Herring, W. (2005b). Threshold-linear estimation of genetic parameters for farrowing mortality, litter size, and test performance of Large White sows. *Journal of Animal Science*, *83*(3). https://doi.org/10.2527/2005.833499x

Araya-Ajoy, Y. G., Westneat, D. F., & Wright, J. (2020). Pathways to social evolution and their evolutionary feedbacks. *Evolution*, *74*(9), 1894–1907. https://doi.org/10.1111/EVO.14054

Bailey, N. W., & Desjonquères, C. (2022). The Indirect Genetic Effect Interaction Coefficient ψ: Theoretically Essential and Empirically Neglected. *Journal of Heredity*, *113*(1). https://doi.org/10.1093/jhered/esab056

Bailey, N. W., & Kölliker, M. (2019). Social runaway: Fisherian elaboration (or reduction) of socially selected traits via indirect genetic effects. *Evolution*, *73*(8). https://doi.org/10.1111/evo.13791

Bailey, N. W., Marie-Orleach, L., & Moore, A. J. (2018). Indirect genetic effects in behavioral ecology: Does behavior play a special role in evolution? In *Behavioral Ecology*. https://doi.org/10.1093/beheco/arx127

Bergsma, R., Kanis, E., Knol, E. F., & Bijma, P. (2008). The contribution of social effects to heritable variation in finishing traits of domestic pigs (Sus scrofa). *Genetics*, *178*(3). https://doi.org/10.1534/genetics.107.084236

Bergsma, R., Mathur, P. K., Kanis, E., Verstegen, M. W. A., Knol, E. F., & Van Arendonk, J. A. M. (2013). Genetic correlations between lactation performance and growing-finishing traits in pigs. *Journal of Animal Science*, *91*(8). https://doi.org/10.2527/jas.2012-6200

Bijma, P. (2010). Estimating indirect genetic effects: Precision of estimates and optimum designs. *Genetics*, *186*(3). https://doi.org/10.1534/genetics.110.120493

Bijma, P., Muir, W. M., Ellen, E. D., Wolf, J. B., & Van Arendonk, J. A. M. (2007). Multilevel selection 2: Estimating the genetic parameters determining inheritance and response to selection. *Genetics*, *175*(1), 289–299. https://doi.org/10.1534/genetics.106.062729

Bijma, P., Muir, W. M., & Van Arendonk, J. A. M. (2007). Multilevel selection 1: Quantitative genetics of inheritance and response to selection. *Genetics*, *175*(1), 277–288. https://doi.org/10.1534/genetics.106.062711

Bijma, P., & Wade, M. J. (2008). The joint effects of kin, multilevel selection and indirect genetic effects on response to genetic selection. *Journal of Evolutionary Biology*, *21*, 1175–1188. https://doi.org/10.1111/j.1420-9101.2008.01550.x

Bouwman, A. C., Bergsma, R., Duijvesteijn, N., & Bijma, P. (2010). Maternal and social genetic effects on average daily gain of piglets from birth until weaning. *Journal of Animal Science*, *88*(9). https://doi.org/10.2527/jas.2009-2494

Brinker, T., Bijma, P., Visscher, J., Rodenburg, T. B., & Ellen, E. D. (2014). Plumage condition in laying hens: Genetic parameters for direct and indirect effects in two purebred layer lines. *Genetics Selection Evolution*, *46*(1). https://doi.org/10.1186/1297-9686-46-33

Brinker, T., Ellen, E. D., Veerkamp, R. F., & Bijma, P. (2015). Predicting direct and indirect breeding values for survival time in laying hens using repeated measures. *Genetics Selection Evolution*, *47*(1). https://doi.org/10.1186/s12711-015-0152-2

Brommer, J. E., & Rattiste, K. (2008). "Hidden" reproductive conflict between mates in a wild bird population. *Evolution*, *62*, 2326–2333. https://doi.org/10.1111/j.1558-5646.2008.00451.x

Canario, L., Lundeheim, N., & Bijma, P. (2017). The early-life environment of a pig shapes the phenotypes of its social partners in adulthood. *Heredity*, *118*(6). https://doi.org/10.1038/hdy.2017.3

Chakrabarty, A., van Kronenberg, P., Toliopoulos, N., & Schielzeth, H. (2019). Direct and indirect genetic effects on reproductive investment in a grasshopper. *Journal of Evolutionary Biology*, *32*(4). https://doi.org/10.1111/jeb.13417

Charmantier, A., Garant, D., & Kruuk, L. E. B. (2014). *Quantitative Genetics in the Wild*. Oxford University Press.

Chen, C. Y., Kachman, S. D., Johnson, R. K., Newman, S., & Van Vleck, L. D. (2008). Estimation of genetic parameters for average daily gain using models with competition effects. *Journal of Animal Science*, *86*(10). https://doi.org/10.2527/jas.2007-0660

Cinar, O., Nakagawa, S., & Viechtbauer, W. (2022). Phylogenetic multilevel meta-analysis: A simulation study on the importance of modelling the phylogeny. *Methods in Ecology and Evolution*, *13*(2). https://doi.org/10.1111/2041-210X.13760

Costa E Silva, J., Potts, B. M., Bijma, P., Kerr, R. J., & Pilbeam, D. J. (2013). Genetic control of interactions among individuals: Contrasting outcomes of indirect genetic effects arising from neighbour disease infection and competition in a forest tree. *New Phytologist*. https://doi.org/10.1111/nph.12035

Craig, J. V., & Muir, W. M. (1996). Group selection for adaptation to multiple-hen cages: Beak-related mortality, feathering, and body weight responses. *Poultry Science*, *75*(3). https://doi.org/10.3382/ps.0750294

David, I., Sánchez, J. P., & Piles, M. (2018). Longitudinal analysis of direct and indirect effects on average daily gain in rabbits using a structured antedependence model. *Genetics Selection Evolution*, *50*(1). https://doi.org/10.1186/s12711-018-0395-9

de Groot, C., Wijnhorst, R. E., Ratz, T., Murray, M., Araya-Ajoy, Y. G., Wright, J., & Dingemanse, N. J. (2023). The importance of distinguishing individual differences in 'social impact' versus 'social responsiveness' when quantifying indirect genetic effects on the evolution of social plasticity. *Neuroscience and Biobehavioral Reviews*, *144*. https://doi.org/10.1016/J.NEUBIOREV.2022.104996

Dewan, I., Garland, T., Hiramatsu, L., & Careau, V. (2019). I Smell a Mouse: Indirect Genetic Effects on Voluntary Wheel-Running Distance, Duration and Speed. *Behavior Genetics*, *49*(1). https://doi.org/10.1007/s10519-018-9930-2

Dickerson, G. (1947). Composition of hog carcasses as influenced by heritable differences in rate and economy of gain. *Iowa Agric Exp Stn Res Bull*, *354*, 492–524.

Dochtermann, N. A., Schwab, T., Anderson Berdal, M., Dalos, J., & Royauté, R. (2019). The Heritability of Behavior: A Meta-analysis. *Journal of Heredity*, *110*(4). https://doi.org/10.1093/jhered/esz023

Dochtermann, N. A., Schwab, T., & Sih, A. (2015). The contribution of additive genetic variation to personality variation: heritability of personality. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1798), 20142201.

Duijvesteijn, N., Knol, E. F., & Bijma, P. (2012). Direct and associative effects for androstenone and genetic correlations with backfat and growth in entire male pigs. *Journal of Animal Science*, *90*(8). https://doi.org/10.2527/jas.2011-4625

Edward, D. A., Poissant, J., Wilson, A. J., & Chapman, T. (2014). Sexual conflict and interacting phenotypes: A quantitative genetic analysis of fecundity and copula duration in drosophila melanogaster. *Evolution*, *68*(6). https://doi.org/10.1111/evo.12376

Ellen, E. D., Bas Rodenburg, T., Albers, G. A. A., Elizabeth Bolhuis, J., Camerlink, I., Duijvesteijn, N., Knol, E. F., Muir, W. M., Peeters, K., Reimert, I., Sell-Kubiak, E., van Arendonk, J. A. M., Visscher, J., & Bijma, P. (2014). The prospects of selection for social genetic effects to improve welfare and productivity in livestock. In *Frontiers in Genetics,* 5(377). https://doi.org/10.3389/fgene.2014.00377

Ellen, E. D., Peeters, K., Verhoeven, M., Gols, R., Harvey, J. A., Wade, M. J., Dicke, M., & Bijma, P. (2016). Direct and indirect genetic effects in life-history traits of flour beetles (Tribolium castaneum). *Evolution*, *70*(1), 207–217. https://doi.org/10.1111/evo.12835

Ellen, E. D., Visscher, J., Van Arendonk, J. A. M., & Bijma, P. (2008). Survival of laying hens: Genetic parameters for direct and associative effects in three purebred layer lines. *Poultry Science*, *87*(2). https://doi.org/10.3382/ps.2007-00374

Evans, S. R., Postma, E., & Sheldon, B. C. (2020). It takes two: Heritable male effects on reproductive timing but not clutch size in a wild bird population. *Evolution*. https://doi.org/10.1111/evo.13980

Fairbairn, D. J., Blanckenhorn, W. U., & Székely, T. (2007). Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism. In *Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism*. https://doi.org/10.1093/acprof:oso/9780199208784.001.0001

Falconer, D. (1981). *Introduction to Quantitative Genetics* (2nd ed.). Longman.

Falconer, D. S., & Mackay, T. F. C. (1996). *Introduction to quantitative genetics* (Longman, Ed.).

Fisher, D. N., Haines, J. A., Boutin, S., Dantzer, B., Lane, J. E., Coltman, D. W., & McAdam, A. G. (2019). Indirect effects on fitness between individuals that have never met via an extended phenotype. In *Ecology Letters* (Vol. 22, Issue 4). https://doi.org/10.1111/ele.13230

Fisher, D. N., & McAdam, A. G. (2019). Indirect genetic effects clarify how traits can evolve even when fitness does not. *Evolution Letters*. https://doi.org/10.1002/evl3.98

Fisher, D. N., Wilson, A. J., Boutin, S., Dantzer, B., Lane, J. E., Coltman, D. W., Gorrell, J. C., & McAdam, A. G. (2019). Social effects of territorial neighbours on the timing of spring breeding

in North American red squirrels. *Journal of Evolutionary Biology*, *32*(6), 559–571. https://doi.org/10.1111/jeb.13437

Fisher, R. (1930). *The genetical theory of natural selection*. Clarendon.

Frank, S. A. (2007). All of life is social. *Current Biology,* 17(16). https://doi.org/10.1016/j.cub.2007.06.005

Germain, R. R., Wolak, M. E., Arcese, P., Losdat, S., & Reid, J. M. (2016). Direct and indirect genetic and fine-scale location effects on breeding date in song sparrows. *Journal of Animal Ecology*, *85*(6). https://doi.org/10.1111/1365-2656.12575

Gienapp, P., Fior, S., Guillaume, F., Lasky, J. R., Sork, V. L., & Csilléry, K. (2017). Genomic quantitative genetics to study evolution in the wild. *Trends in Ecology & Evolution*, 32(12), 897-908.

Grafen, A. (1989). The phylogenetic regression. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *326*(1233). https://doi.org/10.1098/rstb.1989.0106

Griffing, B. (1967). Selection in reference to biological groups. I. Individual and group selection applied to populations of unordered groups. *Australian Journal of Biological Sciences*, *20*, 127–139. https://doi.org/10.1071/BI9670127

Hadfield, J. D., & Wilson, A. J. (2007). Multilevel selection 3: Modeling the effects of interacting individuals as a function of group size. *Genetics*, *177*(1), 667–668. https://doi.org/10.1534/genetics.107.075622

Han, C. S., Tuni, C., Ulcik, J., & Dingemanse, N. J. (2018). Increased developmental density decreases the magnitude of indirect genetic effects expressed during agonistic interactions in an insect. *Evolution*, *72*(11). https://doi.org/10.1111/evo.13600

Hansen, T. F., Pélabon, C., & Houle, D. (2011). Heritability is not Evolvability. *Evolutionary Biology*. https://doi.org/10.1007/s11692-011-9127-6

Hong, J. K., Kim, Y. M., Cho, K. H., Cho, E. S., Lee, D. H., & Choi, T. J. (2019). Genetic association between sow longevity and social genetic effects on growth in pigs. *Asian-Australasian Journal of Animal Sciences*, *32*(8). https://doi.org/10.5713/ajas.18.0789

Hong, J. K., Kim, Y. M., Cho, K. H., Park, J. C., & Lee, D. H. (2017). Reproductive performance of sows selected for divergent social genetic effects for growth. *Animal Reproduction*, *14*. https://doi.org/10.21451/1984-3143-AR946

Houle, D. (1992). Comparing evolvability and variability of quantitative traits. In *Genetics*.

Hsu, W. L., Johnson, R. K., & van Vleck, L. D. (2010). Effect of pen mates on growth, backfat depth, and longissimus muscle area of swine. *Journal of Animal Science*, *88*(3). https://doi.org/10.2527/jas.2009-1879

Hunt, J., Rapkin, J., House, C. M., & Wilson, A. J. (2019). Beyond genes and environments: Indirect genetic effects and the evolution of behaviour. In *Genes and Behaviour: Beyond Nature-Nurture*. https://doi.org/10.1002/9781119313663.ch4

Johnston, S. E., Chen, N., & Josephs, E. B. (2022). Taking quantitative genomics into the wild. *Proceedings of the Royal Society B*, 289(1989), 20221930.

Khaw, H. L., Ponzoni, R. W., Yee, H. Y., Aziz, M. A. bin, & Bijma, P. (2016). Genetic and non-genetic indirect effects for harvest weight in the GIFT strain of Nile tilapia (Oreochromis niloticus). *Aquaculture*, *450*. https://doi.org/10.1016/j.aquaculture.2015.07.033

Kjaer, J. B., & Sørensen, P. (1997). Feather pecking behaviour in White Leghorns, a genetic study. *British Poultry Science*, *38*(4). https://doi.org/10.1080/00071669708417999

Kruuk, L. E. B., Slate, J., & Wilson, A. J. (2008). New answers for old questions: The evolutionary quantitative genetics of wild animal populations. In *Annual Review of Ecology, Evolution, and Systematics* (Vol. 39). https://doi.org/10.1146/annurev.ecolsys.39.110707.173542

Liu, J., & Tang, G. (2016). Investigating the contribution of social genetic effect to longer selection response in a ten generations breeding programme simulated. *Italian Journal of Animal Science*, *15*(4). https://doi.org/10.1080/1828051X.2016.1248868

Luan, S., Luo, K., Chai, Z., Cao, B., Meng, X., Lu, X., Liu, N., Xu, S., & Kong, J. (2015). An analysis of indirect genetic effects on adult body weight of the Pacific white shrimp Litopenaeus vannamei at low rearing density. *Genetics Selection Evolution*, *47*(1). https://doi.org/10.1186/s12711-015-0164-y

Lynch, M., & Walsch, B. (1998). *Genetics and analysis of quantitative traits*. Sinauer.

Mcadam, A. G., Garant, D., & Wilson, A. J. (2014). *Chapter 6. The effects of others' genes: maternal and other indirect genetic effects*. 1–33.

McGlothlin, J. W., Moore, A. J., Wolf, J. B., & Brodie, E. D. (2010). Interacting phenotypes and the evolutionary process. III. Social evolution. *Evolution*, *64*(9), 2558–2574. https://doi.org/10.1111/j.1558-5646.2010.01012.x

Merilä, J., Sheldon, B. C., & Kruuk, L. E. B. (2001). Explaining stasis: Microevolutionary studies in natural populations. *Genetica*. https://doi.org/10.1023/A:1013391806317

Michonneau, F., Brown, J. W., & Winter, D. J. (2016). rotl: an R package to interact with the Open Tree of Life data. *Methods in Ecology and Evolution*, *7*(12). https://doi.org/10.1111/2041-210X.12593

Modlmeier, A. P., Keiser, C. N., Watters, J. V., Sih, A., & Pruitt, J. N. (2014). The keystone individual concept: An ecological and evolutionary overview. In *Animal Behaviour* (Vol. 89). https://doi.org/10.1016/j.anbehav.2013.12.020

Moher, D., Liberati, A., Tetzlaff, J., Altman, D. G., Antes, G., Atkins, D., Barbour, V., Barrowman, N., Berlin, J. A., Clark, J., Clarke, M., Cook, D., D'Amico, R., Deeks, J. J., Devereaux, P. J., Dickersin, K., Egger, M., Ernst, E., Gøtzsche, P. C., … Tugwell, P. (2009). Preferred reporting items for systematic reviews and meta-analyses: The PRISMA statement. In *PLoS Medicine* (Vol. 6, Issue 7). https://doi.org/10.1371/journal.pmed.1000097

Moore, A. J., Brodie, E. D. I., & Wolf, J. B. (1997). Interacting Phenotypes and the Evolutionary Process: I . Direct and Indirect Genetic Effects of Social Interactions. *Evolution*, *51*(5), 1352–1362.

Moore, M. P., Whiteman, H. H., & Martin, R. A. (2019). A mother's legacy: the strength of maternal effects in animal populations. In *Ecology Letters* (Vol. 22, Issue 10). https://doi.org/10.1111/ele.13351

Mousseau, T. A., & Fox, C. W. (1998). The adaptive significance of maternal effects. In *Trends in Ecology and Evolution* (Vol. 13, Issue 10). https://doi.org/10.1016/S0169-5347(98)01472-4

Mousseau, T. A., & Roff, D. A. (1987). Natural selection and the heritability of fitness components. *Heredity*. https://doi.org/10.1038/hdy.1987.113

Muir, W. M. (2005). Incorporation of competitive effects in forest tree or animal breeding programs. *Genetics*. https://doi.org/10.1534/genetics.104.035956

Muir, W. M., Bijma, P., & Schinckel, A. (2013). Multilevel selection with kin and non-kin groups, experimental results with japanese quail (coturnix japonica). *Evolution*, *67*(6). https://doi.org/10.1111/evo.12062

Nakagawa, S., Lagisz, M., Jennions, M. D., Koricheva, J., Noble, D. W. A., Parker, T. H., Sánchez-Tójar, A., Yang, Y., & O'Dea, R. E. (2022). Methods for testing publication bias in ecological and evolutionary meta-analyses. In *Methods in Ecology and Evolution* (Vol. 13, Issue 1). https://doi.org/10.1111/2041-210X.13724

Nakagawa, S., Lagisz, M., O'Dea, R., Pottier, P., Rutkowska, J., Senior, A., Yang, Y., & Noble, D. (2023). orchaRd 2.0: an R package for visualizing meta-analyses with orchard plots. *EcoEvoRxiv*.

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2). https://doi.org/10.1111/j.2041-210x.2012.00261.x

Nathan, R., Monk, C. T., Arlinghaus, R., Adam, T., Alós, J., Assaf, M., ... & Jarić, I. (2022). Big-data approaches lead to an increased understanding of the ecology of animal movement. *Science*, 375(6582), eabg1780.

Nielsen, H. M., Ask, B., & Madsen, P. (2018). Social genetic effects for growth in pigs differ between boars and gilts. *Genetics Selection Evolution*, *50*(1). https://doi.org/10.1186/s12711-018-0375-0

Nielsen, H. M., Monsen, B. B., Ødegård, J., Bijma, P., Damsgård, B., Toften, H., & Olesen, I. (2014). Direct and social genetic parameters for growth and fin damage traits in Atlantic cod (Gadus morhua). *Genetics Selection Evolution*, *46*(1). https://doi.org/10.1186/1297-9686-46-5

Oers, K. Van, & Sinn, D. L. (2014). Quantitative and Molecular Genetics of Animal Personality. In *Animal Personalities*. https://doi.org/10.7208/chicago/9780226922065.003.0007

Ouzzani, M., Hammady, H., Fedorowicz, Z., & Elmagarmid, A. (2016). Rayyan-a web and mobile app for systematic reviews. *Systematic Reviews*, *5*(1). https://doi.org/10.1186/s13643-016-0384-4

Paradis, E., & Schliep, K. (2019). Ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, *35*(3). https://doi.org/10.1093/bioinformatics/bty633

Peeters, K., Ellen, E. D., & Bijma, P. (2013). Using pooled data to estimate variance components and breeding values for traits affected by social interactions. *Genetics Selection Evolution*, *45*(1). https://doi.org/10.1186/1297-9686-45-27

Peeters, K., Eppink, T. T., Ellen, E. D., Visscher, J., & Bijma, P. (2012). Indirect genetic effects for survival in domestic chickens (Gallus gallus) are Magnified in crossbred genotypes and show a parent-of-origin effect. *Genetics*, *192*(2). https://doi.org/10.1534/genetics.112.142554

Petfield, D., Chenoweth, S. F., Rundle, H. D., & Blows, M. W. (2005). Genetic variance in female condition predicts indirect genetic variance in male sexual display traits. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(17). https://doi.org/10.1073/pnas.0409378102

Piles, M., David, I., Ramon, J., Canario, L., Rafel, O., Pascual, M., Ragab, M., & Sánchez, J. P. (2017). Interaction of direct and social genetic effects with feeding regime in growing rabbits. *Genetics Selection Evolution*, *49*(1). https://doi.org/10.1186/s12711-017-0333-2

Postma, E. (2014). Four decades of estimating heritabilities in wild vertebrate populations: improved methods, more data, better estimates? In *Quantitative Genetics in the Wild*. https://doi.org/10.1093/acprof:oso/9780199674237.003.0002

Pujol, B., Blanchet, S., Charmantier, A., Danchin, E., Facon, B., Marrot, P., Roux, F., Scotti, I., Teplitsky, C., Thomson, C. E., & Winney, I. (2018). The Missing Response to Selection in the Wild. In *Trends in Ecology and Evolution* (Vol. 33, Issue 5). https://doi.org/10.1016/j.tree.2018.02.007

R Core Team. (2021). R core team (2021). In *R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www. R-project. org*.

Radersma, R. (2021). Estimating heritability of social phenotypes from social networks. *Methods in Ecology and Evolution*, 12(1), 42-53.

Ragab, M., Piles, M., Quintanilla, R., & Sánchez, J. P. (2019). Indirect genetic effect model using feeding behaviour traits to define the degree of interaction between mates: An implementation in pigs growth rate. *Animal*, *13*(2). https://doi.org/10.1017/S1751731118001192

Rees, J. A., & Cranston, K. (2017). Automated assembly of a reference taxonomy for phylogenetic data synthesis. *Biodiversity Data Journal*, *5*(1). https://doi.org/10.3897/BDJ.5.e12581

Rostellato, R., Sartori, C., Bonfatti, V., Chiarot, G., & Carnier, P. (2013). Comparison between direct and competitive models to investigate variation of carcass and ham quality traits in heavy pigs. *Agriculturae Conspectus Scientificus*, *78*(3).

Rostellato, R., Sartori, C., Bonfatti, V., Chiarot, G., & Carnier, P. (2015). Direct and social genetic effects on body weight at 270 days and carcass and ham quality traits in heavy pigs. *Journal of Animal Science*, *93*(1). https://doi.org/10.2527/jas.2014-8246

Sánchez-Tójar, A., Nakagawa, S., Sánchez-Fortún, M., Martin, D. A., Ramani, S., Girndt, A., Bókony, V., Kempenaers, B., Liker, A., Westneat, D. F., Burke, T., & Schroeder, J. (2018). Meta-analysis challenges a textbook example of status signalling and demonstrates publication bias. *ELife*, *7*. https://doi.org/10.7554/eLife.37385

Santostefano, F., Allegue, H., Garant, D., Bergeron, P., & Réale, D. (2021). Indirect genetic and environmental effects on behaviors, morphology, and life-history traits in a wild Eastern chipmunk population. *Evolution*, *75*(6). https://doi.org/10.1111/evo.14232

Santostefano, F., Wilson, A. J., Niemelä, P. T., & Dingemanse, N. J. (2017). Indirect genetic effects: A key component of the genetic architecture of behaviour. *Scientific Reports*, *7*(1). https://doi.org/10.1038/s41598-017-08258-6

Sartori, C., & Mantovani, R. (2012). Effects of inbreeding on fighting ability measured in Aosta chestnut and Aosta black pied cattle. *Journal of Animal Science*, *90*(9). https://doi.org/10.2527/jas.2011-4010

Scott, J., & Fuller, J. (1965). *Genetics and the Social Behavior of the Dog*. University of Chicago Press.

Shine, R. (1989). Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Quarterly Review of Biology*, *64*(4). https://doi.org/10.1086/416458

Stirling, D. G., Réale, D., & Roff, D. A. (2002). Selection, structure and the heritability of behaviour. *Journal of Evolutionary Biology*, *15*(2), 277–289.

Sun, Y., Ellen, E. D., Van Der Poel, J. J., Parmentier, H. K., & Bijma, P. (2014). Modelling of feather pecking behavior in beak-trimmed and non-beak-trimmed crossbred laying hens: Variance component and trait-based approach. *Poultry Science*, *93*(4). https://doi.org/10.3382/ps.2013-03367

Székely, T., Moore, A. J., & Komdeur, J. (2010). *Social behaviour: genes, ecology and evolution*. Cambridge University Press.

Teplitsky, C., Mills, J. A., Yarrall, J. W., & Merilä, J. (2010). Indirect genetic effects in a sex-limited trait: The case of breeding time in red-billed gulls. *Journal of Evolutionary Biology*. https://doi.org/10.1111/j.1420-9101.2010.01959.x

Trubenová, B., & Hager, R. (2012). Phenotypic and Evolutionary Consequences of Social Behaviours: Interactions among Individuals Affect Direct Genetic Effects. *PLoS ONE*, *7*(11). https://doi.org/10.1371/journal.pone.0046273

Trubenová, B., Novak, S., & Hager, R. (2015). Indirect genetic effects and the dynamics of social interactions. *PLoS ONE*, *10*(5). https://doi.org/10.1371/journal.pone.0126907

Van Vleck, L. D., Cundiff, L. V., & Kocht, R. M. (2007). Effect of competition on gain in feedlot bulls from Hereford selection lines. *Journal of Animal Science*, *85*(7). https://doi.org/10.2527/jas.2007-0067

Viechtbauer, W. (2010). Conducting Meta-analysis in R with the metafor package. *Journal of Statistical Software*, *36*(3).

Wade, M. J. (1976). Group selection among laboratory populations of Tribolium. *Proceedings of the National Academy of Sciences of the United States of America*, *73*(12). https://doi.org/10.1073/pnas.73.12.4604

Wade, M. J. (1977). An Experimental Study of Group Selection. *Evolution*, *31*(1). https://doi.org/10.2307/2407552

Wade, M. J., Bijma, P., Ellen, E. D., & Muir, W. (2010). Group selection and social evolution in domesticated animals. *Evolutionary Applications*, *3*, 453–465. https://doi.org/10.1111/j.1752-4571.2010.00147.x

West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. Oxford University Press.

Westgate, M. J. (2019). revtools: An R package to support article screening for evidence synthesis. In *Research Synthesis Methods* (Vol. 10, Issue 4). https://doi.org/10.1002/jrsm.1374

Westneat, D. F., & Fox, C. (2010). *Evolutionary behavioral ecology*. Oxford University Press.

Wilson, A. J. (2014). Competition as a source of constraint on life history evolution in natural populations. *Heredity*, *112*(1), 70–78. https://doi.org/10.1038/hdy.2013.7

Wilson, A. J., Gelin, U., Perron, M., & Réale, D. (2009). Indirect genetic effects and the evolution of aggression in a vertebrate system Indirect genetic effects and the evolution of aggression in a vertebrate system. *Proceedings of the Royal Society B: Biological Sciences*, *276*, 533–541. https://doi.org/10.1098/rspb.2008.1193

Wolf, J. B., Brodie, Cheverud, J. M., Moore, A. J., & Wade, M. J. (1998). Evolutionary consequences of indirect genetic effects. *Trends in Ecology and Evolution*, *13*(2), 64–69.

Wood, J. L. A., Yates, M. C., & Fraser, D. J. (2016). Are heritability and selection related to population size in nature? Meta-analysis and conservation implications. In *Evolutionary Applications* (Vol. 9, Issue 5). https://doi.org/10.1111/eva.12375

854 Wu, P., Wang, K., Yang, Q., Zhou, J., Chen, D., Liu, Y., Ma, J., Tang, Q., Jin, L., Xiao, W., Lou, P., Jiang,
855 A., Jiang, Y., Zhu, L., Li, M., Li, X., & Tang, G. (2019). Whole-genome re-sequencing association
856 study for direct genetic effects and social genetic effects of six growth traits in Large White
857 pigs. *Scientific Reports*, *9*(1). https://doi.org/10.1038/s41598-019-45919-0

858 Yang, Y., Noble, D. W., Spake, R., Senior, A. M., Lagisz, M., & Nakagawa, S. (2023). Measuring
859 biological generality in meta-analysis: a pluralistic approach to heterogeneity quantification
860 and stratification. *EcoEvoRxiv*. Preprint. https://doi.org/10.32942/X2RG7X

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Data and code availability statement

All data and code are available at the following GitHub repository (https://github.com/ASanchez-Tojar/meta-analysis_IGEs). Upon acceptance, all data and code will be provided with a doi via Zenodo.

Conflict of interest statement

The authors declare no competing interests.

894 ## Tables

895 **Table 1.** List of studies (n = 47) from which data was extracted and included in our meta-analysis on indirect genetic effects.

Study ID	Year	Journal	Number of effect sizes (k)	Species	Reference
IGE0057	2015	Genetics Selection Evolution	1	*Penaeus vannamei*	(Luan et al., 2015)
IGE0144	2013	Agriculturae Conspectus Scientificus	3	*Sus scrofa*	(Rostellato et al., 2013)
IGE0195	2012	Journal Of Animal Science	3	*Sus scrofa*	(Duijvesteijn et al., 2012)*
IGE0196	2016	Journal Of Animal Ecology	1	*Melospiza melodia*	(Germain et al., 2016)
IGE0197	2016	Evolution	1	*Tribolium castaneum*	(Ellen et al., 2016)
IGE0199	2019	Journal Of Evolutionary Biology	3	*Chorthippus biguttulus*	(Chakrabarty et al., 2019)
IGE0202	2015	Journal Of Animal Science	10	*Sus scrofa*	(Rostellato et al., 2015)
IGE0203	2014	Genetics Selection Evolution	19	*Gadus morhua*	(Nielsen et al., 2014)*
IGE0242	2007	Journal Of Animal Science	8	*Bos taurus*	(Van Vleck et al., 2007)*
IGE0243	2010	Journal Of Animal Science	3	*Sus scrofa*	(Hsu et al., 2010)*
IGE0253	2012	Journal Of Animal Science	1	*Bos taurus*	(Sartori & Mantovani, 2012)
IGE0291	2008	Journal Of Animal Science	1	*Sus scrofa*	(Chen et al., 2008)*
IGE0292	2016	Journal Of Animal Breeding And Genetics	3	*Neovison vison*	(Alemu et al., 2016)
IGE0294	2005	Journal Of Animal Science	1	*Sus scrofa*	(Arango et al., 2005)
IGE0347	1997	British Poultry Science	6	*Gallus gallus*	(Kjaer & Sørensen, 1997)
IGE0380	2016	Aquaculture	1	*Oreochromis niloticus*	(Khaw et al., 2016)
IGE0385	2019	Asian-Australasian Journal Of Animal Sciences	1	*Sus scrofa*	(Hong et al., 2019)
IGE0391	2013	Journal Of Animal Science	3	*Sus scrofa*	(Bergsma et al., 2013)*

IGE0406	2005	Proceedings Of The National Academy Of Sciences Of The United States Of America	16	*Drosophila serrata*	(Petfield et al., 2005)
IGE0468	2019	Behavior Genetics	24	*Mus musculus*	(Dewan et al., 2019)
IGE0483	2018	Evolution	6	*Gryllus bimaculatus*	(Han et al., 2018)
IGE0493	2019	Ecology Letters	1	*Tamiasciurus hudsonicus*	(Fisher, Haines, et al., 2019)
IGE0494	2019	Animal	1	*Sus scrofa*	(Ragab et al., 2019)
IGE0501	2009	Proceedings Of The Royal Society B-Biological Sciences	5	*Peromyscus maniculatus sonoriensis*	(Wilson et al., 2009)*
IGE0505	2014	Genetics Selection Evolution	3	*Neovison vison*	(Alemu et al., 2014)*
IGE0507	2012	Genetics	4	*Gallus gallus*	(Peeters et al., 2012)*
IGE0509	2010	Journal Of Evolutionary Biology	1	*Chroicocephalus scopulinus*	(Teplitsky et al., 2010)
IGE0515	2017	Scientific Reports	1	*Gryllus bimaculatus*	(Santostefano et al., 2017)
IGE0537	2017	Genetics Selection Evolution	2	*Oryctolagus cuniculus*	(Piles et al., 2017)
IGE0572	2018	Genetics Selection Evolution	5	*Oryctolagus cuniculus*	(David et al., 2018)
IGE0598	2010	Journal Of Animal Science	1	*Sus scrofa*	(Bouwman et al., 2010)*
IGE0640	2014	Poultry Science	2	*Gallus gallus*	(Sun et al., 2014)
IGE0654	2007	Genetics	1	*Gallus gallus*	(Bijma et al., 2007)
IGE0657	2013	Evolution	1	*Coturnix japonica*	(Muir et al., 2013)*
IGE0746	2014	Genetics Selection Evolution	8	*Gallus gallus*	(Brinker et al., 2014)*
IGE0752	2015	Genetics Selection Evolution	4	*Gallus gallus*	(Brinker et al., 2015)
IGE0786	2017	Animal Reproduction	1	*Sus scrofa*	(Hong et al., 2017)
IGE0824	2014	Evolution	2	*Drosophila melanogaster*	(Edward et al., 2014)
IGE0852	2019	Journal Of Evolutionary Biology	1	*Tamiasciurus hudsonicus*	(Fisher, Wilson, et al., 2019)

IGE0857	2015	Proceedings Of The Royal Society B: Biological Sciences	1	*Aegithalos caudatus*	(Adams et al., 2015)
IGE0858	2018	Genetics Selection Evolution	2	*Sus scrofa*	(Nielsen et al., 2018)
IGE0889	2008	Poultry Science	3	*Gallus gallus*	(Ellen et al., 2008)*
IGE0920	2008	Genetics	5	*Sus scrofa*	(Bergsma et al., 2008)
IGE0927	2017	Heredity	1	*Sus scrofa*	(Canario et al., 2017)
IGE1023	2013	Genetics Selection Evolution	2	*Gallus gallus*	(Peeters et al., 2013)
IGE1038	2019	Scientific Reports	6	*Sus scrofa*	(Wu et al., 2019)
IGE1050	2008	Evolution	1	*Larus canus*	(Brommer & Rattiste, 2008)

* References included in the qualitative review performed by Ellen et al. (2014: Table 4 in that review).

Figures

Figure 1. Indirect genetic effects occur when the genotype of one individual influences the expression of a phenotype in a conspecific, mediated by social interactions.

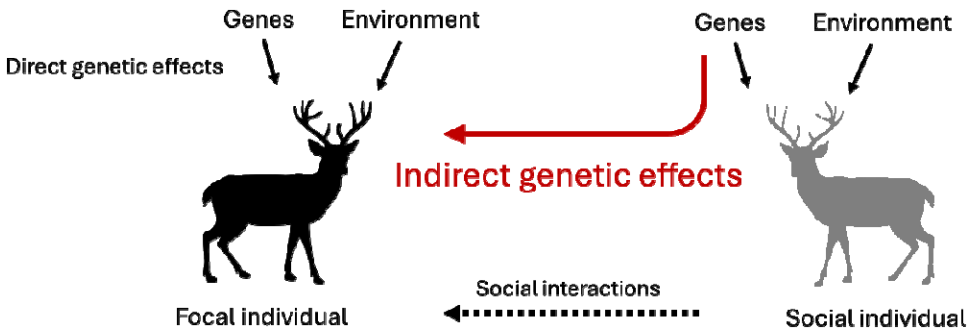
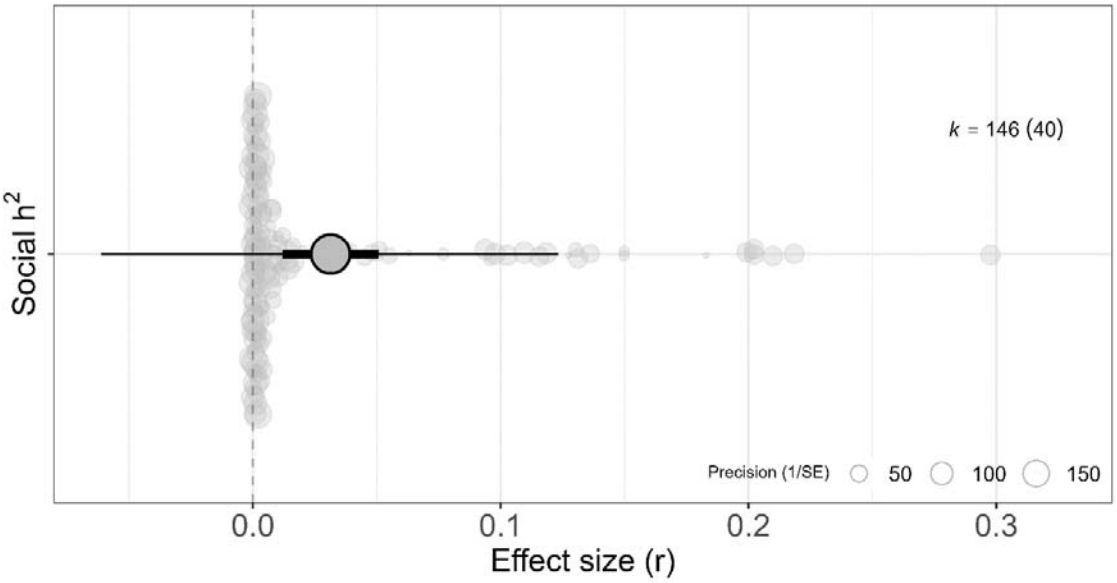
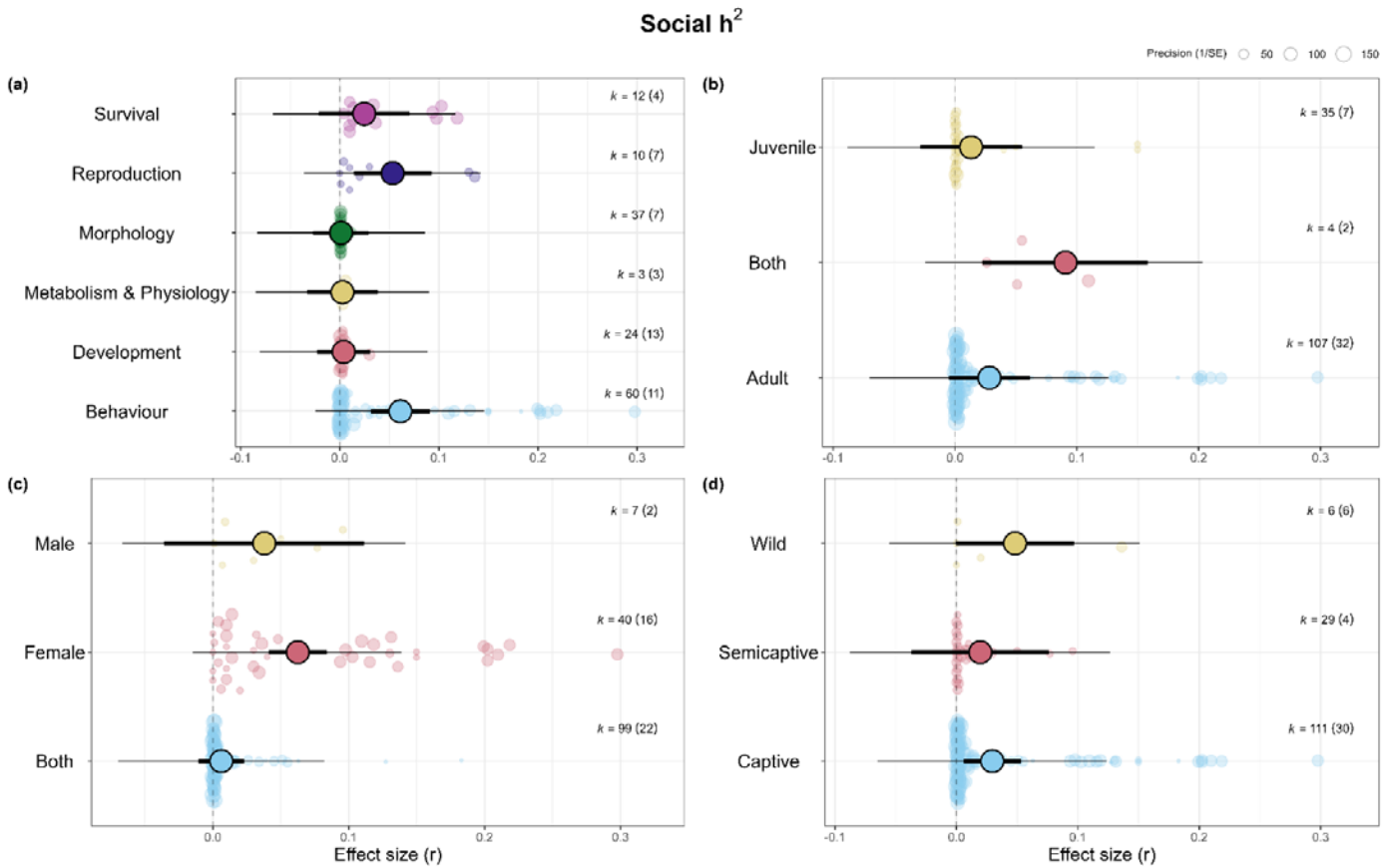


Figure 2. Social heritability (*social* h^2) from a phylogenetic multilevel meta-analysis with 40 studies and 146 effect sizes (Aim 1). Orchard plot showing the back-transformed meta-analytic mean as *r*, 95% confidence intervals (thick whisker), 95% prediction intervals (thin whisker) and individual effect sizes (*r*) scaled by their precision (semitransparent circles). *k* corresponds to the number of effect sizes, the number of studies is shown in brackets.



907 **Figure 3.** Social heritability (*social* h^2) meta-analytic estimates from phylogenetic multilevel uni-moderator meta-regressions testing the following
908 moderators (Aim 2): (a) Trait category, (b) Age, (c) Sex, (d) Population type. Orchard plot showing the back-transformed meta-analytic mean as *r*, 95%
909 confidence intervals (thick whisker), 95% prediction intervals (thin whisker) and individual effect sizes (*r*) scaled by their precision (semitransparent circles).
910 *k* corresponds to the number of effect sizes, the number of studies is shown in brackets.



911

Figure 4. IGEs and DGEs meta-analytic estimates from phylogenetic multilevel uni-moderator meta-regressions (Aim 3) comparing: (a) V_A vs. V_{IGE}, (b) narrow-sense h^2 vs. *social* h^2, and (c) I_{DGE} vs. I_{IGE} (evolvability). Orchard plot showing the back-transformed meta-analytic mean as *r*, 95% confidence intervals (thick whisker), 95% prediction intervals (thin whisker) and individual effect sizes (*r*) scaled by their precision (semitransparent circles). *k* corresponds to the number of effect sizes, the number of studies is shown in brackets.

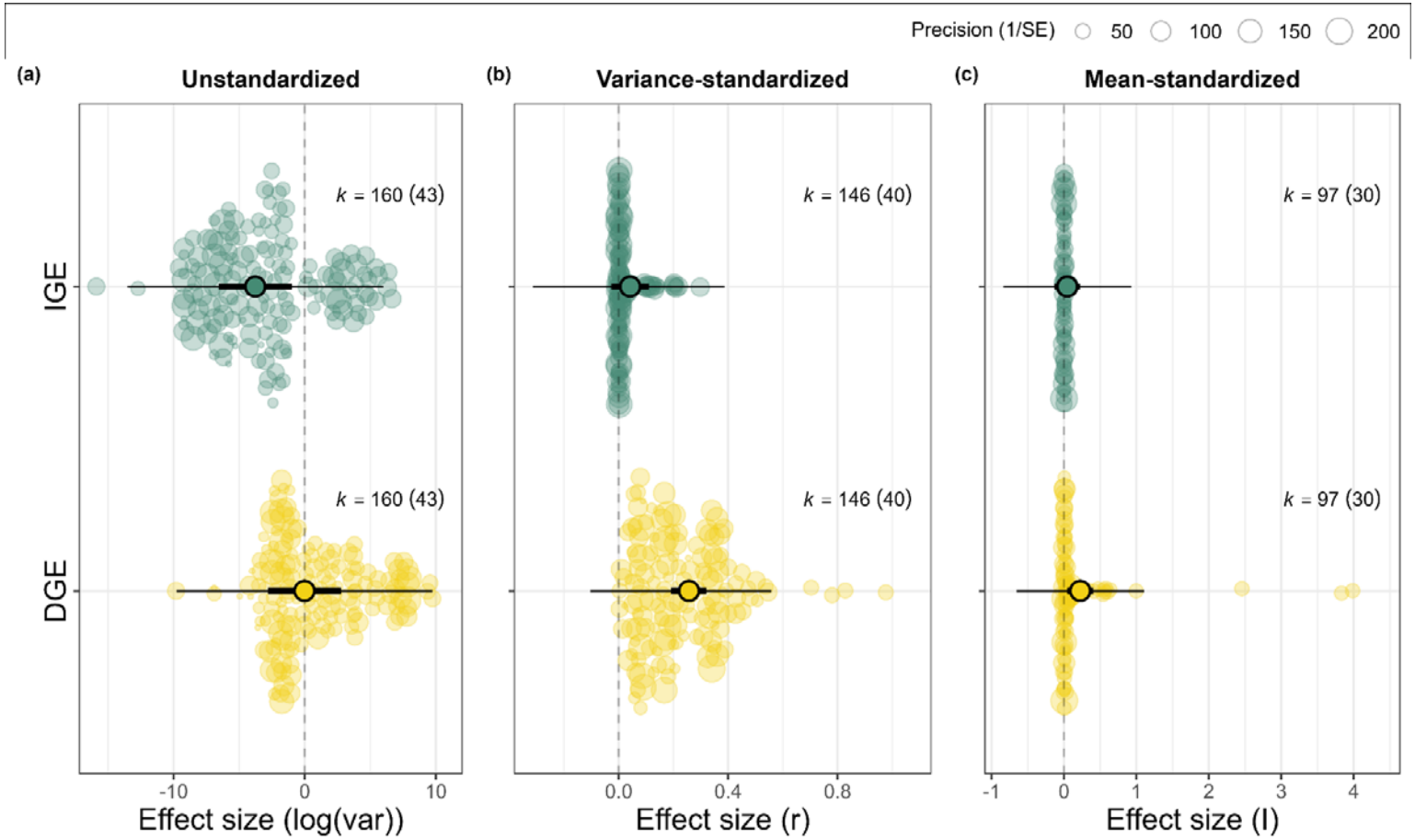
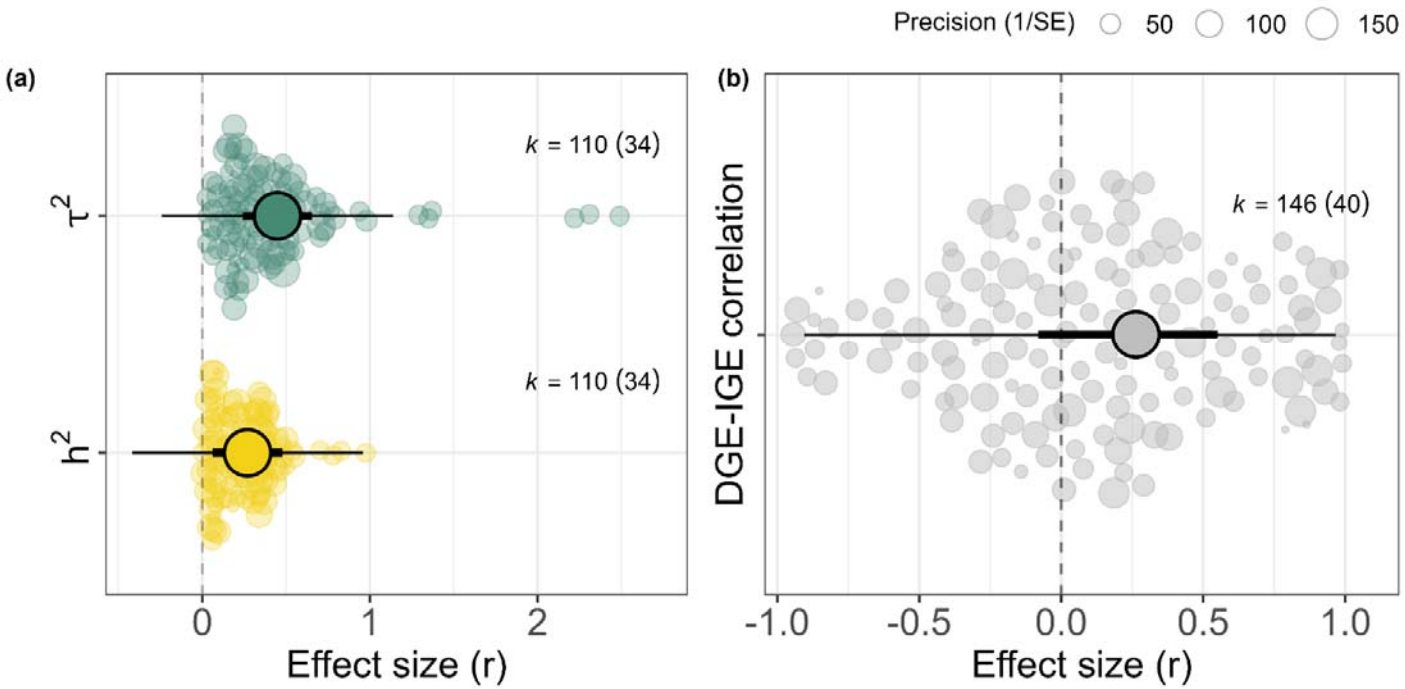



Figure 5. Meta-analytic estimates for Aim 4: (a) phylogenetic multilevel meta-regression comparing narrow-sense heritability (h^2) to total heritable variance (τ^2); (b) phylogenetic multilevel meta-analysis of $r_{DGE\text{-}IGE}$. Orchard plot showing the original (a) and back-transformed meta-analytic mean as *r*, 95% confidence intervals (thick whisker), 95% prediction intervals (thin whisker) and individual effect sizes (*r*) scaled by their precision (semitransparent circles). *k* corresponds to the number of effect sizes, the number of studies is shown in brackets.