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Predictors of past avian translocation outcomes inform feasibility of future efforts under climate change

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ABSTRACT

Conservation translocations – the intentional movement of individuals from one area to another for conservation purposes – provide a potential response to climate change, but can be costly and risky. To help improve translocation outcomes and assess their feasibility as a climate adaptation tool, we analyzed past conservation translocations (176 bird species at 680 sites globally) as a proxy for future efforts. To determine predictors of annual survival of released birds, we used generalized linear mixed models. Species with larger bodies and relative brain size had higher survival. Survival was also higher in protected areas, with subsequent releases at a site, for more recent years, and where the initial cause of decline was removed (n = 435 releases). Of particular relevance to climate-motivated translocations, longer distance translocations decreased survival; there was no evidence that greater climate differences between source and release sites (n = 117 releases), or releases beyond the indigenous range ("managed relocation", n = 435 releases), reduced survival. We also assessed how reproduction varied with release rates (birds/year) and species' generation lengths. Species with long generation lengths released at high rates had similar reproductive success to species with short generation lengths released at low rates. These findings can improve conservation translocation decisions by informing expected outcomes for target species, and identifying site features and management practices that maximize the likelihood of success. We also provide an empirical assessment of potential challenges of using conservation translocations in response to climate change, including evidence that longer distance translocations may be less feasible than shorter distance translocations.

1. Introduction

Climate change threatens species with extinction (Urban, 2015), and conservation translocations offer a potential response (Hoegh-Guldberg et al., 2008; McLachlan et al., 2007; Richardson et al., 2009; Seddon, 2010). Conservation translocations are the intentional movement of individuals from one area with release in another for conservation purposes. They include reinforcements (releasing individuals into an existing population), reintroductions (releasing individuals to a previously occupied site in the indigenous range), and managed relocations (releasing individuals beyond the indigenous range, i.e. "assisted colonization" and "assisted migration", IUCN/SSC, 2013). Under climate change, longer distance translocations and managed relocation could help dispersal-limited species track moving climate envelopes and respond to habitat loss (Hoegh-Guldberg et al., 2008).

While the particular motivation (i.e. climate change) may be new, conservation translocations are a long-standing conservation strategy (Seddon, 2010). They have been successful in preventing global extinctions and creating new populations of vulnerable and conservation-dependent species (Miskelly and Powlesland, 2013; Van Houtan et al., 2009). However, conservation translocations can be costly, labor intensive (Jones and Kress, 2012), contentious (Hardy-Short and Short, 2000; Richardson et al., 2009), and have high failure rates (Dodd and Seigel, 1991; Fischer and Lindenmayer, 2000). Given their potentially increasing use under climate change, determining what leads to their success or failure is critical for improving outcomes and determining when expected benefits outweigh costs (Rout et al., 2013).

Past conservation translocations offer a valuable proxy for future efforts; here, we synthesize historical efforts in order to address two objectives. Our first objective is to identify the species, site, and release factors that predict survival and reproduction in translocated populations. Our second objective is to assess factors that may challenge the

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use of conservation translocations in response to climate change.

Our first objective aims to help managers determine if conservation translocation is feasible for a particular species, and for a given species, inform decisions about where and how it is released (Rout et al., 2013). Indeed, previous syntheses have examined predictors of success in our study taxa (birds, e.g. Ducatez and Shine, 2019; Fischer and Lindenmayer, 2000; Griffith et al., 1989; Jones and Kress, 2012; White et al., 2012; Wolf et al., 1996, 1998). However, with the exception of Ducatez and Shine (2019), these studies are either taxonomically narrow (e.g. Psittacines) or extremely broad (e.g. animals), are geographically-limited (e.g. Mediterranean), use un-quantified self-assessment of success (which may be biased, Fischer and Lindenmayer, 2000), or comprise significantly smaller datasets than the one we used. Ducatez and Shine (2019) used the same database we do to analyze how translocation outcomes relate to life history traits, which we examine in addition to factors related to release decisions and methodology.

Our second objective is to assess three factors relevant to the feasibility of conservation translocations as a climate adaptation tool: whether or not a species is released outside the indigenous range (managed relocations, vs. reintroductions/reinforcements), geographic distance between the source and release site, and climate matching between the source and release site. While historical conservation translocations were generally not undertaken in response to climate change, they offer useful test cases of the relevance of these factors to translocation outcomes.

There are many concerns about managed relocation as a climate adaptation response (Hewitt et al., 2011; Mueller and Hellmann, 2008; Richardson et al., 2009). Here, we address concerns regarding feasibility – the potential for higher failure rates and therefore wasted resources and individuals of rare and endangered species (Kreyling et al., 2011; Richardson et al., 2009).

Unlike historical conservation translocations motivated by other threats, climate-motivated conservation translocations are intended to create directional range shifts to track moving climate envelopes. Given this premise, it is critical to assess the impact of geographic distance on translocation outcomes. Release sites must be far enough away to constitute a worthwhile range shift, but not so far that varying environmental conditions preclude establishment. Moreover, longer distances may predict worse translocation outcomes than managed relocation per se. For example, long-distance translocations may release individuals at sites within the species range to which they are not adapted; similarly, nearby translocations to a suitable but previously un-colonized site would nevertheless be managed relocation. The latter may be especially prevalent amongst dispersal-limited species, the likely candidates for managed relocation.

Matching the source and release site climate may be important for translocation success, especially if populations are adapted to local climates or are climatically sensitive, the latter of which would be expected for climate-motivated translocations. If precise climate matching is critical to translocation success, this would present several unique challenges. Difficulties would include predicting climate impacts and species responses at local scales, precisely timing translocations, as release site climates improve while source site climates deteriorate and populations decline (McDonald-Madden et al., 2011), and the potential that suitable climates (i.e. good matches) will disappear entirely (Williams et al., 2007).

Despite these potential challenges to translocating species in response to climate change, very few studies analyze historical conservation translocations to directly question if these factors influence translocation outcomes. Managed relocation has been used in response to non-climate threats such as habitat loss and invasive species (Seddon, 2010), but only a few studies compare past managed relocations to within-range translocations. Moreover, these studies have varied findings; managed relocations had lower success than within-range translocations in one set of cases (Griffith et al., 1989; Wolf et al., 1996, 1998), but not others (Van Houtan et al., 2009; White et al., 2012). Similarly, we know of no studies that directly test the impact of geographic distance or climate matching on conservation translocation outcomes.

We concentrate on survival and reproduction for several reasons. Survival is the most common obstacle to translocation success listed by practitioners in North America (Brichieri-Colombi and Moehrenschlager, 2016). Survival and reproduction are both required to produce the positive population growth needed to establish a viable population. Assessing survival and reproduction separately allows partitioning of translocation outcomes into processes that can be managed (Ducatez and Shine, 2019). Finally, using quantifiable outcome metrics reduces the impact of unclear definitions of success and biased reporting by practitioners and in published literature (Fischer and Lindenmayer, 2000).

We focus our analysis on birds, which are a useful study taxon for several reasons. Birds are disproportionately translocated, perhaps because they are considered charismatic, resulting in financial and public support (Seddon et al., 2005). Moreover, these translocation efforts are well-documented (Bajomi et al., 2010). Finally, climate-motivated conservation translocations in birds have already been proposed (e.g. Chauvenet et al., 2013; Morrison et al., 2011) and carried out (e.g. VanderWerf et al., 2018). Therefore, improved understanding of avian translocations in the face of climate change is important to both current and future conservation practice.

2. Methods

2.1. Data sources

The Avian Reintroduction and Translocation (ART) Database was constructed from a wide range of peer-reviewed and gray literature, and personal communication with practitioners (Lincoln Park Zoo, 2012). The database has a nested structure: a single species can be released at multiple sites, and at each site the species can be released multiple times ("releases").

The version we used from October 2012 documents 2359 releases between 1903 and 2010. We removed releases back to the source site, translocations not intended to create or augment permanent, self-sustaining populations (i.e. temporary translocations and translocations of surrogate, non-target species used as practice in advance of target species), and translocations using experimental methods (i.e. those recorded as "trials"). Thereafter, the database included the release of 65,299 individual birds of 176 species across 680 sites and 2185 releases.

The database documents translocations to 44 countries in six continents, but particularly focuses on English-speaking countries and temperate latitudes (Fig. A1), suggesting that many tropical efforts are missing. We believe that the focus on New Zealand is proportional to historical translocation practice in this country (Armstrong et al., 2015). We discuss how geographic bias in the database might impact our findings in the discussion.

We analyzed two outcome variables in the database: the number of surviving birds one year after release (from here on "survival rate") and whether any released birds successfully fledged young (from here on "reproduction"). We compiled model predictors from a variety of sources on bird biology and site characteristics (Table 1, Appendix A Sections 2–10).

2.2. Survival models

Most releases in the database (75% of $n = 2185$) lack survival outcomes, and the availability of predictors of interest varied, so we created two models to answer two related questions and best utilize available data. Our first model maximized sample size ("full model"), and our second used a smaller dataset with available predictors that

Table 1
Fixed effect predictors included in survival rate models. The symbols + and − indicate variables hypothesized to increase or decrease survival rate, respectively, X indicates variables included based on a priori hypotheses, * indicates variables included in the distance model because they were significant or marginally significant ($p < 0.1$) in the full model, and 0 indicates variables that were considered but ultimately excluded (see text). See text and Appendix A for details on modeling approach and methods for calculating variables.

	Definition/units	Variable type (transformation)	Hypothesized impact	Reasoning/example evidence from previous studies	Full model	Distance model
Species variables						
Body mass	Grams[a,c]	Continuous (log)	+	Ducatez and Shine, 2019	X	*
Relative brain size	Log-log brain size–body mass residual[c]	Continuous	+	Sol et al., 2012	X	0
Generation length	Mean age of reproductive individuals, years[b]	Continuous (log)	+	"Slow-lived" species have higher survival: Ducatez and Shine, 2019	0	
Habitat generalism	Number of habitat types[b,c]	Ordinal (log)	+	Cassey et al., 2008; Sol et al., 2012	X	
Migratory tendency	Altitudinal migrant, full migrant, or nomadic, vs. non-migratory[b,c]	Binary	−	Cassey et al., 2008	X	*
Site variables						
Threat addressed	Threat that caused initial population decline fully vs. partially or not addressed at release site[d]	Binary	+	Cassey et al., 2008; Fischer and Lindenmayer, 2000; Wolf et al., 1996	X	0
Within a protected area	Based on the ART Database[d], site name, and/or World Protected Area Database[c,e]	Binary	+	A proxy for higher habitat quality and/or protection from anthropogenic threats: Griffith et al., 1989; Wolf et al., 1996, 1998	X	*
Managed relocation	Release beyond the indigenous species range, vs. reintroduction or reinforcement[c,d]	Binary	−	Griffith et al., 1989; Wolf et al., 1996, 1998	X	0
Geographic distance	Geographic distance between source and release site (wild releases only), km	Continuous (log(x + 1))	−	Incorporates differences in environmental conditions that vary linearly in space, and longer transit times: Cassey et al., 2008		X
Climate distance	Standardized Euclidean distance in climate space between source and release site (wild releases only)[c]	Continuous (square root)	−	Describes differences in climate conditions between source and release sites: Cassey et al., 2008		X
Release variables[d]						
Calendar years before present	Years before 2019	Ordinal (log)	−	Accounts for improvements in reintroduction science and management: Seddon and Armstrong, 2016	X	*
First year at site	Release within the first year of releases at the site	Binary	−	Practitioners may use untested protocols or face unforeseen circumstances in the first year. In subsequent years, prior releasees may aid in learning or create an anchoring effect: IUCN/SSC, 2013; Miskelly and Gummer, 2013	X	*
Release rate	i.e., "propagule pressure": (number released including current release)/(years since the first release at site +1)	Continuous (log)	+	Cassey et al., 2008; Fischer and Lindenmayer, 2000; Griffith et al., 1989; Wolf et al., 1996, 1998	X	
Wild	Release of wild birds only; no captive-hatched or -reared releasees	Binary	+	Fischer and Lindenmayer, 2000; Griffith et al., 1989; Wolf et al., 1996	X	Wild-only

[a] Dunning, 2007.
[b] BirdLife International, 2016.
[c] See Appendix A for (additional) sources and/or methods.
[d] Lincoln Park Zoo, 2012.
[e] IUCN and UNEP-WCMC, 2017.

were particularly relevant to translocations in response to climate change ("distance model", see below). We removed 15 releases of five seabird species from both models. This is because seabirds' distinct life histories and the unique methods used in their translocations, such as hand-rearing following translocation as eggs or chicks, before spending multiple years at sea (Jones and Kress, 2012), might alter survival rates and the factors that predict them.

We modeled survival rate using generalized linear mixed models with binomial outcomes and a logit link. For each release, the binomial outcome was the number of surviving birds vs. number of deaths one year after release. Models included random effects for species and site, to account for non-independence where a species was released at multiple sites or over multiple releases at the same site. After transforming and rescaling our predictors, we fit models using the lme4 package (Bates et al., 2015) in R (R Core Team, 2017). We calculated p-values for fixed effects using likelihood ratio tests, defining significance as $p < 0.05$ and marginal significance as $p < 0.1$. We calculated the marginal and conditional R^2, based on fixed effects alone and fixed and random effects together, respectively (Nakagawa and Schielzeth, 2013). For our detailed modeling procedure, see Appendix A (Section 11).

2.2.1. Full model

In order to maximize sample size, this model included translocations of captive-hatched or -reared birds ("captive") as well as those of wild birds only ("wild"), and widely-available predictors hypothesized to impact survival (Table 1). We chose these predictors based on previous studies of avian conservation translocations as well as the establishment of exotic species, given parallels between these two processes (Cassey et al., 2008). Body mass and generation length were highly correlated ($r = 0.75$, $n = 68$ species, $p = 2.6e-13$), so we used only body mass. Our final model included 434 releases of 4479 individual birds of 68 species across 136 sites (n sites = 38 New Zealand, 33 US, 9 Australia, 9 France, and 47 in other countries). We tested whether an additional random effect for biogeographic realm significantly improved the model fit using a likelihood ratio test; it did not and was excluded.

2.2.2. Distance model

This model focused on predictors particularly relevant to the feasibility of climate-motivated conservation translocations: geographic distance and climate distance (the difference in climate between source and release sites). This model was limited to releases of wild birds; translocations of captive birds rarely have a source site listed in the ART database, which is needed to calculate geographic and climate distance (methods below). We could not include managed relocation (vs. reinforcement/reintroduction) as a predictor in this model, as there were only four cases in this subset of the data (although it was included in the larger full model).

We calculated the geographic distance between source and release sites using the R package geosphere (Hijmans, 2017). To characterize climate distance, we focused on temperature and precipitation extremes and variation, which can impact avian survival directly, for example via heat stress, and indirectly, for example via changes in habitat (Jenouvrier, 2013). We also reasoned that changes in extremes and variability would be more impactful within a single year than changes in averages, which might have slower, cumulative effects on released birds. We extracted nine such bioclimatic variables (BIO2, BIO4–7, BIO12–15) from 1970 to 2000 for each source and release site from WorldClim version 2 at 30 arc-second resolution (Fick and Hijmans, 2017, see Appendix A Section 10 for detailed methods). We then removed highly correlated variables ($r > 0.7$, Fig. A2) so that covarying climate variables were not double-counted in our climate distance metric. This left us with six variables: BIO2, BIO5, BIO6, and BIO13–15. We calculated climate distance as the standardized Euclidian distance between these six variables at each source and release site (Fig. A3).

To control for variables we found to be important in the full model, we included in the distance model five variables that were significant or marginally significant ($p < 0.1$) in the full model and that had data for >85% of releases in the distance model data set (body mass, migratory status, protected area, calendar year, and release within the first year at the release site, Table 1). Our final model included 117 releases of 1996 wild birds of 45 species across 74 sites (n sites = 37 New Zealand, 12 US, 6 Australia, 6 UK, and 13 in other countries).

2.2.3. Post hoc analyses

To determine whether our findings for species traits might have been impacted by phylogenetic non-independence, we first calculated survivability as each species' random effect coefficient obtained from a version of the full (or distance) model with site and release factors only. We then compared two phylogenetic generalized least squares models of species' survivability. One model had no phylogenetic structure. In the other, the strength of the phylogenetic structure, as measured by Pagel's Lambda (Pagel, 1999), was determined using maximum likelihood (see Appendix A Section 12 for detailed methods).

We found that calendar year of release and migratory tendency were significant predictors in the full model (which included both wild and captive birds) but not the distance model (which included wild birds only, Fig. 2). To explore this difference, we added the interactions wild × migratory and wild × calendar year to the full model, to see if such interactions were significant. We further explored whether migratory tendency was associated with factors that were differently accounted for between the two models. Specifically, we explored whether migratory tendency was associated with geographic distance and climate distance (which were in the distance model only), or relative brain size and threat addressed (which were significant in the full model but excluded from the distance model due to insufficient data, Table 1) using t- and chi-squared tests.

2.3. Reproduction analysis

Because the ART database does not distinguish whether reproduction is attributed to currently- or previously-released birds, we aggregated reproduction success within each site, defined as whether or not successful reproduction (fledging of young) ever took place at the site. Beyond bias towards reporting of translocation successes (Fischer and Lindenmayer, 2000), this aggregation further favored successes when combined with missing data. This is because a single release with successful reproduction in combination with missing outcomes (e.g. 1-0-0-NA) could be identified as a site-level success, while a similar series of reproductive failures and missing outcomes (e.g. 0-0-0-NA) could not be conclusively classified as a site-level failure.

Since this analysis could only be done at the site level, we devised a simplified analysis focusing on two predictors we hypothesized would most impact reproductive success: release rate and generation length. We aggregated release rate by totaling the number of birds released at the site divided by the range of release years, then categorized release rates as "high" (median and above) vs. "low" (below median). We similarly categorized species' generation lengths as "long" (median and above) vs. "short" (below median). We then compared reproduction in all four combinations of low and high release rates and short and long generation lengths. We also tested the correlation between generation length and release rate, to determine whether practitioners tend to release more individuals of species with short generation lengths. Our data set for this analysis included 129 species across 315 sites.

3. Results

3.1. Dataset summary

The most commonly translocated taxonomic order was Passeriformes (31% of $n = 176$ species, Fig. 1), which make up ~60% of bird species globally and 48% of extinct, threatened, and near-threatened bird species (BirdLife International, 2016). The majority of

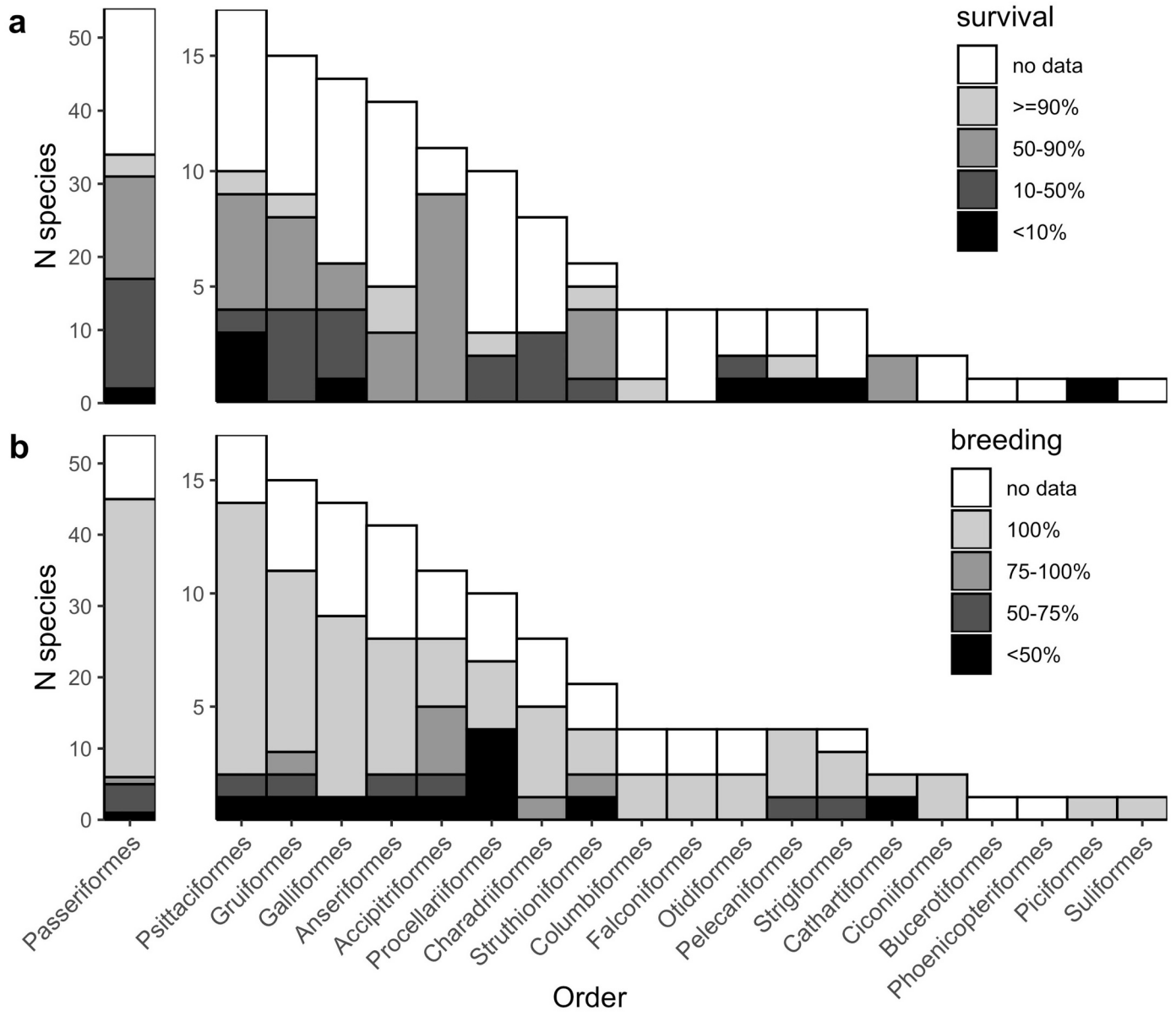

Fig. 1. Number of species translocated by taxonomic order.
(a) For each species, shading indicates percent of birds surviving one year after release out of all birds with survival outcome data.
(b) For each species, shading indicates the percent of sites with successful reproduction out of sites with reproduction outcome data. Sixty percent of species with 100% reproduction success had reproduction outcome data at only one site.
For both, $n = 176$ species. Note the separate y-axis scale for Passerines.

species in the database (58%) were listed by the IUCN as threatened or near-threatened, 40% were "least concern", and three were extinct or extinct in the wild (Guam Rail *Hypotaenidia owstoni*, Hawaiian Crow *Corvus hawaiiensis*, and Bridled White-eye *Zosterops conspicillatus*, n = 176 species, BirdLife International, 2016). Based on the database, the threats that led to translocations were habitat loss (61%), invasive species (46%), hunting (35%), poisoning (21%), and disease and reduced food resources (<5% each, $n = 617$ sites).

Documented releases occurred in 44 countries, especially New Zealand (42%) and the US (27%, $n = 680$ sites), and in corresponding temperate latitudes (Fig. A1). The median number of birds released per year at a site was 13.0, for a median total of 30 birds per site ($n = 671$ sites). Of 6875 released birds with survival data, 51% survived one year after release ($n = 550$ releases). Forty-eight percent of releases were of wild vs. captive birds ($n = 2163$ releases). The median translocation distance for wild releases was 105 km and ranged from 1 to 4325 km ($n = 276$ sites). Reintroductions, reinforcements, and managed relocations comprised 66, 18, and 7% of efforts, respectively; the remaining 9% were within the indigenous range but we could not decipher whether they were reinforcements or reintroductions ($n = 679$ sites). Geographic and climate distance were correlated ($r = 0.47$, $p < 2.2e-16$, $n = 287$ sites); visual inspection showed that managed relocations occurred across a wide range of geographic and climate distances (Fig. A4).

3.2. Survival models

3.2.1. Full model

In the full model (marginal $R^2 = 0.43$, conditional $R^2 = 0.18$), higher survival rates were predicted for species with larger body mass and relative brain size (brain mass relative to body mass), sites where the initial threat had been addressed, releases of wild (vs. captive)

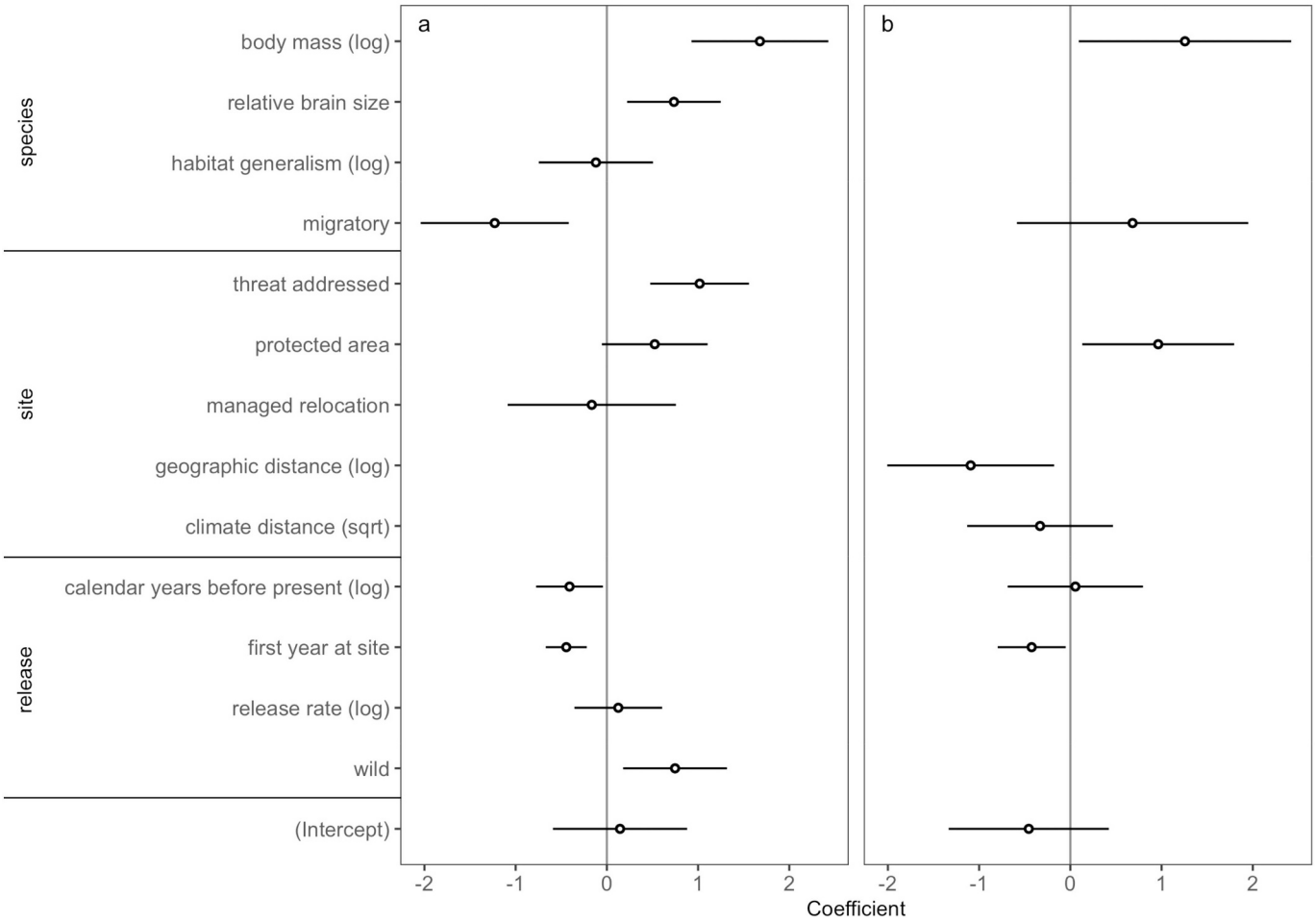

Fig. 2. Variables predicting survival of translocated birds one year after release. Circles represent coefficients and lines represent 95% confidence intervals of generalized linear mixed models with binomial outcomes. Positive coefficients predict improved survival of translocated birds, and negative coefficients predict the opposite. Models also include random effects for site and species. Continuous predictors are scaled to allow direct comparison of coefficients (Gelman, 2008), which are on the log-odds scale. Results are also presented in Table A2.
(a) Full model. $n = 434$ releases of 4479 wild and captive birds across 136 sites and 68 species.
(b) Distance model. $n = 117$ releases of 1996 wild birds across 74 sites and 45 species.

birds, and releases in more recent years (Fig. 2a, Table A1). Releases into protected areas tended to have increased survival, although this result was only marginally significant ($p = 0.083$). In contrast, migratory species and releases within the first year of releases at a site had decreased survival rates. Habitat generalism, release rate, and managed relocation did not predict survival; the rarity of managed relocations in the modeled data (9% of $n = 136$ sites) may have made it difficult to detect an impact for this factor. Because the modeled coefficients are log-odds ratios of rescaled variables, we translate the coefficients into predicted survival rates in Table A1, which may be more useful to practitioners.

3.2.2. Distance model

In the distance model (marginal $R^2 = 0.11$, conditional $R^2 = 0.42$), increasing geographic distance, but not climate distance, predicted decreasing survival rates (Fig. 2b, Table A1). Unlike the full model, migratory tendency and calendar year did not predict survival.

3.2.3. Post hoc analyses

We found no evidence that species' shared phylogenies impacted our finding for species traits in the full model. Phylogenetic correction affected the body mass estimate in the distance model, but the change relative to the nonphylogenetic model was minor (Appendix A Section 12, Fig. A9).

We found a significant, positive interaction for wild-sourced birds × calendar year after adding it to the full model (Fig. A5), indicating more recent improvements in survival rates for captive-sourced birds than wild birds. Visual inspection of plots showed a similar pattern (Fig. A6).

We found no interaction for wild-sourced birds × migratory tendency when we added it to the full model (Fig. A5). Compared to non-migratory species, migratory species were associated with translocations over longer geographic distances and destinations where initial threats had been addressed. Thus, our contrasting findings for migratory species between the full and distance models may be due to differences in how our model formulations accounted for these confounding predictors (see Appendix A Section 13).

3.3. Reproduction analysis

Species with long generation lengths released at high rates had comparable reproductive success (89%, $n = 61$ sites) to species with short generation lengths released at low rates (88%, $n = 59$ sites, Fig. 3). Species with longer generation lengths were released at lower rates ($r = -0.28$, $p = 5.1e-07$, $n = 315$ sites, Fig. 3).

4. Discussion

Our synthesis of a large, single-taxa database of historical

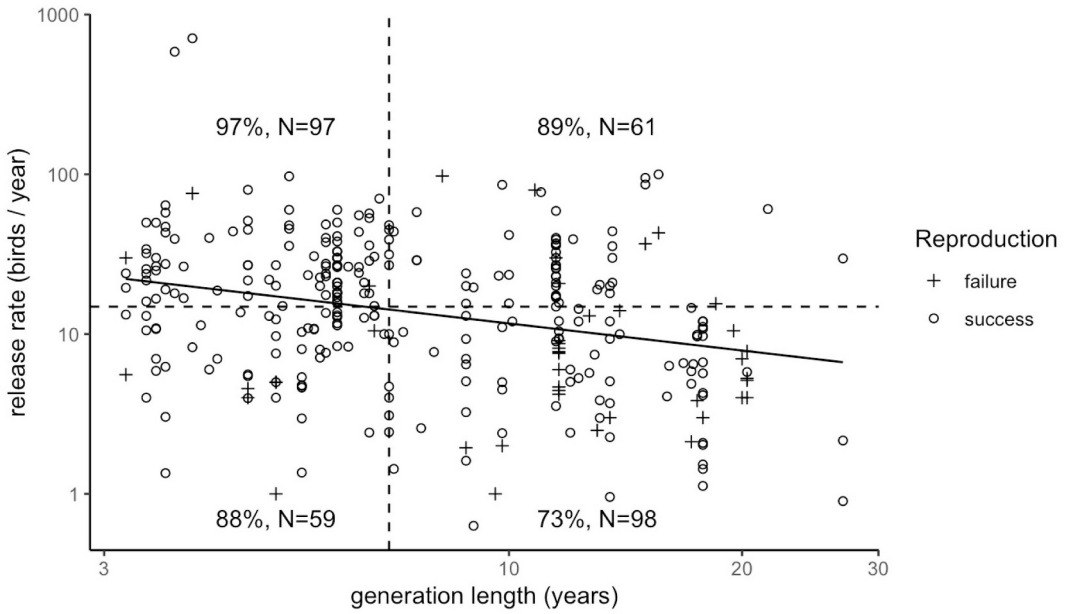

Fig. 3. Reproduction success (open circle) or failure (plus sign) by species generation length and release rate at each translocation site. Dashed lines represent median values for each axis (median generation length = 7 years, median release rate = 14.8 birds/year). Labels indicate the percent of sites with successful reproduction and sample sizes for each quadrat (total n = 129 species at 315 sites), and show that species with long generation lengths released at high rates had similar reproductive success to species with short generation lengths released at low rates. The solid line is a best-fit regression line to visualize the negative correlation between generation length and release rate ($r = -0.28$, $p = 5.1e-07$, n = 315 sites). Note that both axes are on the log scale.

conservation translocations has important implications for the improvement of conservation translocation practice and the use of these actions into the future. Our findings can help prioritize species for conservation translocations and inform decisions about the sites and approaches that maximize the chance of success. Our findings can also help anticipate translocation outcomes; realistic estimates of the probability of success can be compared to costs to estimate cost effectiveness (Rout et al., 2009, 2013) and help determine when other actions might be preferable. These understandings are particularly important given the likely increasing use of conservation translocations in response to climate change. Moreover, our analysis addresses specific challenges for using translocations for climate adaptation.

4.1. Species traits

Greater body mass and relative brain size predicted improved survival after translocation (Fig. 2), while short generation lengths predicted reproductive success (Fig. 3). Large body mass and relative brain size are thought to buffer individuals from extrinsic factors (Sol et al., 2012). Relative brain size predicts establishment success in introduced birds, perhaps by allowing behavioral innovation in novel environments (Sol et al., 2012); we expect a similar mechanism in conservation-motivated releases of individuals to new sites. To our knowledge, this is the first time relative brain size has been tested and shown to be predictive of conservation translocation outcomes.

Large body size predicted improved survival, but was correlated with longer generation length, which predicted decreased reproduction. Ducatez and Shine (2019) similarly found that "slow" life history traits improved post-release survival but decreased reproductive success, and vice versa for "fast" life history traits. Both survival and reproduction are critical for establishing a viable population, so for a given species, managers should focus on whichever of survival or reproduction is most likely to limit success. Nevertheless, as long as overall population growth is positive, species with intrinsically low survival or slow reproduction can be successfully translocated with enough time, resources and individuals.

Migratory species had reduced survival in the full model but not the distance model (Fig. 2). This discrepancy may in part be due to practices that are confounded with migratory species (geographic distance and threats addressed, see Appendix A Section 13), and which were accounted for differently in the two models. This illustrates the difficulty in teasing apart predictors of success when the experimental "treatments" are unevenly distributed and likely chosen based on practitioner expectations.

4.2. Site and release factors

Several factors that improved survival are amenable to management: addressing the initial threat, choosing release sites that are protected and closer to the source site, and continuing to release individuals after the first year of efforts at a site (Fig. 2, see also Table A1 for example survival rate predictions based on these varying management choices). Practitioners tasked with translocating a species with expected low survival (e.g. small-bodied or -brained species) may be able to compensate by focusing on such factors that are within their control.

Similarly, managers may be able to compensate for expected slow reproduction in species with long generation lengths by releasing more birds per year (Fig. 3). However, gathering a large number of individuals of rare and endangered species may be a challenge. This problem is amplified for species with longer generation lengths, which were more often released at low rates (Fig. 3). While practitioners may be tempted to spread individuals across multiple sites to hedge bets, our findings imply that for species with long generation lengths, practitioners might instead favor releasing more individuals at a single site to increase the release rate. However, given the data's coarse resolution and bias (see methods), and the fact that low release rate may be conflated with poorly-resourced efforts (Armstrong and Seddon, 2008), our findings should be confirmed with higher-resolution data and where it is possible to account for the amount of resources.

Birds released during the first year of efforts at a site had lower survival than those released in subsequent years (Fig. 2), aligning with improved outcomes in longer translocation programs (Griffith et al., 1989). Site-specific learning by practitioners may improve survival

rates, highlighting the importance of adaptive management in translocations (Rout et al., 2009). Additionally, repeat releases may allow newly released birds to learn from previous releasees (IUCN/SSC, 2013) or create an anchoring effect, whereby individuals tend to settle near conspecifics (Miskelly and Gummer, 2013). Regardless of the mechanism, this finding implies that poor outcomes in the first year may be best met with additional years of effort.

Releases in the full model began in the early 1970s and have shown improved survival outcomes since then (Fig. 2a). These improvements likely stem from advances in management and the maturation of the field (Seddon and Armstrong, 2016). However, we found a significant interaction for wild × calendar year (Figs. A5 and A6), such that the predicted benefit of releasing wild over captive birds (Fig. 2a) diminished in recent years. It may be that advancements in the field have disproportionately improved methods for translocating captive birds and preparing them for release (Tetzlaff et al., 2019).

Our survival models have relatively low marginal R^2 values, meaning that the factors we chose explained some variation in outcomes, but outcomes cannot be reliably predicted based on these variables alone. This is unsurprising given the parallel difficulties in predicting invasive species establishment (Sol et al., 2012), and suggests that other factors that may impact translocation outcomes should be kept in mind (e.g. soft. vs. hard releases, training, Tetzlaff et al., 2019). The comparatively large conditional R^2 values and relatively large variance for the species and site random effects (Table A1) underscore the importance of translocation context – the unique combination of species, sites, and practitioners – in a given translocation outcome. This context-dependence heightens the value of expert opinion, accessible and standardized documentation of translocation methods and outcomes, and the facilitation of such efforts via groups like the IUCN Conservation Translocation Specialist Group.

4.3. Implications for translocations under climate change

It is tempting to assume that geographic distance and climate distance (the difference in climate between source and release sites) can serve as proxies for each other, and that managed relocations occur at longer geographic and climate distances. However, geographic and climate distance were correlated but not equivalent, and managed relocations occurred across a wide range of geographic and climate distances (Fig. A4). Thus, practitioners should consider all three attributes (geographic distance, climate distance and managed relocation), as well as others, when choosing release sites.

Longer distance translocations predicted decreased survival in translocated birds (Fig. 2b). All else being equal, choosing a release site 100 km instead of 10 km away reduced an average bird's chances of survival from 78% to 64% according to our model (Table A1). However, the distances needed to keep pace with climate change may not be much larger than a typical historical translocation (median ~100 km). We can compare a 100 km translocation to the velocity of climate change predicted by Loarie et al. (2009). In biomes with fast climate velocities (1.26 km/yr) – those where climate-motivated translocations are most likely – a typical 100 km translocation corresponds to the distance the climate will shift in ~80 years. Given this relatively long time horizon, the challenge may not be the distances themselves, but rather determining which time horizon to match and direction to move, since climate variables may not move at the same rate or in the same direction (Ackerly et al., 2010). All of this suggests that longer distance translocations may be both less successful and often unnecessary, and that more attention should be paid to the idea of sequential, shorter distance translocations in response to climate change.

Geographic distance was a better predictor of survival than climate distance (Fig. 2b), suggesting that spatial variation in non-climatic factors (e.g. geophysical features, ecological communities) impact survival more than climate per se. However, our inability to detect an independent impact for climate matching should be interpreted cautiously, for several reasons. First, climate-motivated translocations are likely to focus on more climate-sensitive species than previous translocations. Second, under relative climatic stability, practitioners in the past may have been more successful at matching source and release site climates, compared to future situations under climate change. Third, our dataset's latitudinal bias underrepresents tropical species (Fig. A1), some of which may be relatively sensitive to climate distance given their narrow climatic niches (Khaliq et al., 2014). Finally, we were tasked with finding a generic metric of climate distance for all species in our model; in contrast, any given species will respond to a specific set of climate variables. We encourage future studies of individual species with known physiologically-linked climatic tolerances.

While relatively rare in the database, managed relocations did not have different survival rates than other translocations (Fig. 2a), suggesting that moving species beyond their indigenous range does not decrease survival compared to reintroductions and reinforcements. However, their small sample size may have limited our ability to detect a pattern.

4.4. Conclusions

While we were motivated by the potential increasing use of conservation translocations in response to climate change, our findings are relevant to all conservation translocations, regardless of the proximate threat. Given ubiquitous, inevitable climate impacts, all future translocations should consider climate impacts (e.g. long-term climate stability) as well as geographic and climate distance when picking release sites.

Managers should assess whether a given species is a better survivor or breeder and then tailor their efforts, expectations, timelines, and budgets accordingly (Ducatez and Shine, 2019). For example, for a species with projected low survival (e.g. small body and relative brain size), managers should focus resources on factors that improve survival. These include addressing the initial threat, choosing a protected release site relatively near to the source site, and continuing releases after the first year. For a species with projected low reproduction (e.g. a large-bodied, long-lived species), managers might instead focus resources on factors that increase the probability of reproduction, such as gathering and releasing more birds per year at a single site. Similarly, an assessment of climate impacts might cause an adjustment of timelines and expectations. A practitioner might initially prioritize a relatively nearby release site, but plan for future monitoring and potential further translocations to track a moving climate envelope. Overall, we hope our analysis can help predict the outcomes of conservation translocations with varied strategies. This could inform cost-effectiveness estimates for varying translocation choices, and promote comparison to other potential interventions, ultimately improving conservation outcomes.

Future research should assess conservation translocations in tropical and non-English speaking countries, which are underrepresented here. Given that initial successes may eventually fail (Seddon, 1999), especially in the face of shifting climates, additional research should also explore how managed relocation, geographic distance, and climate distance impact the long-term viability of translocated populations. We also suggest research on the feasibility of sequential shorter distance translocations in response to climate change. Finally, we analyzed the feasibility of translocations for target species only, without regard to potential impacts on recipient ecosystems, which is a common concern about managed relocation (Hewitt et al., 2011; Mueller and Hellmann, 2008). While impacts on recipient sites are less documented, the vast history of conservation translocations, including managed relocations, could be used to explore these concerns using a similar approach to the one presented here.

Conservation translocations are not new, but are in fact a long-standing intervention for securing threatened populations and reducing extinction risks. Synthesizing this historical experience is critical to improving current and future efforts in the face of climate change and

other threats. We hope this approach can help move beyond philosophical debates about the use of conservation translocation as a climate adaptation response, and towards a more nuanced, empirical perspective. Such a perspective will be key for thoughtfully pursuing their promise as a conservation tool in response to climate change.

CRediT authorship contribution statement

Sarah A. Skikne: Conceptualization, Methodology, Formal analysis, Data curation, Investigation, Writing - original draft, Writing - review & editing. **Abraham L. Borker**: Conceptualization, Methodology, Investigation, Writing - review & editing. **Ryan S. Terrill**: Methodology, Formal analysis, Writing - review & editing. **Erika S. Zavaleta**: Conceptualization, Methodology, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary text, figures and tables (Appendix A) and modeled survival data (Appendix B) can be found online at https://doi.org/10.1016/j.biocon.2020.108597.

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