Title: The fitness consequences of wildlife conservation translocations: A meta-analysis

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Abstract

Conservation translocation is a common strategy to offset mounting rates of population declines through the transfer of captive-reared or relocated organisms to imperiled populations. However, these programs have been criticized for low success rates and husbandry practices that produce individuals with genetic and performance deficits. We assessed the disparity in post-release performance of translocated organisms relative to wild-resident conspecifics through a meta-analysis of 826 performance comparisons from 172 studies representing nine animal classes (101 species). We found that translocated organisms have 70% decreased odds of out-performing their wild-resident counterparts, supporting published claims of systemic issues hampering conservation translocation. Pre-release animal enrichment significantly reduced performance disparities, whereas our results suggest no overall effects of captive generation time or the type

of fitness surrogate measured. Conservation managers should consider evaluations of post-release performance using sympatric (resident-control) and allopatric (true-control) wild-reference groups to ensure translocated animals contribute to recipient population growth and viability.

Introduction

Rates of floral and faunal species loss in the new Anthropocene signal the onset of a sixth global mass extinction [1,2]. Among vertebrates, extinction rates in the last century increased 100 times above pre-industrial levels [3] and recorded population size declines have averaged 68% in the last 50 years [4]. Continued species loss will have irreversible consequences for ecosystem services and resiliency. Slowing the rate of species loss will require eliminating existing threats (e.g., disease, poaching) and extensive habitat preservation and restoration [5,6]. While environmental threats are being addressed, supportive breeding and translocation programs have been proposed to maintain species and their roles in the ecosystem [7,8].

Animal conservation translocations (ACTs) are a common strategy intended to directly offset species extinction through the supplementation of threatened populations and the repatriation of extirpated populations [9]. ACT programs supplementing extant populations in their indigenous range are called reinforcements, and can be grouped into two categories [10,11]. First, *in situ* reinforcements (ISRs) collect and transport wild organisms to another natural area for the benefit of the recipient conspecific population. Second, *ex situ* reinforcements (ESRs) incorporate a captive phase lasting from less than one generation (i.e., head-starting) up to several generations (i.e., captive breeding) before release. Despite immense efforts across a wide array of taxa to employ ACTs and document their efficacy in the literature, it is still unknown whether translocated individuals are as capable as their wild conspecifics at contributing to population viability and preventing extinctions.

To date, ACTs have had many notable successes and a quantifiable impact on global extinction rates [12,13]. Nevertheless, ACTs are often considered a halfway technology with logistical and systemic shortcomings that have led to generally low success rates [14,15]. In

particular, multiple studies indicate that ACTs might produce individuals with inherent genetic and performance-related deficits that compromise ACT program goals and reduce recipient population viability [16,17]. These deficits are most severe in ESRs involving multiple captive generations since the capture of ESR founders acts as a bottleneck on genetic diversity. Even with a stringent captive breeding structure, factors inherent to husbandry practices (e.g., small effective population size, inbreeding depression, relaxed purifying selection) increase the likelihood of fixation of undesirable alleles and a loss of allelic heterozygosity [7,18,19]. A large influx of captive-born individuals into the wild with such genetic properties can swamp genetic diversity of locally adapted populations and reduce effective population sizes despite an overall increase in numbers [20]. However, such genetic deficits require multiple generations of captive breeding to accumulate which suggests alternative factors contribute to fitness reductions observed in ESRs lasting a generation or less [17,21].

A fundamental criticism of ESRs is that non-natural conditions present in captivity can influence individual phenotypes, diminishing post-release performance relative to wild conspecifics [19,22,23], where animal performance is defined as a measure of some critical life history character (e.g., growth rate, survival, fecundity) that correlates with individual fitness [24]. In a variety of taxa, ESRs lasting a generation or less negatively influence post-release performance metrics such as anti-predator behavior [25], dispersal [26], growth [27], survival [28], and reproductive success [21]. Such phenotypic mismatches can arise via domestication selection, where trait values that are selected for in captivity are maladaptive when expressed in a natural environment [29,30]. The unintentional selection for domesticated phenotypes in artificial environments is likely a major contributor to reduced performance of ESRs, since it can alter phenotype distributions within a single generation [21,27]. In the absence of domestication selection,

phenotypic plasticity during less than one generation of captive development and rearing can lead to similar deviations from the wild-type in anatomical, physiological, and behavioral traits [29,31]. Moreover, certain plastic phenotypic deviations have an epigenetic basis, thereby potentially influencing performance of future generations regardless of their developmental environment [32].

By virtue of the use of wild-born organisms and lack of a captive component, ISRs are lauded as a less intrusive and a generally more successful translocation strategy than ESRs [14,33–35]. However, failure rates for ISRs are still notably high and potentially a consequence of similar issues that affect ESRs. At the population-level, supplementing existing populations with conspecifics from other wild populations can lead to maladaptive gene flow or outbreeding depression of the recipient population and a reduction in meta-population genetic diversity [36,37]. At the individual-level, relocation can impact post-release performance either directly through transportation-related stress [38] or indirectly through energetic costs of establishment [39], errant dispersal and homing behaviors [40], diminished social structure [41], and phenotypic mismatches within the novel ecosystem [31].

Exposing captive organisms to some form of enrichment is the most intuitive strategy to counteract phenotypic mismatch, and a reasonable compromise when ISRs are not possible. We use the term enrichment broadly to refer to a variety of supportive measures [14] employed by ACTs to offset any maladaptive behavior, physiology, or physical injury incurred during captivity and/or translocation [23,41]. Some examples include fostering pre-release organisms with experienced conspecifics [42], simulating *in situ* environments with naturalistic enclosures or antipredator training [43], implementing a soft-release phase where supplemental feeding and/or shelter are provided [44], or simply reducing the length of the captive phase [26,45]. Literature reviews

suggest that enriched ESR cohorts are more successful post-release compared to un-enriched cohorts [14,23], but the lack of a wild-reference group in the synthesized findings makes it difficult to conclude whether enrichment strategies produce translocated organisms that are indistinguishable from wild conspecifics with respect to post-release fitness [46].

Finally, the metric used to gauge relative performance can vary in its representation of fitness, thereby shaping study conclusions [24]. The lifetime reproductive success of an individual is the ideal measure of fitness when focusing on population dynamics and phenotypic adaptation, but lifetime reproductive success and the component life history traits that determine it (e.g., survival and fecundity) are difficult to measure in natural conditions. Consequently, fitness is often approximated using traits that typically correlate with fitness (e.g., body size, body constitution, movement). However, the extent to which correlates and components of fitness covary and ultimately relate to lifetime reproductive success remains uncertain [24]. For example, Mulder et al. found that while translocated and wild-resident desert tortoises (*Gopherus agassizii*) had similar body condition and survivorship four years post-release, translocated males fathered none of 92 offspring for which paternity was determined [47]. This suggests that survival is a potentially inappropriate component of fitness to gauge ACT success in adult organisms with high adult survivorship. Conservation translocations should consider multiple relevant fitness components during project assessment to identify potential life-history trade-offs and avoid misleading conclusions [24].

The translocation literature has grown to a point that quantitative reviews are necessary to summarize the high volume of papers, while also accounting for heterogeneity and bias [48]. Seminal reviews have evaluated ACT efficacy from the published literature and via mail-in questionnaires sent to conservation program managers [11,14,33]. In both approaches, the response

variable (translocation success versus failure) reduces a highly nuanced outcome to a binary classification based in part on unstandardized criteria (e.g., creation of a self-sustaining population) and professional opinion. These syntheses are an invaluable resource for applied conservation and management, but their largely narrative format is not conducive to quantitative synthesis across broad and multifactorial datasets while accounting for bias and heterogeneity among studies. Meta-analysis is well equipped to gauge translocation efficacy based on the post-release performance of animal subjects [23,43,49–51]. Previous meta-analyses are limited to comparisons among translocated cohorts and fail to include a wild-reference group (but see [22]), therefore, they cannot address whether translocated individuals are as capable as their wild conspecifics at contributing to population viability.

Here, we present the first comprehensive meta-analysis to assess conservation translocation programs through the synthesis of studies involving direct, post-release comparisons of translocated and wild-resident conspecifics. We further expand on previous reviews by sampling the literature broadly across macroscopic animal groups and assess relative post-release performance using multiple fitness surrogates. Our primary objective is to quantify the disparity in post-release performance of translocated organisms relative to wild-resident conspecifics across animal taxa and to determine whether several organismal and methodological factors influence this disparity. Our systematic review and meta-analysis show that across a broad array of taxa (826 effect sizes from 101 species representing 49 families), translocated organisms have 70% decreased odds of out-performing their wild-resident counterparts. Pre-release animal enrichment strategies significantly reduced performance disparities among translocated and wild organisms, whereas *in situ* vs. *ex situ* reinforcement strategy, captive generation time, and the type of fitness surrogate measured did not influence relative post-release

performance. Conservation managers should standardize the use of wild-resident controls and multiple performance metrics in their assessments of potential conservation translocation strategies.

Table 1. Total number of log odds ratio (LOR) estimates collected, organized by taxonomic class and the fitness surrogate used as a metric for performance.

	Movement	Constitution	Growth	Survival	Reproduction	**Total**
Bivalvia	0	0	0	6	0	**6**
Gastropoda	0	3	5	9	6	**23**
Malacostraca	0	4	0	14	5	**23**
Echinoidea	1	1	0	0	0	**2**
Actinopterygii	38	43	26	158	81	**346**
Amphibia	4	2	0	3	0	**9**
Reptilia	101	12	26	55	9	**203**
Aves	14	12	0	59	38	**123**
Mammalia	18	13	2	46	12	**91**
Total	**176**	**90**	**59**	**350**	**151**	**826**

Results

After filtering based on the inclusion criteria, our dataset comprised 826 unique effect sizes for relative performance of translocated organisms and their wild-resident conspecifics (223 ESR and 603 ISR comparisons) collected from 172 peer-reviewed studies investigating 101 unique species (Table 1; Supplementary Table S1). We calculated standardized effect sizes as log odds ratios (LORs) of performance metrics for translocated versus wild-resident cohorts such that positive values indicate translocated individuals exhibited higher relative performance than wild-resident conspecifics. We analyzed the LORs and subsets of these data using three linear mixed effects meta-analytical models with fixed effect moderator variables to determine the impact of organismal and methodological factors plus random effects to attribute sources of variation among effect sizes.

Translocated organisms generally exhibited poorer performance following release compared to wild-resident conspecifics. The primary model's overall log odds ratio (LOR mode: -0.98; CrI: -1.62 to -0.36) was converted to an odds ratio by exponentiating across the posterior distribution, indicating that translocated organisms have 69.9% decreased odds of out-performing their wild-resident counterparts (OR mode: 0.30; CrI: 0.18 to 0.66). By quantifying the proportion of posterior samples with LOR estimates greater than or equal to zero, we infer that translocated organisms had an overall 0.002 probability of out-performing wild-resident conspecifics following release (Fig. 1). Disparity in post-release performance did not vary widely across taxonomic classes, but instead all classes generally exhibited negative LOR effect sizes, suggesting poor performance of translocated organisms relative to wild-residents across taxa (Supplementary Table S2). Similarly, relative post-release performance was largely unaffected by ESR vs. ISR translocation strategy.

In studies involving mixed-sex cohorts, comparisons based on fitness components tend to have lower LOR marginal posterior mode estimates than comparisons based on fitness correlates, but widely overlapping credible intervals across fitness components and correlates indicate a consensus in the interpretation of relative under-performance of translocated cohorts across a variety of performance metrics (Supplementary Table S2). More variable effect size outcomes observed in sex-specific comparisons might suggest the presence of unequal life-history consequences to translocation among sexes, but low sample sizes in constitution-, growth-, and survival-based estimates, and uneven taxonomic representation in movement-based estimates preclude conclusive interpretations.

Due to limited reporting of key moderator variables across studies, we analyzed subsets of the data in two additional models to assess whether the amount of captive ancestry or the presence of enrichment, respectively, influenced relative post-release performance of translocated cohorts. In general, LOR marginal posterior mode estimates were similar for the overall model effects and for parameters that also appeared in the primary model 1 above (Supplementary Tables S3-S4). Therefore, we limit the remainder of our reporting to model-specific parameters.

Post-release performance was generally lower among translocated cohorts compared to wild residents, regardless of the amount of captive ancestry. Post-release performance was largely unaffected by the length of captive ancestry, except for comparisons based on constitution and growth. In ISR studies involving constitution-based comparisons, we observed that relocated organisms without any captive ancestry had a lower probability (0.00; OR mode: 0.06; OR CrI: 0.03 to 0.21) of out-performing wild-resident conspecifics relative to head-started (0.15; OR mode: 0.58; OR CrI: 0.24 to 1.33) and captive-bred cohorts (0.25; OR

mode: 0.28; OR CrI: 0.03 to 2.49; Supplementary Table S3). Comparisons with growth-based estimates exhibited a similar pattern, but these growth-related comparisons for relocated, head-started, and captive-bred cohorts were based on reduced datasets of only two, eight, and one studies, respectively.

Post-release performance of translocated organisms generally benefitted as a result of enrichment. To test the influence of enrichment strategies on relative post-release performance among translocated and wild cohorts, we analyzed a subset of studies that gathered data from both enriched and unenriched cohorts within the same experimental design and compared their post-release performances relative to a common wild-control group. Unenriched translocated organisms had a 0.07 probability of out-performing their wild-resident conspecifics (OR mode: 0.07; CrI: 0.003 to 1.16), whereas enriched translocated organisms had a 0.58 probability of out-performing their wild counterparts (OR mode: 0.55; CrI: 0.01 to 9.95; Fig. 2; Supplementary Table S4).

The dataset exhibited a high overall taxonomic signal but low heterogeneity at individual taxonomic levels. Here we summarize the heterogeneity statistics from model 1, representing the full dataset (Supplementary Table S5 for heterogeneity summary statistics of all three models). Heterogeneity values from individual taxonomic levels were relatively small and even in magnitude, but their combined taxonomic signal accounted for 59.9% (CrI: 46.8% to 74.4%) of total heterogeneity. Study- and group-level effects accounted for 21.8% (CrI: 12.0% to 34.3%) and 11.9% (CrI: 8.14% to 18.4%) of total heterogeneity, respectively.

Discussion

Our meta-analysis gauged the efficacy of conservation translocation programs based on direct, *in situ* comparisons of animal performance between translocated organisms and wild-resident conspecifics. We synthesized estimates of relative performance based on five fitness-surrogate categories across 101 unique species spanning nine taxonomic classes. Our findings indicate that translocated organisms tend to under-perform relative to their wild counterparts, and that this pattern is largely independent of taxonomic class or the type of fitness surrogate measured. This supports previous claims for the existence of systemic issues across ACTs and suggests that translocated organisms are often at a major disadvantage following release. Under-performance of translocated cohorts was also consistent regardless of translocation strategy or the amount of captive ancestry, with some caveats. Finally, post-release performance was markedly improved in translocated cohorts exposed to pre-release enrichment relative to unenriched cohorts. Here we explore the implications of our findings and make recommendations for future translocation program assessment and monitoring procedures.

The unexpected lack of variation in effect sizes across taxonomic classes hints at a general influence of ACTs on animals, which is in direct odds with the large proportion of study heterogeneity explained by taxonomic rank (Supplementary Table S5). The high taxonomic signal (64.29%) indicates that taxonomic position explains a majority of variation in effect sizes, which would lead us to expect large differences in relative performance values among higher taxonomic groups. For example, Dochtermann et al. observed a consistent pattern in a phylogenetic meta-analysis quantifying behavioral heritability: Little difference in effect size among species and a low phylogenetic signal [52]. However, we see the proportion of heterogeneity explained by individual taxonomic tiers is consistently low, which could explain the minimal differentiation in effect sizes at the level of taxonomic class. This suggests that

heterogeneity incurred at different taxonomic levels is not necessarily cumulative and might be more accurately quantified in a phylogenetic framework. Regardless, comparative studies assessing biological patterns at the broadest taxonomic scales should adopt a mixed phylogenetic and taxonomic approach until an appropriate phylogeny with empirically-derived branch lengths can be resolved [53,54].

Our meta-analysis highlights a clear bias in taxonomic representation among ACTs, with most studies involving charismatic species or those with economically important fisheries. Most notably, there is a significant lack of ACTs involving amphibians that meet our inclusion criteria. Amphibian populations are experiencing global declines and will likely require human interventions in the form of ACTs to avoid extirpation [40]. Recent quantitative reviews describe a positive trend in the success of amphibian translocations relative to earlier benchmarks [40,55]. However, these efforts fail to consider comparisons among translocated and wild-resident conspecifics as a potential index for project feasibility. Recent amphibian studies using this comparative approach have provided novel insights regarding the multi-generational influence of ACTs as well as potential pitfalls of cryopreservation techniques on ACT feasibility [56,57]. Future assessments of translocation success should include simultaneous monitoring of a wild-control group from the donor and/or recipient populations as an additional criterion for determining project feasibility and success.

Our primary model showed high consistency in effect sizes across fitness surrogates, indicating that phenotypic traits considered as correlates of overall fitness have the potential to characterize performance differences among translocated and wild-resident cohorts. We initially predicted that fitness correlates would exhibit less consistent disparities across animal cohorts since fitness correlates are less reliable proxies of fitness than fitness components [58]. One

explanation for the observed pattern is that fitness surrogates can vary in how well they reflect overall individual fitness based on the relative length and positioning of the measurement interval within the organism's lifespan [24]. Additionally, the lack of differences in fitness surrogate effects may be due to unaccounted-for differences in life-history strategies within and among study systems. Life-history theory suggests that the uneven allocation of finite resources results in life-history trade-offs among fitness components such that maximizing one fitness component can decrease overall lifetime reproductive success (e.g., increased annual fecundity decreases annual survival)[59]. Future ACT studies and meta-analyses on the topic should incorporate multiple fitness components at different life stages to assess relative quality of released organisms, such that the covariance among fitness components and thus the presence of fitness trade-offs or differing life-history strategies can be tested at the within-study level [24].

We were not able to evaluate sex-by-fitness surrogate interactions in the full dataset because so few studies reported sex-specific effects. However, sufficient data from reptile studies suggest that estimates of relative performance based on movement were substantially lower for both male- and female-only cohorts relative to estimates from mixed-sex cohorts, indicating greater disparity in post-release performance relative to wild conspecifics when males and females were analyzed separately. Only when accounting for sex do our findings align with the established relationship between maladaptive post-release movement patterns and reduced survival in the herpetofaunal literature [40,60]. The influence of sex on post-release performance is also poorly represented in the primary literature and rarely synthesized in subsequent reviews [61]. To our knowledge, no other quantitative literature review or meta-analysis examining translocation efficacy has included sex as a moderating factor, despite well-documented and systematic differences in life history and ecology among the sexes [62].

We observed similar levels of under-performance among translocated cohorts relative to wild conspecifics, regardless of whether translocated organisms were ISR (0 captive generations), head-started (ESR with < 1 captive generation), or captive-bred (ESR with > 1 captive generation). This contrasts with existing quantitative reviews describing a negative relationship between captive ancestry and fitness, with ISRs performing relatively better than ESRs [14,35]. One explanation for this discrepancy is the poor reporting in the literature of ESR captive histories and animal origins which precluded us from conducting a more powerful assessment of the effect of captive ancestry. As such, our head-starting vs. captive-rearing levels possibly misclassified cohorts with ambiguous or mixed captive histories, which could explain the lack of significant performance deficits commonly reported in long-term captive-breeding populations [21]. Additionally, past reviews have used an arbitrary measure of success to characterize performance, which could skew model outcomes. Our findings suggest that while ISRs avoid the maladaptive selective pressures associated with extended captivity, managers should still be wary of individual- and population-level stressors characteristic of ISRs that can lead to disparities in post-release performance like those observed in ESRs. This underscores the necessity of ACT programs to report the capture histories of their organisms, and to conduct multi-generational monitoring to ensure accurate measures of meaningful life-history traits.

Disparity in post-release performance among translocated and wild individuals was significantly reduced when translocated organisms were exposed to some form of pre-release enrichment. This finding highlights the growing relevance of the behavioral ramifications of *in situ* and *ex situ* reinforcements, where genetic management has historically been the only factor informing best husbandry and breeding practices [16,46]. Our findings agree with those from other meta-analyses showing that enriched, translocated organisms generally had higher performance

than non-enriched, translocated conspecifics in a variety of taxa [23,50]. Since few studies incorporating pre-release enrichment also fulfilled our inclusion criteria by directly comparing translocated cohorts to wild-resident conspecifics, we were not able to refine our categorization of different enrichment strategies. Despite that, our study provides the broadest evidence yet—and the first synthesized evidence to incorporate wild-control groups—that pre-release enrichment strategies have the potential to reduce post-release performance disparities between translocated and wild-resident organisms.

Conservation biology is in the midst of a revolutionary push for more evidence-based decision-making to replace historically anecdotal- or experience-driven strategies [63]. Formal meta-analysis is an important tool for synthesizing existing literature and directing new veins of inquiry, particularly in the field of conservation, where translocation studies are numerous but statistical power is limited by low sample sizes [64]. Our findings show that *in situ* reinforcements (ISRs) and *ex situ* reinforcements (ESRs) produce organisms that under-perform and should therefore be implemented only after careful consideration of the recipient population's trajectory and the existing environmental threats at the recipient site. For example, if a wild population is declining due to extrinsic threats, then the release of under-performing translocated conspecifics is unlikely to reverse declines [5]. Alternatively, if environmental threats have been removed, then the allelic diversity of a remnant wild population could benefit from the influx of translocated cohorts, despite certain performance deficits [13,56]. Pilot studies employing the post-release comparative techniques analyzed in this study could therefore use relative post-release performance, population demographics, and environmental forecasts to predict the efficacy of ACT programs. Future conservation efforts must clarify their goals and consider other

ecosystem-level restoration or mitigation efforts as alternative or complementary strategies to ACTs.

Despite a number of successful efforts, animal conservation translocations have experienced historically low success rates, without significant improvement observed over time [65]. That said, the often-wide credible intervals in our findings suggest there are opportunities in which ACTs can produce viable individuals and contribute to recipient populations. We recommend that ACT managers include sympatric (resident-control) and allopatric (true-control) wild-reference groups in their programs to properly evaluate post-release performance of translocated organisms, and assess any negative density-dependent impacts of ACTs on resident conspecifics [46,66]. Managers should also take advantage of next-generation sequencing technologies and parentage assignment software to promote long-term, multi-generational monitoring of relative reproductive success and other fitness surrogates [21]. Finally, we encourage ACT managers to explore the natural history of their study organisms for tailored opportunities to maximize post-release performance by implementing pre-release behavioral or environmental enrichment.

Methods

Literature search and inclusion criteria

We conducted our literature review, screening, and analysis according to PRISMA guidelines (Supplementary Fig. S1)[67]. We searched the literature using Web of Science, including all databases (1/1/1900-8/23/2019), for peer-reviewed studies concerning conservation translocations with some reference to a wild-resident group used as a control. Our query was:

TS = ((conservation OR reintroduc* OR repatriat* OR releas* OR supplementation OR transloc*) AND ("captive?born" OR "captive?breed*" OR "captive?bred" OR "captive?rais*" OR "captive?rear*" OR fisher* OR hatcher* OR "head$start*" OR relocat*) AND (native OR resident OR wild))

We also screened studies reviewed in Stuparyk et al. for inclusion because our primary Web of Science query did not encompass the terminology used in several ISR studies concerning relocations intended to mitigate human-animal conflicts [22]. After screening (Supplementary Fig. S1; Supplementary Table S1), the resulting 589 full-text papers—along with 28 additional papers synthesized by Stuparyk et al.[22]—were assessed for our required inclusion criteria: At least one direct, quantitative comparison of a fitness component (growth, survival, reproduction) or fitness-correlated trait (movement, body constitution) between one translocated (either ESR or ISR) and one wild-resident animal group. The comparison(s) must have been made in a natural setting following the release of the translocated cohort into an area occupied by wild-resident conspecifics of comparable age and size distributions. We excluded papers making comparisons based on ambiguous traits without the author(s) clearly defining a relationship to fitness. These ambiguous traits include, but are not limited to, stable isotope or itemized diet analysis [68], habitat use [69], behavioral ethograms [70], or varying morphotypes [71]. Papers were also excluded if they did not contain the necessary descriptive statistics to calculate effect sizes (see “effect size extraction” below) and corresponding authors did not respond to email requests for supplementary statistics. Finally, we excluded papers assessing the influence of translocations on population genetic indices, as these datasets do not involve distinct animal groups and sample sizes that are necessary to calculate effect sizes.

We quantified the disparity in performance between wild-resident and translocated cohorts using two effect size metrics. In studies comparing animal groups based on mean estimates of continuous traits (*e.g.*, growth rate, survivorship, clutch size), we calculated standardized mean differences (SMD)[72]. For comparisons based on counts of dichotomous outcomes (e.g., full vs. empty stomachs, proportion recaptured, successful vs. unsuccessful nests), we calculated log odds ratios (LOR)[73]. Effect sizes were calculated using the function *escalc* in the R package *metafor* [74]. From each paper, we extracted descriptive statistics necessary to calculate effect sizes for all relevant fitness-related comparisons from the published and supplemental texts and data tables, from additional materials requested from corresponding authors, and from relevant figures and plots using the R package *digitize* [75].

We converted all SMD estimates to LORs for more intuitive interpretation of effect size magnitudes [76]. Log odds ratios are centered at zero and were calculated such that positive values indicate translocated individuals exhibited better relative performance than wild-resident individuals, and negative values indicate translocated individuals under-performed relative to wild individuals. In traits where lower values indicate better performance (e.g., rate of mortality, parasite load), raw trait values were multiplied by negative one for consistent interpretation.

We extracted several study-level and estimate-level attributes to evaluate our predictions in the final statistical model. Comparisons were assigned a study ID based on the paper from which they were extracted and a group ID to distinguish unique groups of organisms within each study. Identical group ID values were assigned to comparisons involving measures of different traits in the same organisms [77]. We also retrieved taxonomic class, order, family, genus, and species names of all assessed organisms from the Integrative Taxonomic Information System database [78]. We identified the fitness-related trait under consideration in each comparison and

reclassified each into one of five broad categories: Movement, body constitution, growth, survival, and reproduction. We also identified the predominant sex (i.e., female-only, male-only, or mixed-sex) of organisms in each comparison. We characterized the amount of captive ancestry of translocated individuals represented in each comparison using two separate variables. First, we distinguished comparisons according to whether the translocation program involved a captive phase or not (i.e., *in situ* reinforcement vs. *ex situ* reinforcement strategy). In those studies that described the amount of captive ancestry among translocated cohorts, we further classified captive ancestry using an ordered set of categories: 1) ISR organisms without any captive ancestry, 2) ESR organisms with wild-origin parents not raised in captivity, and 3) ESR organisms with one or more direct ancestral generation raised in captivity. Finally, we classified the absence/presence (0/1) of enrichment techniques for select comparisons according to the circumstances of each paper. Due to the arbitrary nature of enrichment treatments across our dataset, we only assessed enrichment efficacy within studies that included post-release performance comparisons with wild-resident conspecifics for both enriched and unenriched translocated cohorts.

Statistical analysis

We first fit a meta-analytical taxonomic mixed model [53,79] to quantify the overall effect size—relative post-release performance among translocated and wild-resident cohorts—across the entire dataset, and also assess how individual-level (i.e., sex, taxonomic group) and study-level (i.e., fitness surrogate, ESR vs. ISR strategy) factors influence this outcome (model 1; Supplementary Table S2). We modeled the LOR responses as a function of categorical fixed effects for sex, taxonomic class, fitness surrogate, and study strategy. We examined two-way

interactions between sex and fitness surrogate, and between sex and strategy to determine whether these individual- and study-level factors had sex-specific relationships with relative post-release performance. We also included a two-way interaction between fitness surrogate and strategy to examine whether post-release performance in various fitness-related traits is influenced by translocation strategy.

To assess the potential influence of domestication selection on the relative post-release performance of translocated cohorts, we used a second, similar model to analyze a subset of studies that specified the number of captive generations experienced by translocated cohorts (model 2; Supplementary Table S3). We fit model 2 by substituting the fixed effect of strategy from model 1 with captive ancestry, a categorical fixed effect with three levels classifying the focal ACT cohort as either part of an ISR (without any captive ancestry), a head-starting program (ESR with < 1 generation in captivity), or a captive-breeding program (ESR with > 1 direct ancestral generations in captivity). We were unable to analyze captive ancestry as a continuous variable due to a lack of reporting of exact ancestral generation times, and due to cohorts of potentially mixed ancestry. Model 2 also included categorical fixed effects for sex, taxonomic class, fitness surrogate, and captive ancestry, and two-way interactions between sex and fitness surrogate, sex and captive ancestry, and between fitness surrogate and captive ancestry.

Finally, we developed model 3 to test the influence of enrichment strategies on relative post-release performance among wild and translocated cohorts by analyzing a subset of studies that gathered relative post-release performance data with a wild-control group from both enriched and unenriched cohorts within the same experimental design (Supplementary Table S4). In model 3, we included categorical fixed effects for sex, taxonomic class, fitness surrogate, ESR

vs. ISR strategy, and enrichment. We also included two-way interactions between enrichment and sex, enrichment and surrogate, and enrichment and strategy.

In all models, we included several random effects terms to account for different sources of non-independence among effect sizes. To account for shared taxonomy [53,79], we included all Linnaean taxonomic ranks below the level of class as separate random effect terms in each model. Taxonomic class was maintained as a fixed effect to quantify average differences in post-release performance across broad, recognizable animal groups of potential relevance to translocation managers. We chose the nested taxonomic random effects approach over the incorporation of a phylogenetic covariance matrix because the taxonomic breadth of our dataset precluded access to a comprehensive phylogeny with empirically-derived branch lengths [53,80] and the goals of our analyses are not concerned with estimating the extent of correlated evolution. We included study and group identities as two additional random effects terms in all models to account for non-independence of effect sizes within studies and among repeated measures of unique organisms [77]. We also included a term to model the variance in sampling errors for each effect size (Supporting Information SI 1). To assess the overall dispersion of our effect sizes and thus the generalizability of the findings of our models, we calculated total model heterogeneity (Supplementary Table S5) [81]. Since measures of heterogeneity tend to be high in ecological studies assessing diverse taxa [82], we further calculated the heterogeneity apportioned across the aforementioned taxonomic and study-specific random effect terms to more clearly explain patterns of dispersion in effect sizes [83].

Models were fit in a Bayesian framework using a Markov chain Monte Carlo (MCMC) algorithm as implemented in the R package *MCMCglmm* (Supporting Information SI 1) [84]. We address whether conservation programs produce organisms that perform similarly to or better

than wild-resident conspecifics after release by calculating the total probability that the log odds ratio for a particular comparison is greater than or equal to zero. We also report the marginal posterior mode and 95% highest posterior density credible interval (CrI) of the odds ratio (OR) by exponentiating posterior distributions of log odds ratios. We used the R package *emmeans* to report the marginal values of individual parameters and overall model effects to account for the influence of other model parameters [85]. All derived parameters are calculated across the entire posterior distribution to carry through all uncertainty.

We performed several meta-analysis validation tests to assess our dataset and findings for publication bias and influential outliers (Supporting Information SI 2-4) [86]. As we found no changes in our major findings after rerunning all models with identified outliers excluded (Supplementary Tables S6-S8), and because we considered outlying estimates to be representative of legitimate patterns in animal performance, we conducted the final analysis with all outliers included [87].

Data Availability

All data and R code are available from Zenodo Digital Repository: https://doi.org/10.5281/zenodo.7535746.

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Author contributions

Conceptualization: IPG and MEW; **Data curation:** IPG and MEW; **Formal analysis:** IPG, with input from AEW and MEW; **Investigation:** IPG; **Project administration:** MEW; **Visualization:** IPG and MEW; **Writing - original manuscript:** IPG; **Writing - review and editing:** AEW and MEW.

Competing Interests

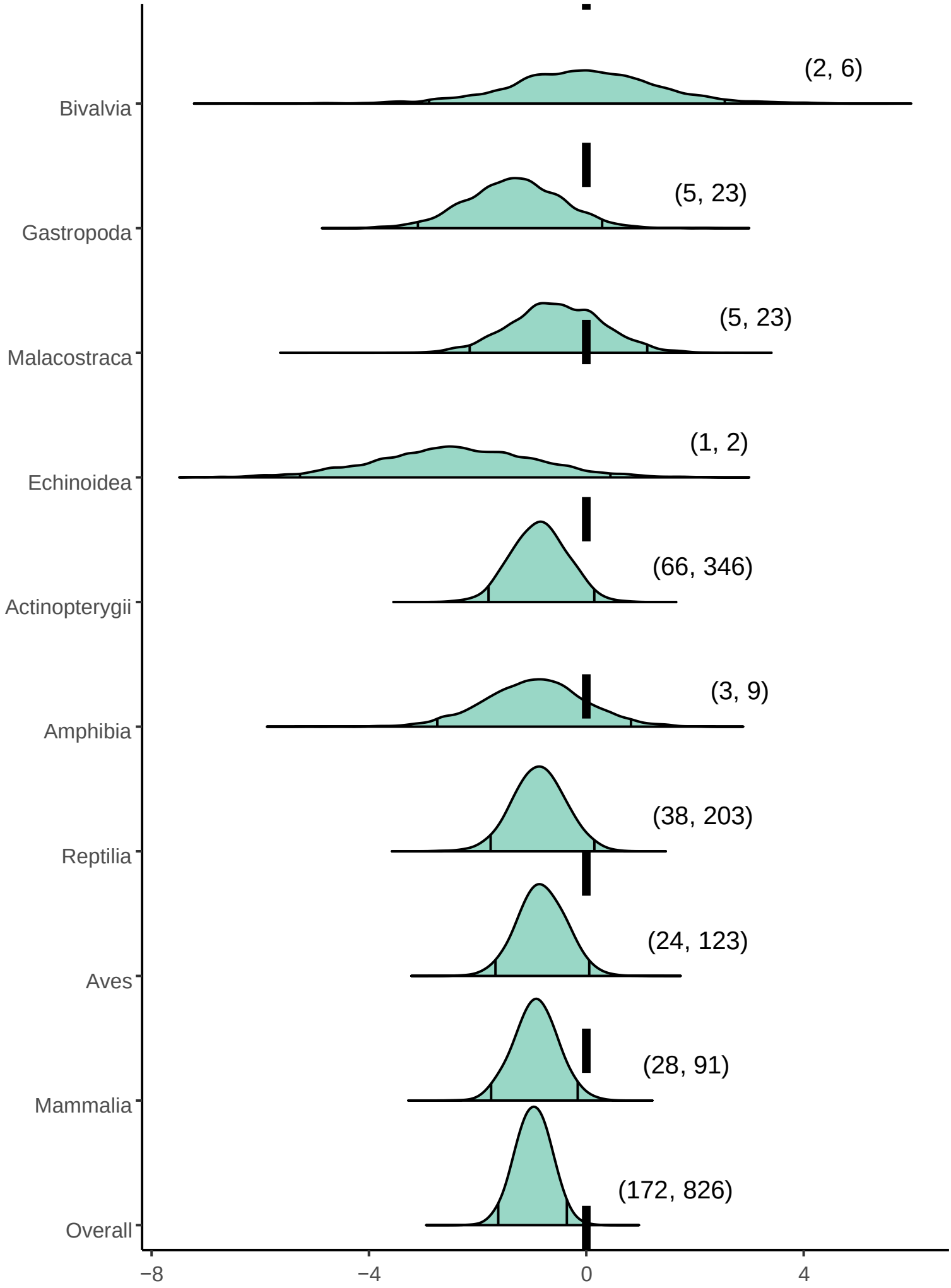
The authors declare no competing interests.

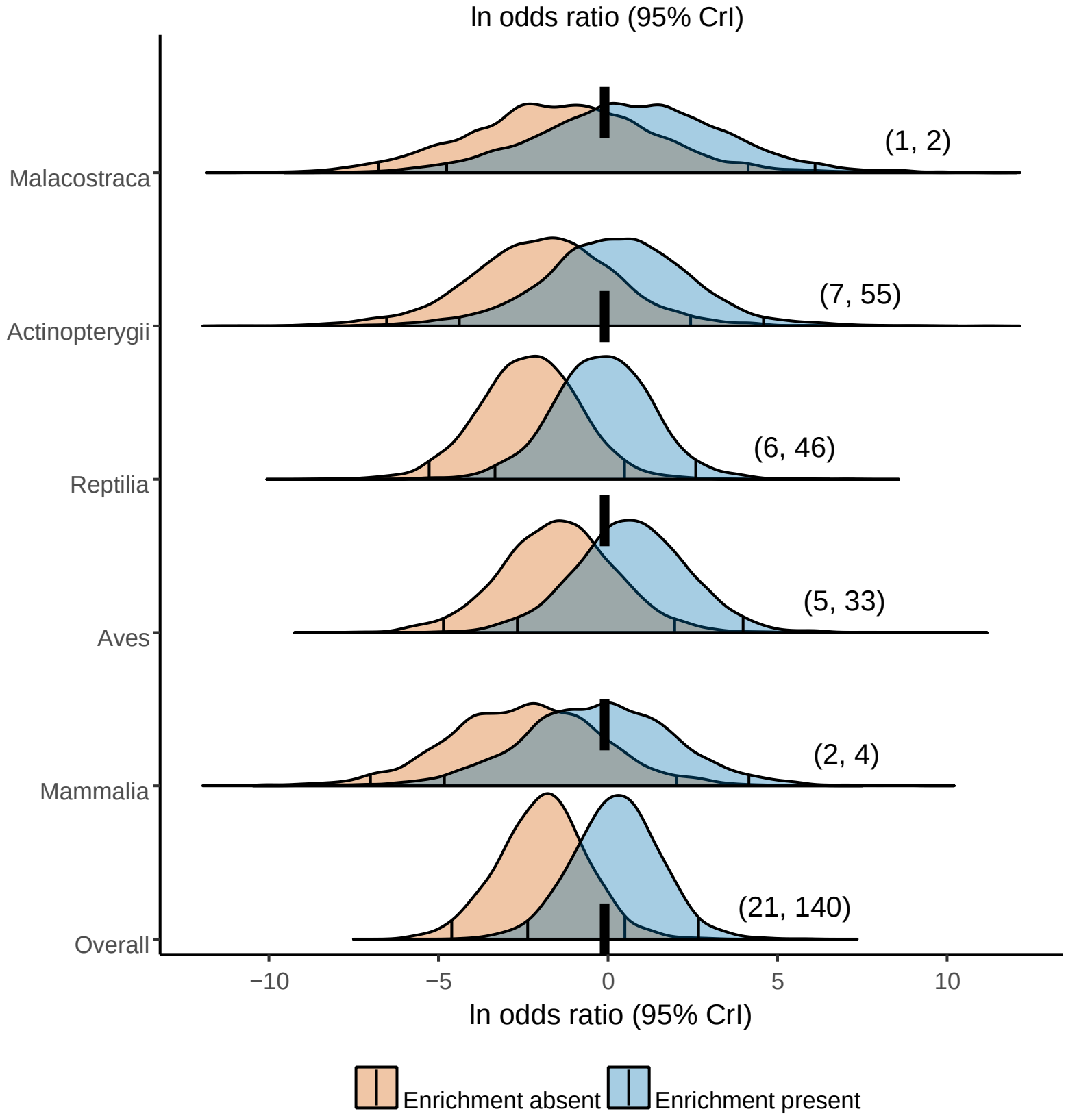
Figure Legends

Figure 1. Marginal posterior distributions of log odds ratios (ln odds ratio) plotted across taxonomic classes. Values greater than zero (vertical dotted line) indicate that translocated organisms out-performed wild-resident conspecifics, and negative values indicate translocated organisms under-performed. Vertical lines within each density plot indicate the 95% credible intervals (CrI). The parenthetical statements indicate the number of studies and the number of individual comparisons comprising each density plot, respectively.

Figure 2. Marginal posterior distributions of log odds ratios (ln odds ratio) plotted across taxonomic classes. Values greater than zero (vertical dotted line) indicate that translocated organisms out-performed wild-resident conspecifics, and negative values indicate translocated organisms under-performed. Blue density plots represent comparisons in which translocated organisms received some form of pre-release enrichment, whereas tan density plots represent comparisons where translocated organisms were unenriched. Vertical lines within each density

plot indicate the 95% credible intervals (CrI). The parenthetical statements indicate the number of studies and the total number of comparisons between enriched/unenriched and wild cohorts organized by taxonomic class.


Bivalvia
(2, 6)
Gastropoda
(5, 23)
Malacostraca
(5, 23)
Echinoidea
(1, 2)
Actinopterygii
(66, 346)
Amphibia
(3, 9)
Reptilia
(38, 203)
Aves
(24, 123)
Mammalia
(28, 91)
Overall
(172, 826)
−8
−4
0
4


ln odds ratio (95% CrI)
Malacostraca
Actinopterygii
Reptilia
Aves
Mammalia
Overall
(1, 2)
(7, 55)
(6, 46)
(5, 33)
(2, 4)
(21, 140)
−10
−5
0
5
10
ln odds ratio (95% CrI)
Enrichment absent
Enrichment present