Ungeneralizable generalizations? A meta-meta-analysis of the influence of taxonomic bias on the study of behavior.

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Abstract

Meta-analysis is a powerful tool for synthesizing behavioral research and identifying general patterns. However, are the conclusions we draw from these analyses truly representative across animal groups? Alternatively, are our conclusions shaped by taxonomic biases in the underlying research? For example, in animal behavior, vertebrates are often overrepresented in the research we conduct. This taxonomic imbalance raises concerns about the validity of generalizations drawn in the field, especially from meta-analyses. To examine this issue, we examined the meta-analyses published in Animal Behaviour, Behavioral Ecology, and Behavioral Ecology and Sociobiology from 2000 – 2024. We then conducted a "meta-meta-analysis" to calculate the degree to which overall effects in prior meta-analytical results may have been mis-estimated due to taxonomic bias. We found that taxonomic biases in the primary research strongly influence effect size estimates in meta-analyses and can lead to improper inferences and generalizations. On average, meta-analytical averages are mis-estimated by ~35% ($p << 0.01$) and significance changes in about 25% of instances when sampling is taxonomically representative. Because meta-analyses aggregate data, they propagate the biases present in an area of research, leading to potentially incorrect generalizations. Addressing this taxonomic bias is critical to generalizations that describe the true richness of animal behavior.

Introduction

A major goal of animal behavior research is to understand why animals behave the way they do from both proximate and ultimate perspectives (Tinbergen 1963). Drawing general conclusions to answer such questions across species can be challenging and meta-analyses have emerged as the primary tool for doing so. However, the inferences drawn from any analysis, including meta-analyses, are reliant on whether the data being used are an appropriate sample (Gurevitch and Hedges 1999, Jennions et al. 2013, Konno et al. 2020). Put another way, if the data going into behavioral meta-analyses are not representative of animal behavior broadly, then the resulting inferences may be incorrect.

Biases in the data used in meta-analyses is a topic that has been extensively explored (e.g. Dickersin 2005, Rothstein et al. 2005). However, most of this discussion has focused on issues like the well-known “file drawer problem” and time-lag bias. The file drawer problem concerns publication bias wherein “statistically significant” findings are more likely to be published (reviewed by Dickersin 2005). This bias leads to the absolute magnitude of effect sizes being overestimated. Time-lag bias refers to the general observation that effect sizes tend to decrease over time (Trikalinos and Ioannidis 2005), as has been found in ecology generally (Jennions and Møller 2002). Time-lag bias leads to the absolute magnitude of effect sizes being overestimated early in a field’s development. While not trivial, both types of biases can be at least partially addressed statistically within meta-analyses (Nakagawa and Santos 2012, Nakagawa et al. 2022).

More generally, and potentially more importantly, we do not have a good idea of how taxonomically biased the data going into meta-analyses might be (Gurevitch and Hedges 1999). However, for animal behavior research, we do know that individual research projects are conducted in a highly taxonomically biased manner. Rosenthal et al. (2017) examined papers published in *Animal Behaviour* between 1953 and 2015 and found that vertebrates were strongly over-represented (Figure 1A). At the coarsest level, vertebrates represent only 5% of animal species but were the focus of study in 71% of surveyed studies. Even within vertebrates there was considerable bias in what animals were studied (Rosenthal et al. 2017): endotherms were far more frequently studied than expected based on their taxonomic representation (Figure 1B) and well over 50% of all studies were on birds or mammals (Figure 1B). When invertebrates were specifically studied, most behavioral research was conducted in a single order (Hymenoptera, Rosenthal et al. 2017). Interestingly, this bias in favor of vertebrates is reduced in sexual selection and sexual conflict research. Zuk et al. (2014), found that roughly 30 percent of sexual selection and 50 percent of sexual conflict research is conducted with insects. However, even in these areas of study, vertebrates remain over-represented and over 20 percent of the work done on insects was from a single genus (i.e. Drosophila, Zuk et al. 2014).

This potential for biased inferences also has impacts beyond our basic understanding of behavior. From an applied perspective, as discussed by Rosenthal et al. (2017), taxonomic bias in the study of behavior can affect conservation and management efforts, understanding population dynamics, and understanding zoonotic disease risk. Consequently, evaluating the presence of taxonomic bias in animal behavior meta-analyses and considering how such bias may affect the inferences we draw is of considerable importance. Specifically, it is necessary to know whether the conclusions we draw from meta-analyses are representative and generalizable.

We sought to address this concern by asking two questions: First, is the taxonomic bias identified by Rosenthal et al. (2017) also present in the data used in meta-analyses? Second, does taxonomic bias lead to misestimation and incorrect inferences in meta-analytical results?

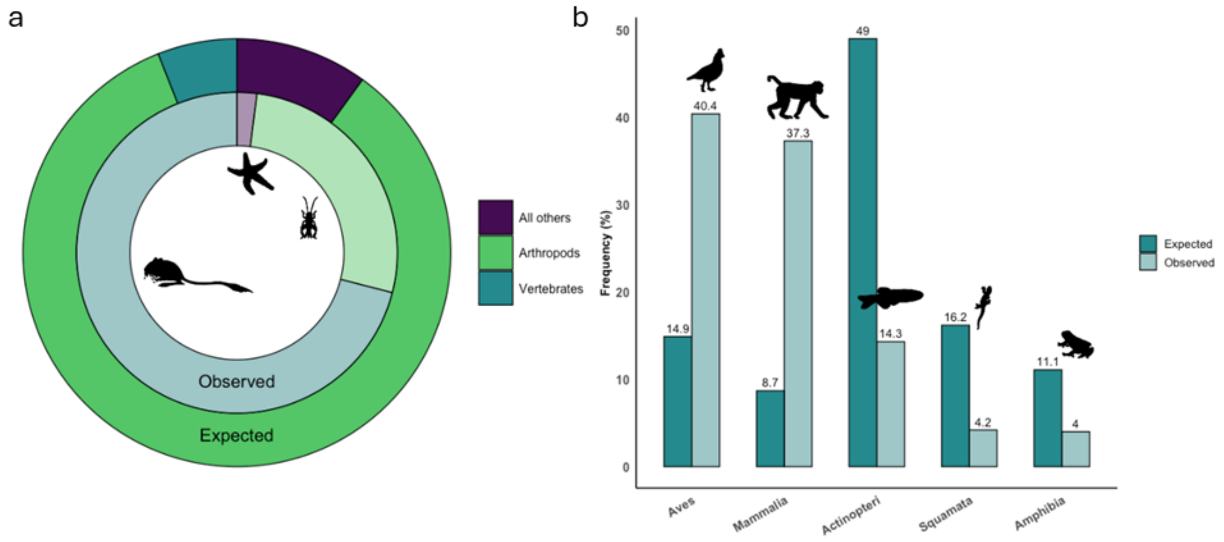

Figure 1. Taxonomic bias in the animals used in the study of animal behavior as identified by Rosenthal et al. (2017) both in general (a) and just within vertebrates (b).

Methods

To answer these two questions, we identified the meta-analyses published in three leading behavioral journals. We then determined the taxonomic representation of the constituent studies used in these meta-analyses and how estimates from these meta-analyses would change if the data were sampled in a taxonomically representative manner.

Identifying meta-analyses

To identify meta-analyses in animal behavior, we searched the journals Animal Behaviour, Behavioral Ecology and Sociobiology, and Behavioral Ecology for meta-analyses published in 2000 – 2024 using Web of Science (Core Collection, Science Citation Index Expanded). We used the search string TS=(meta-anal* OR meta OR meta anal*). This search returned 118 articles and was conducted on 4 February 2025. The titles and abstracts of these articles were then screened based on two search criteria: 1) the study had to have been identified by the authors as a meta-analysis, and 2) the study had to have been focused on non-human animals. Based on these search criteria, we identified a total of 75 articles for secondary screening (sensu Foo et al. 2021).

During the secondary screening we verified that the 75 articles met our inclusion criteria. Additional inclusion criteria at this stage were that the meta-analyses were not taxonomically restricted (e.g. focused solely on primates) and that available data were sufficient to estimate effect size means for vertebrates and invertebrates. When data were not available from online sources, we requested the data directly from the authors. This ultimately led to a sample size of 15 articles and 43 estimates (Figure 2, Table 1).

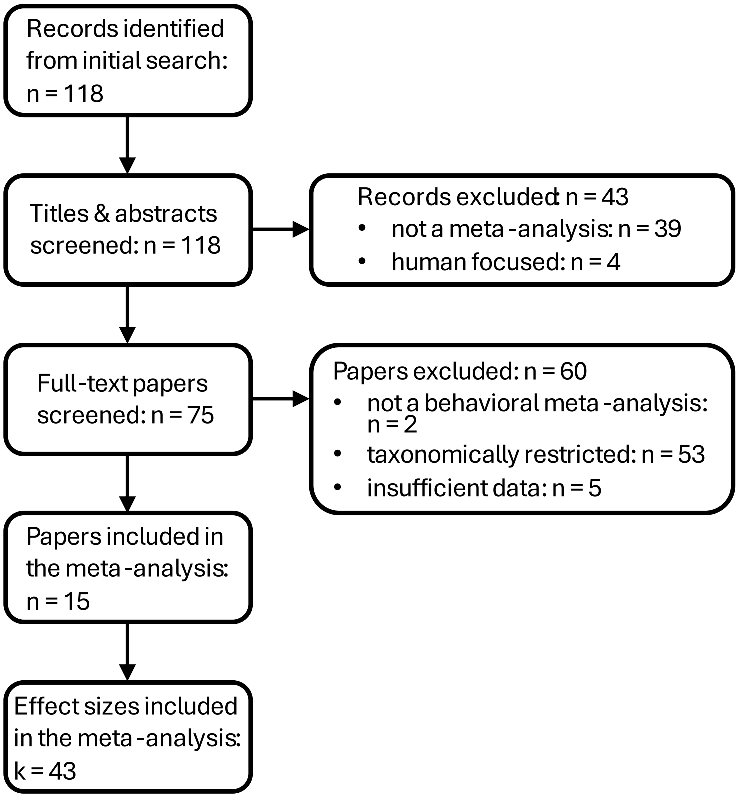

Figure 2. PRISMA diagram of included studies and effect size estimates

Identifying taxonomic representation

For each article we determined whether specific estimates within a meta-analysis were from vertebrates or invertebrates. We then compared this representation of estimates to that expected based on known animal diversity. Because of the expected lack of non-vertebrate estimates (Figure 1a) and the large number of non-vertebrate phyla, we compared the representation of vertebrates and invertebrates. We compared this representation based on the taxonomic diversity without accounting for differences in abundance.

Estimating taxonomic misestimation of meta-analytical results

To determine the degree to which taxonomic representation could lead to misestimation of meta-analytical results, we compared meta-analytic grand means to estimates of what those means would be if estimates were drawn proportionally from the diversity of Animalia. We did so by calculating the marginalized means for each included meta-analysis under the assumption of taxonomically representative sampling (sensu Nakagawa et al. 2023).

For example, consider a meta-analysis based on 100 estimates with 75 estimates coming from vertebrates and 25 from invertebrates. This degree of taxonomic mis-representation is consistent with the findings of Rosenthal et al. (2017). Assuming equal precision of estimates, the grand mean effect size in this meta-analysis would be primarily driven by the mean for vertebrates: if the mean effect size for vertebrates were 0.5 and the mean for invertebrates was -0.5, the overall "grand mean" would be 0.25. However, this overall mean is taxonomically biased as vertebrates only represent around 5% of all animals (vertebrates: 4.74%; Catalogue of Life, 2025). If the estimates in this hypothetical example were drawn proportionally from the animal kingdom, the grand mean would instead have been estimated as -0.45.

We estimated the marginalized means given the observed data ("data-proportional") and under taxonomic representative sampling ("taxonomic-representative") with the `metafor` package in R (Viechtbauer 2010, Viechtbauer and López‐López 2022, Nakagawa et al. 2023). This process is known as "poststrafication" and is often used in recalibrating survey results (Gelman et al. 2021). Using the `predict` function of `metafor`, we estimated the marginalized taxonomic-representative value with an assumption of 5% of estimates being from vertebrates and 95% of estimates being from invertebrates. This also allowed us to estimate the uncertainty around the taxonomic-representative mean (Viechtbauer and López-López 2022).

Many of the constituent studies conducted multiple meta-analyses and we attempted to replicate as many of those as possible. In all cases we attempted to replicate the original analyses either using code originally provided by the authors or de novo code based on the described methods and as the effect sizes used or described by the authors. When possible, this included the inclusion of phylogenetic error structure. For each meta-analysis we estimated the data-proportional (μ_{dp}) and taxonomic-representative (μ_{tr}) overall mean estimates and their uncertainties. We also determined the statistical significances ($\alpha < 0.05$) of μ_{dp} and μ_{tr}.

Data analysis

For each meta-analytical estimate pair from a study, we compared the data-proportional versus taxonomic-representative estimates to quantify the relative, proportional effect of taxonomic misrepresentation on overall effects in meta-analysis. To do so, we calculated the absolute value of the log ratio (Hedges et al. 1999):

$$\left| log \frac{\mu_{tr}}{\mu_{dp}} \right|$$

we used the absolute value as this allowed comparison across studies regardless of whether data-proportional or taxonomic-representative estimates were larger. This also allowed us to compare estimates across meta-analyses even when those original meta-analyses used different effect sizes. The two limitations of this approach are that it does not allow analysis in cases where the signs of estimates change and the use of absolute values can result in over-estimation of magnitudes (Morrissey 2016, see below). Fortunately, sign changes only occurred for 3 of the 43 pairs of estimates (see results).

As an additional analysis, we also calculated the absolute difference between data-proportional and taxonomic-representative estimates. Because the constituent meta-analyses used different effect sizes themselves (i.e. Zr, log-odds ratios, and various standardized mean differences), we first transformed all effect sizes to Zr following equations in Borenstein et al. (2009). We then calculated the absolute value of the differences between data-proportional and taxonomic-representative Zr scores.

For both the relative and absolute differences between pairs, the standard deviation of the differences was estimated as:

$$\sqrt{sd_{dp}^2 + sd_{tr}^2 - 2sd_{dp} \times sd_{tr} \times r}$$

where sd_{dp} and sd_{tr} are the estimate standard deviations of the overall meta-analytical means (reported in the `metafor` outputs as standard errors) and r represents the correlation between the uncertainties (because the uncertainties are based on the same datasets). For the differences in Zr scores, we used the estimated uncertainties in the above equation. For the absolute value of log ratios, sd_{dp} and sd_{tr} were calculated as $sd_{dp}/\ \mu_{dp}$ and $se_{tr}/\ \mu_{tr}$, respectively. r is not analytically known but is between 0 and 1 and so was set to 0.8. This did not substantively affect our conclusions or estimation (Supplemental Materials).

To estimate the overall effect of taxonomically biased sampling on meta-analytical inferences, we next fit a random effects meta-analysis with the study an estimate was drawn from as a random effect to the absolute standardized mean differences. We also included individual estimate identity as a random effect because each estimate was based on a different sample size and often addressing a different question. The overall effect size was estimated while weighting by the inverse of the standardized mean difference's sampling variance (Borenstein et al. 2009). We evaluated the magnitude and uncertainty of the grand mean as indicative of taxonomic bias in meta-analytical inferences. A significant grand mean would indicate significant taxonomic bias in meta-analytical estimates.

Importantly, calculating the grand mean of absolute values results in positive bias (Morrissey 2016). Therefore, we used an "analyze-then-transform" approach following Morrissey (2016). To do so, we transformed the meta-analytic grand means of the magnitude of taxonomic bias (x_{gm}) and its uncertainty (se_{gm}) according to a folded normal distribution as:

$$x_{folded} = se_{gm}\sqrt{\frac{2}{\pi}} \times e^{\left(\frac{-x_{gm}^2}{2se_{gm}^2}\right)} + x_{gm} \times \mathbf{erf}\left(\frac{x_{gm}}{\sqrt{2se_{gm}^2}}\right)$$

$$sd_{folded} = x_{gm}^2 + se_{gm}^2 + x_{folded}^2$$

where x_{folded} is the transformed grand mean and sd_{folded} is its standard deviation. **erf** is the Gauss error function. Uncertainties of parameters from linear models, like those provided by the `metafor` package, are reported as standard errors but these values specifically refer to the standard deviation of the parameter's sampling distribution and so were used here in lieu of standard deviations. We calculated the folded values for both the relative and absolute analyses.

We next conducted a heterogeneity analyses to determine the contributors to variability in taxonomic bias. We determined whether there was significant heterogeneity among estimates based on Cochran's Q and its significance. We then calculated the proportion of variation (I^2) attributable to sampling error, to study differences, and to estimate differences within studies (Nakagawa and Santos 2012).

Because we were analyzing differences between marginal means, as opposed to original findings, there are not clear expectations of publication bias or approaches to testing for such bias. Moreover, because our estimates were constrained to be positive, typical funnel plots and trim-and-fill analyses were not appropriate. Given the lack of either a basis or methods, we did not conduct publication bias tests.

All analyses were conducted in the R statistical language (v4.5.0, R_Core_Team 2025).

Data availability

All data and analysis code are available at **link**.

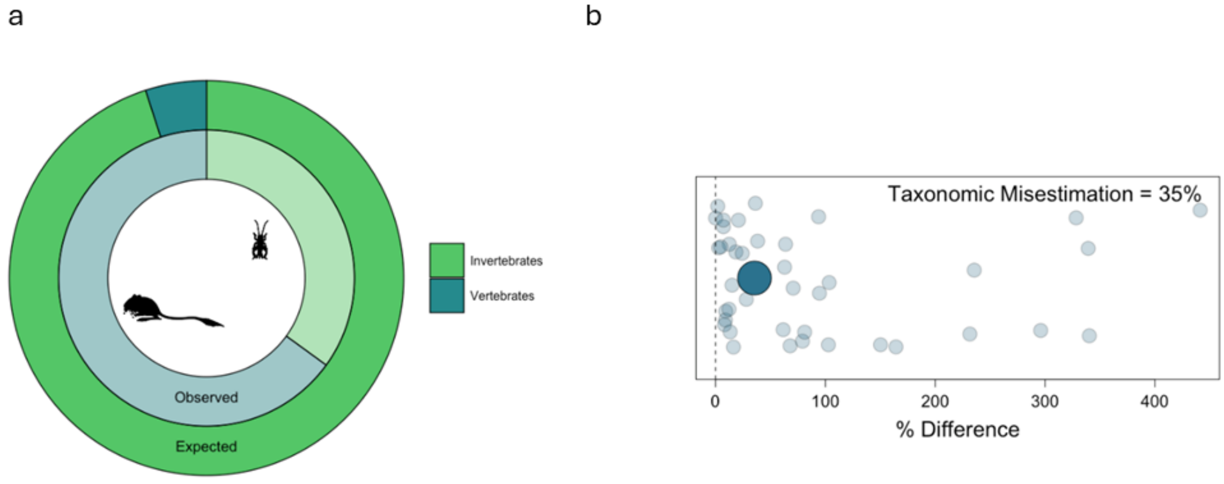

Figure 3. a) Data included in meta-analyses by taxa. b) Overall (large dot) and individual estimates (small dots) of the percentage misestimation due to taxonomic misrepresentation (uncertainty around this misestimation is smaller than the point).

Results

Taxonomic Representation of Data in Meta-Analyses

We found that the data used in behavioral meta-analyses was highly taxonomically biased in favor of vertebrates (Figure 3a, Table 1). 65% of the estimates used in meta-analyses were from vertebrates, slightly less than the bias observed more broadly in behavioral research (Rosenthal et al. 2017), but far, far greater than the 5% expected according to taxonomic representation.

Relative Effect of Taxonomic Misrepresentation on Meta-Analytical Inferences

The meta-analytical mean, after transformation due to the folded distribution, of absolute log ratios was 0.30 (s.e. = 0.08, $p << 0.01$; Figure 4). Put another way, meta-analytical means are, on average, misestimated by 35% (Figure 3b). Significance changed between the data-proportional and taxonomic-representative estimates for 10 of 43 estimate pairs (Figure 4), though the signs of effects only changed for 3 pairs.

There was significant heterogeneity among estimates ($Q_{df:39} = 102.15$, $p << 0.01$). Of this heterogeneity, most was attributable to sampling variance ($I^2 = 0.69$). But there was also considerable heterogeneity among studies ($I^2 = 0.13$) and among estimates within studies ($I^2 = 0.19$).

Absolute Effect of Taxonomic Misrepresentation on Meta-Analytical Inferences

The meta-analytical mean of absolute differences between Zr scores was 0.15 (s.e. = 0.06, $p = 0.01$). However, one estimate pair differed by around 3 times more than the next largest difference (Figure S1). When excluded, the difference dropped to 0.098 (se = 0.026) and remained significant ($p < 0.01$). Whether with or without this extreme data point, these effects translate to substantive differences in more conventional effect sizes: a difference between Zr scores of 0.15 corresponds to a difference of 0.29 between correlations and a difference of 0.091 converts to a difference in correlations of 0.20. There was significant heterogeneity among estimates ($Q_{df:41} = 2.1\times 10^5$, $p << 0.01$) but 99% of this heterogeneity was attributable to sampling variance with no appreciable heterogeneity among studies or estimates ($I^2 < 0.01$).

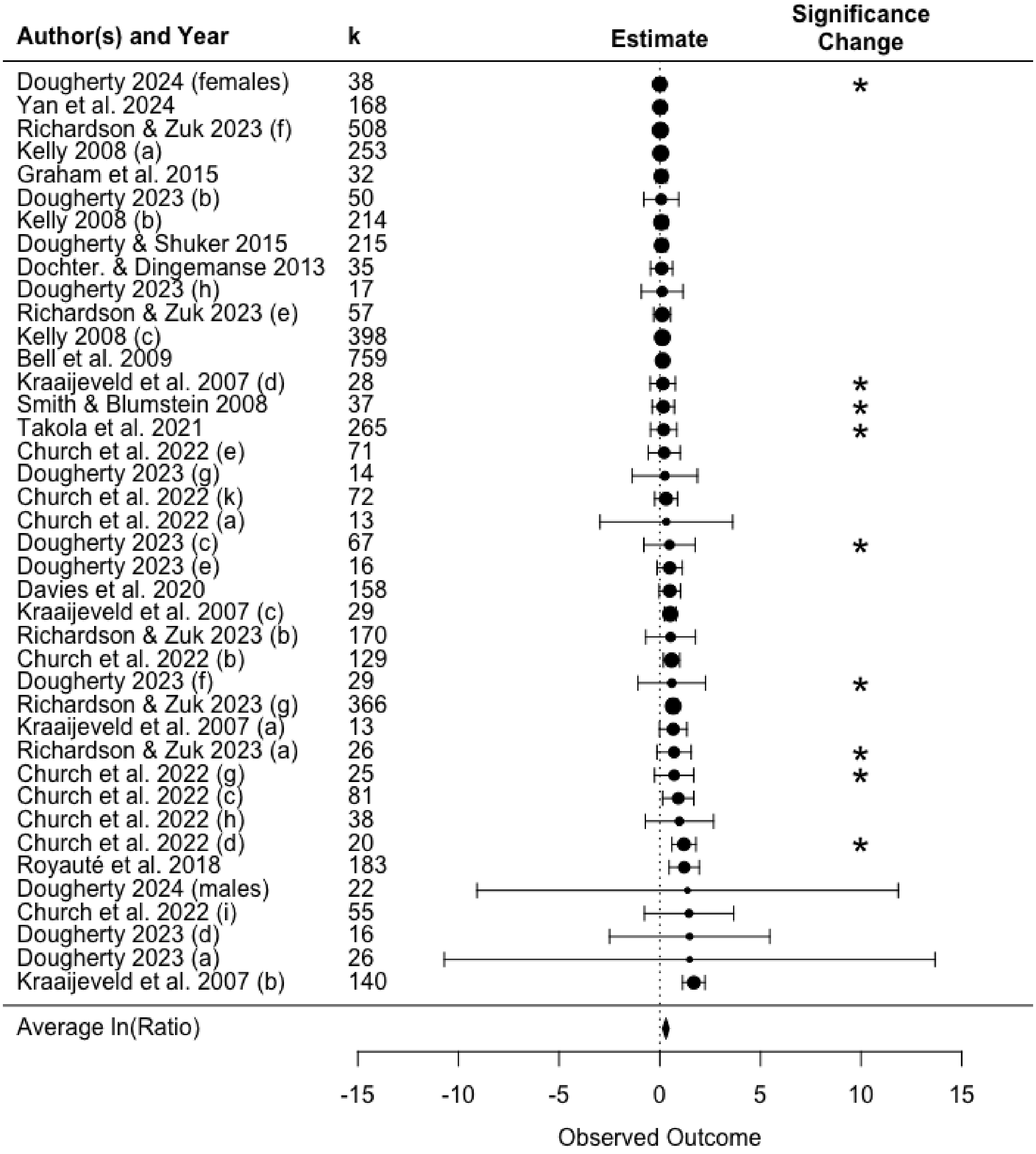

Figure 4. Within-study estimates and standard errors of the relative magnitude of taxonomic bias on meta-analytical estimates.

Discussion

We found that the degree of taxonomic bias on meta-analytical estimates in the study of animal behavior was surprisingly large (Figure 3). Specifically, our results demonstrate that meta-analytical means from behavioral meta-analysis are misestimated by around 35%. The observed magnitude of misestimation also led to changes in significance for around 25% of estimates. This degree of an effect can lead to incorrect inferences being drawn.

Our analysis of the absolute magnitude of the effect on meta-analytical estimates demonstrates a somewhat smaller impact of taxonomic bias. However, this is not entirely unexpected because effect sizes estimated in meta-analyses are typically quite small (Møller and Jennions 2002, Low-Décarie et al. 2014) and so absolute differences will necessarily be constrained to also be small. Even in absolute terms, this bias still translates into substantial difference in the magnitudes of effects, changing correlations by around 0.3. Further, we were initially concerned with relative and inferential impacts, which cannot be determined from absolute differences.

As one example, consider the findings of Royauté et al. (2018). We use this example as one of us (NAD) was the senior author of that study and so as to not single out other authors. In Royauté et al. (2018), the authors concluded that correlations between behaviors and physiological or life-history traits were not in the direction expected according to the “pace-of-life” syndrome (POLS) hypothesis proposed by Réale et al. (2010). This was a novel and surprising finding given the intuitive predictions of POLS and its dramatic impact on discussions of how behavior might be integrated with physiology and life-history. The conclusion in that paper was based on the meta-analytical mean, estimated as r = 0.06 (95% CI: -.01 : 0.14), which was predicted to have been positive according to POLS. However, as reported by Royauté et al. (2018), there was a significant difference between vertebrates and invertebrates regrading support for POLS. There also was substantial taxonomic bias in the data that went into Royauté et al.'s (2018) analysis. Here, via the estimation of marginal means adjusting for taxonomic bias, we see that if the sampling of vertebrates and invertebrates was taxonomically proportional, the meta-analytical mean would have been estimated as r = 0.22 and would have been significantly different than zero. While this is a relatively modest absolute difference in estimates, it is a large relative difference (~2.4 times, Figure 4). This ends up resulting in a substantive reinterpretation of the evidence for POLS: If the data going into the original analysis were consistent with actual taxonomic representation, and the estimates of the original analysis hold, this would have been taken as meta-analytical support for POLS. We suspect similar changes in conclusions might be drawn from other meta-analyses if taxonomic bias were to be similarly addressed.

Importantly, changes in interpretation as discussed above are dependent on how robust our marginal mean estimates are for invertebrates. This is not currently clear and, across the included meta-analyses, the poor representation of invertebrates (Figure 3a, Table 1) necessarily means that these estimates have greater uncertainties than do estimates for vertebrates. Also, because of the poor representation of invertebrates in behavioral studies, the diversity *within* invertebrates could not be captured in our analysis. Because invertebrates are also not proportionally sampled (Zuk et al. 2014), our field's meta-analytical conclusions may be even more biased than revealed here.

While changes in interpretation due to taxonomic bias might be discouraging, they also are of intrinsic interest. Sub-group analysis (Borenstein et al. 2009), a long-standing part of meta-analyses in other fields and stratification, would allow the evaluation of when a hypothesis like POLS holds in some taxonomic groups and not others.. For example, it is also perhaps more interesting to ask why POLS holds in invertebrates but not vertebrates rather than simply asking whether the hypothesis is supported in general. Such analyses may allow for greater insight than currently provided by most behavioral meta-analyses

This example and our overall finding confirms concerns raised by others. In particular, Gurevitch and Hedges (1999) discussed how researcher biases and taxonomic preferences in the generation of original data have the potential to affect subsequent meta-analytical inferences. However, the degree to which this was an actual problem was not clear until our analysis here. This is a concerning problem but not a new one. As discussed by Rosenthal et al. (2017), taxonomic bias in the study of animal behavior is pervasive and pronounced (their data are recreated in Figures 1a & 1b).

It is also worth emphasizing that relatively few studies could be included in our analyses and, as a result, the effects of taxonomic bias might therefore be even more severe. Specifically, 53 meta-analyses published in Animal Behaviour, Behavioral Ecology, and Behavioral Ecology and Sociobiology were taxonomically restricted (Figure 2). Put another way, the taxonomic bias in the 15 studies included here necessarily underestimates the bias present in the 53 studies for which bias could not even be estimated. In some cases taxonomic restriction may be because a specific hypothesis applies to, for example, mammals but not reptiles. However, it is also possible that this represents a secondary opportunity for researchers to express taxonomic preferences (Gurevitch and Hedges 1999). Taxonomically restricted meta-analyses, when not necessary, will further reduce the generality of conclusions.

If a broad goal of animal behavior research is to increase our general understanding of behavior, our results demonstrate that taxonomic bias should be a major concern. If, instead, we are primarily interested in examining personally interesting examples of behavior, the bias is of less importance. Regardless, a primary aim of meta-analyses *is* to draw generalizable inferences. Our results suggest that the taxonomic bias inherent in the behavioral literature makes this generalization difficult. This may profoundly affect how right and wrong we are about our understanding of behavior. Addressing this bias will require individual researchers to consider whether their study system choices will increase the generality of our field's understanding.

Acknowledgements

We thank the authors of behavioral meta-analyses for providing data either via public repositories or upon request. MAS was supported by the Department of Biological Sciences and the Environmental and Conservation Sciences Program at North Dakota State University. NAD was supported during this work by the National Science Foundation (IOS-2222929).

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Table 1. Behavioral meta-analyses included in the current analyses

Study ID	Number of included analyses	Number of estimates in each analysis	Number of estimates for vertebrates	Number of estimates for invertebrates	Author(s) (Year)
K9	4	13	4	9	Kraaijeveld et al. (2007)
		140	135	5	
		29	26	3	
		28	23	5	
B11	1	759	493	266	Bell et al. (2009)
T40	1	265	261	4	Takola et al. (2021)
D44	3	38	2	36	Dougherty (2024)
		22	4	18	
Y46	1	168	47	121	Yan et al. (2024)
S56	1	37	31	6	Smith and Blumstein (2008)
D64	1	35	30	5	Dochtermann and Dingemanse (2013)
D67	1	215	92	123	Dougherty and Shuker (2015)
D85	1	158	125	33	Davies et al. (2020)
C87	10	13	12	1	Church et al. (2022)
		129	85	44	
		81	74	7	
		20	19	1	
		71	56	15	
		26	25	1	
		25	22	3	
		38	35	3	
		55	49	6	
		72	29	43	
R89	7	26	9	17	Richardson and Zuk (2023)
		170	61	109	
		52	24	28	
		8	4	4	
		57	43	14	
		508	92	416	
		366	325	41	
D90	8	26	8	18	Dougherty (2023)
		50	27	23	
		67	41	26	
		16	6	10	
		13	13	3	
		29	22	7	

		14	5	9	
		17	6	11	
		253	187	66	
K102	3	214	168	46	Kelly (2008)
		398	339	59	
G106	1	32	3	29	Graham et al. (2015)
R110	1	183	145	38	Royauté et al. (2018)

Supplementary Materials

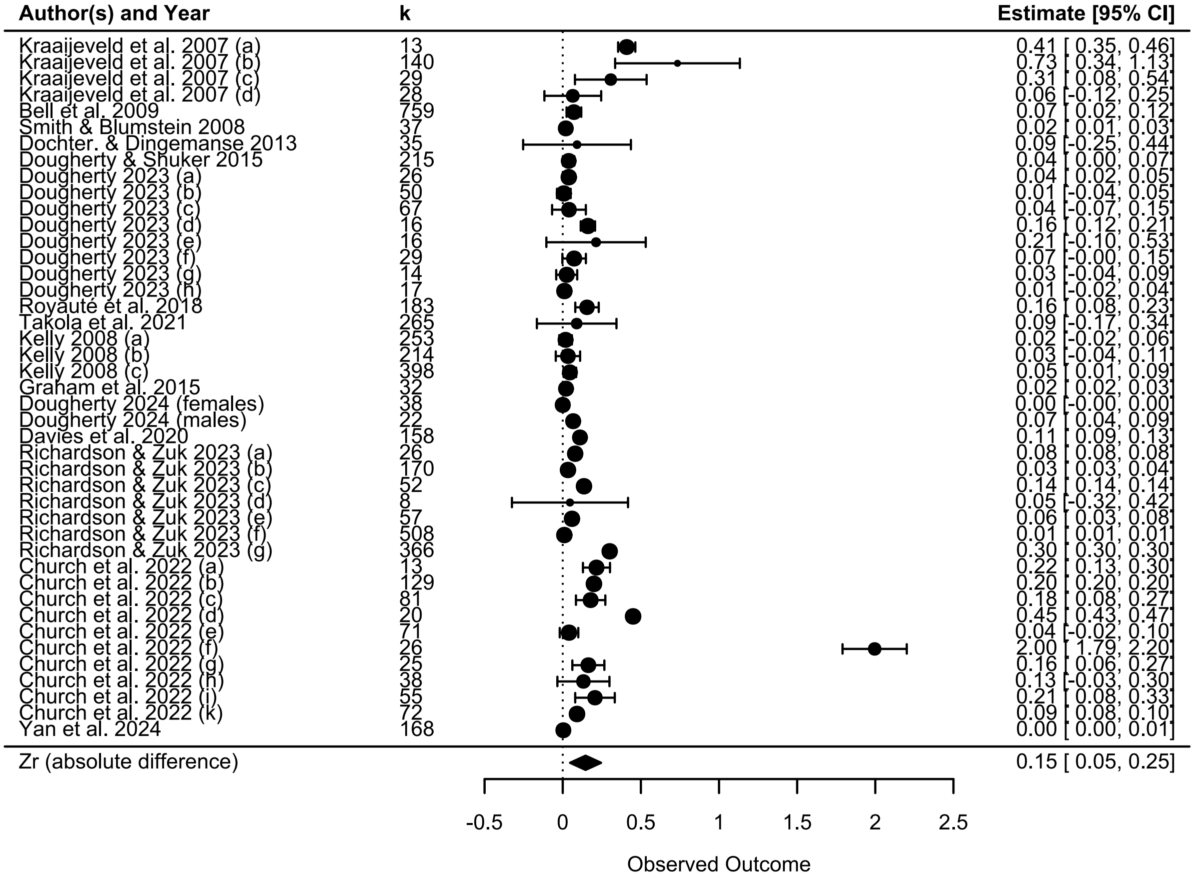

Figure S1. Within-study estimates and standard errors of the magnitude of taxonomic bias (absolute differences) on meta-analytical estimates.

Supplementary Analysis: Effect of *r* on sampling variance.

Because we estimated the standard deviation of estimates as:

$$\sqrt{sd_{dp}^2 + sd_{tr}^2 - 2sd_{dp} \times sd_{tr} \times r}$$

it was possible that choices about the value of *r* might influence the ultimate meta-meta-analytical results. We know that *r* is much greater than 0 since the same data were being used for the data-proportional and taxonomic-representative estimates. However, we don't know if this value is exactly 1. We *a priori* decided to use a value of 0.8 since the value is necessarily large but also calculated meta-analytical means over a range of values for *r* (Figure S2). A higher *r*, corresponding to a more conservative estimte of the standard deviation, led to an increase in the meta-analytical estimate but did not change significance or our overall interpretation.

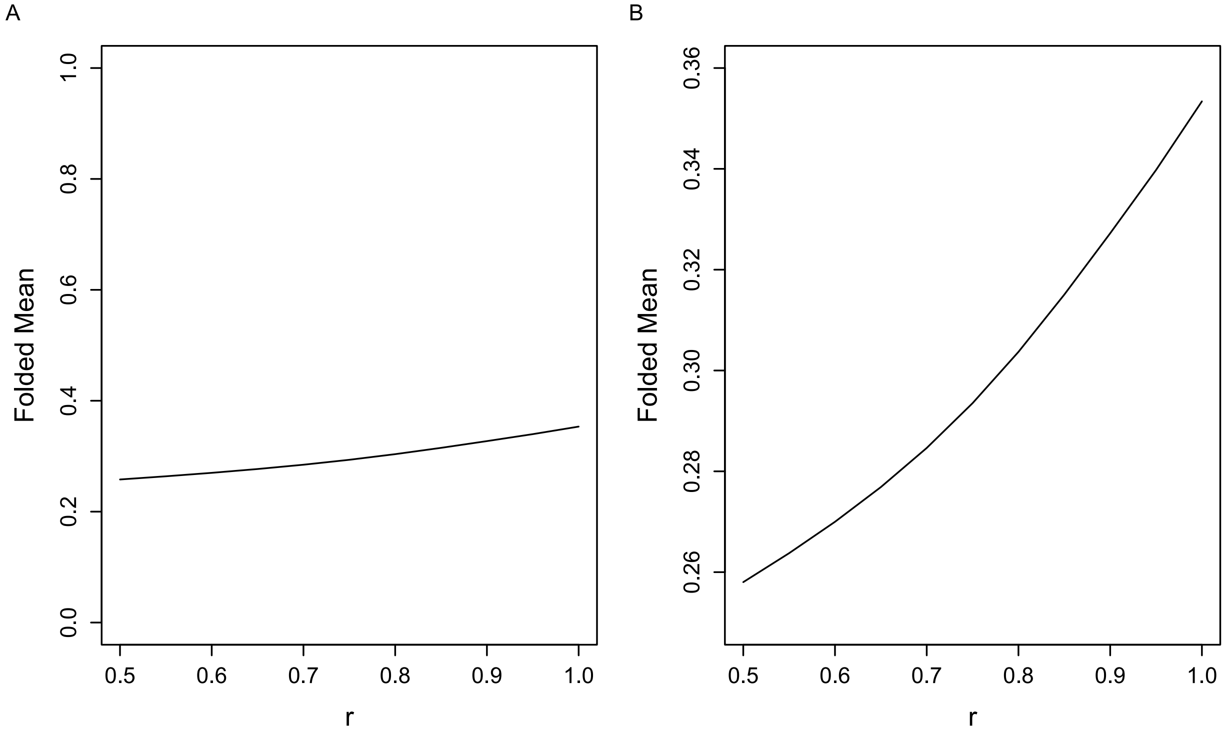

Figure S2. Change in the estimated folded mean for a range of values for *r*. A and B differ only in the scale of the y axes.