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Palabras clave: estocasticidad demográfica, estrategia de minimización de riesgos, hipótesis del crecimiento poblacional, historia de vida lenta-rápida, pronosticador del éxito de invasión, reintroducción, regulador de la historia de vida

Resumen. Los intentos por identificar los pronosticadores y los mecanismos del éxito de invasión han sido debilitados por la poca calidad de los datos, principalmente porque el monitoreo no inicia inmediatamente después de los eventos de introducción. Para superar este tema, usamos datos a partir de las reubicaciones por conservación de especies amenazadas de aves. Analizamos la información de más de 1,200 eventos de reubicación para más de 150 especies de aves y así investigar cómo los atributos de las historias de vida afectan el establecimiento de la población medido con base en tasas de supervivencia y reproducción. La posición de las especies a lo largo del continuo de historias de vida lenta-rápida fue un pronosticador importante para el éxito de la reubicación. Las especies con historias de vida rápidas tuvieron una menor posibilidad de sobrevivir (tanto a corto como a mediano plazo) y una mayor probabilidad de reproducirse exitosamente que las especies con historias de vida lentas. La división temporal del esfuerzo reproductivo (número de puestas por año) también afectó la probabilidad del éxito de la reproducción. Nuestros resultados ilustran cómo los programas de reintroducción motivados por la conservación pueden proporcionar sustitutos para los estadios iniciales del proceso de invasión, permitiendo pruebas empíricas a partir de la teoría de la historia de vida e informando a los administradores.

Life-history traits and the fate of translocated populations

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Running head: Life-history traits and translocations

Keywords: bet hedging, demographic stochasticity, invasion success predictors, life-history buffer, population growth hypothesis, reintroduction, slow-fast life history

Article impact statement: After translocations for conservation purposes, bird survival and breeding success depend on their life history.

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Abstract

Attempts to identify predictors and mechanisms of invasion success have been weakened by poor data quality, mostly because monitoring does not begin immediately after introduction events. To overcome this issue, we used data from conservation translocations of threatened bird species. We analyzed information on >1,200 translocation events of >150 bird species to investigate how life-history traits affect population establishment measured based on rates of survival and reproduction. Species position along the slow-fast life-history continuum was a key predictor of translocation success. Species with fast-paced life histories were less likely to survive (over both short and mid-term) and more likely to breed successfully than species with slow life histories. The temporal partitioning of reproductive effort (number of clutches per year) also affected the probability of successful reproduction. Our results illustrate how conservation-motivated reintroduction programs can provide proxies for the initial stages of the invasion process, enabling empirical tests of predictions from life-history theory and informing management.

Introduction

Much scientific research has been conducted to predict and explain the attributes of invasive species that result in successful invasion (e.g., Sol et al. 2012; Capellini et al. 2015; Allen et al. 2017). Although many correlates of invasion success have been identified, these analyses are weakened by the poor quality of data available (Mack et al. 2000). First, many invasions occurred long before detailed records were kept. Second, unsuccessful translocations are unlikely to be recorded, especially for unintentional movements of species. Presumably, most translocated individuals die and never come to the attention of scientists. This bias compromises attempts to compare successful and unsuccessful translocations. The lack of detailed information on the early postcolonization history of invasive populations means

researchers must characterise invasion success qualitatively (successful or unsuccessful) and cannot partition determinants of that outcome into processes such as survival and reproduction (Sol & Maspons 2016).

To overcome those problems, one can use a data set different from the ones usually considered in invasion biology. Wildlife management authorities frequently conduct intentional translocations to reestablish threatened taxa in areas from which they have been extirpated or nearly extirpated (Ewen et al. 2012; Seddon et al. 2014). In some of these programs, the early phases of population growth (or decline) have been carefully surveyed (Sutherland et al. 2010; Lincoln Park Zoo 2012). This situation thus provides a proxy for studying the elusive initial stages of invasion, whereby a small number of individuals arrives in a new area. Although invasion and intentional translocation have large differences (e.g., they involve different species or different levels of adaptive mismatch in the new area, see Discussion), their processes are similar because they involve the settlement of a few individuals in a new area. We used an extensive data set on conservation-motivated translocations to explore the extent to which the survival and reproductive output of the colonisers is linked to life-history traits. Such links are predicted by life-history theory (Lewontin 1965; Sæther et al. 2004; Sol & Maspons 2016) and consistent with some empirical analyses of invader success (Sol et al. 2012; Capellini et al. 2015; Allen et al. 2017), but our analysis allowed a more nuanced exploration of the processes at work in a population translocated to a novel environment.

Demographic stochasticity is expected to increase the risk of extinction in small populations (Soule & Wilcox 1980; Lande 1993). By allowing rapid population growth, a fast life-history strategy (high fecundity at the expense of a low survival) is expected to favor a quick escape from the zone of high extinction risk (population-growth hypothesis [Lewontin 1965]). In contrast, the life-history-buffer hypothesis supposes species with a slow life-

history strategy are less prone to stochastic fluctuations and thus are less sensitive to demographic stochasticity (Sæther et al. 2004). These 2 contrasting hypotheses involve different demographic mechanisms: increased breeding rate for the population-growth hypothesis and increased survival for the life-history-buffer hypothesis. Considering the effects of life history on these specific demographic parameters, instead of on overall establishment success, allowed us to directly test these 2 hypotheses. If both hypotheses are valid, we expected that translocated populations of a species with a fast life history would exhibit higher breeding success but lower survival than species with a slow life history.

In addition to demographic stochasticity, environmental uncertainty may be another cause of extinction after introduction because of the challenges imposed by the exploration and collection of information on a new environment (e.g., Lande 1993; Ovaskainen & Meerson 2010). Under this scenario, an ability to spread reproductive output over time may enhance reproductive success and potentially survival via bet hedging (e.g., Frank & Slatkin 1990; Starrfelt & Kokko 2012; Sol & Maspons 2016). Species producing multiple clutches per year should then have higher breeding success than single-clutching taxa.

Methods

Translocation data

We used the Avian Reintroduction and Translocation database compiled by Lincoln Park Zoo (2012). This standardized database contains data on release events collected from a wide range of sources, including peer-reviewed and gray literature and collaborators and managers of reintroduction projects. It contains information on 2,359 translocation events conducted from 1903 to 2012 for 201 different species. Failure rates are high overall (Fischer & Lindenmayer 2000), underlining the need to understand the mechanisms behind the response of populations to translocation.

We extracted information on all translocation events that included data on the number of individuals released and the presence or absence of conspecifics in the reintroduction area. We then extracted events for which at least 1 of the 5 following monitoring parameters was provided: survival at 1 week, 1 month, or 1 year after release; whether breeding occurred; and whether breeding was successful. Our final data set included 1,249 events for 157 different species. For each event, we extracted data on the number of individuals released, whether conspecifics were present before the release, and the 5 parameters in which we were interested. Potential effects of monitoring duration were tested (Supporting Information).

Life-history traits

We searched the bird literature for data on life-history traits for each of the 157 species in our reintroduction dataset. We obtained body mass data from (Dunning 2007) and life-history traits from the HBW Alive website (del Hoyo et al. 2017). We collected data on maximum longevity, clutch size, age at first reproduction, and number of clutches per year to characterize the slow-fast continuum of life histories, from species with delayed maturation and long lifespans to early-maturing species with short lifespans, and the temporal partitioning of reproductive events, from frequent small clutches to infrequent large clutches. A measure similar to the latter (the brood value) has been shown to predict invasion success in birds (Sol et al. 2012).

Analyses

Using the PCA function in the FactoMineR (Lê et al. 2008) R package, we first performed a principal component analysis (PCA) on body mass and the 4 life-history traits to reduce the data set on life-history traits to a smaller number of independent dimensions. As expected, this procedure generated axes characterizing the slow-fast life history continuum and the

temporal partitioning of reproductive events. We then extracted the main components of this PCA to use as descriptors of life-history strategy in our models. Data for all life-history traits were available for 75 species on which we could run the PCA.

We then built generalized linear mixed models with Markov chain Monte Carlo (MCMC) techniques with the R package MCMCglmm (Hadfield 2010). As response variables, we included either survival after 1 week, survival after 1 month, survival after 1 year, breeding attempt, or breeding success. The first 2 principal components of the life-history PCA were included as fixed effects, as were the number of individuals introduced (propagule pressure [Colautti et al. 2006]) and the presence or absence of conspecifics at the release site (a binary variable). The 3 survival variables were fitted with a multinomial² distribution, as recommended by Hadfield (2010) for proportions, and we used a categorical distribution for the 2 binary variables (breeding attempt and breeding success, also following Hadfield [2010]). Random factors added in the models included phylogenetic position and species identity and biogeographic region (13 categories plus 1 category for species occupying 2 or more regions) (Ducatez et al. 2014).

We sampled 100 phylogenetic trees from BirdTree.org (2012) for the species in our data set. Species in our data set were selected based on data from the complete avian phylogeny of (Jetz et al. 2012) and Ericson et al.'s (2006) phylogenetic backbone. (These trees were used as different phylogenetic hypotheses for the evolutionary relatedness of the species present in the reintroduction database. Each model described above was run 100 times with each of these different trees, and we averaged the parameters calculated over these 100 different phylogenies.

For all models, the MCMC chains were run for 110,001 iterations with a burn-in interval of 10,000 to ensure satisfactory convergence. We sampled 1000 iterations to estimate parameters for each model. Autocorrelation levels among samples were <0.1 in all cases. We

fixed the covariance structure and used weakly informative priors (improper prior with $\nu = 0.02$) for the variance (Hadfield 2010). All explanatory variables were standardized to a mean of 0 and a variance of 1.

In an additional set of analyses, we ran similar models but replaced the principal components with each life-history trait separately, building 1 model per life-history trait and demographic parameter, to explore the effects of specific traits on each demographic parameter. Our initial analyses with the PCA axes were limited by the number of species for which all life-history traits were available, but this second set of analyses allowed us to increase the sample size because we could include all species for which information on the trait of interest was available, even when other data were not. We used the same methods as described above to assess the effects of each life-history trait on the survival and reproductive outputs of translocated populations (i.e., same random and fixed covariates included, same treatment of phylogenetic uncertainty, same iterations and burn-in interval for the Monte-Carlo chains). We included only a single life-history trait in each model both to limit collinearity effects and because the combined effects of life-history traits were already considered in models including the principal components.

The number of species and reintroduction events for each analysis varied according to the availability of data on life-history traits and postrelease demography. Sample sizes are in Tables 1 and 2. The data set is provided as Supporting Information.

Results

Releases of gamebirds were included in the database and were considered in our analyses because their exclusion did not affect the conclusions (Supporting Information). We extracted 2 components with eigenvalues >1 from the PCA on life-history traits (Supporting Information). The first component explained 51.16% and the second 21.17% of the total

variance in life history. Body mass, maximum longevity, and age at first reproduction loaded positively on the first axis, whereas clutch size and number of clutches per year loaded negatively. The first axis thus provided a measure of a species' position on the slow-fast life-history continuum. Clutch size and number of clutches per year loaded on the second axis, which segregated species laying a few large clutches from species laying many smaller clutches. This second axis thus depicted the spread of reproductive output across time; species producing many small clutches had a lower PC2 value.

The first PCA axis predicted survival after 1 week and 1 month (but not 1 year) and breeding attempt and breeding success (Table 1, Fig. 1). Species with slow life histories (high PC1 score) had higher survival, but were less likely to attempt breeding or to breed successfully. The second axis negatively predicted survival after 1 month, but none of the other demographic parameters. Individuals from species with more and smaller clutches had a higher rate of survival 1 month after release. The number of individuals released (propagule pressure) had a negative effect on survival after 1 week (but not on any of the other parameters), and the presence of conspecifics at the release site increased survival after 1 week and 1 month, but did not significantly affect the other parameters (Table 1).

Larger-bodied species had higher survival over the first week and the first month. Species that delay reproduction until later in life were less likely to attempt to breed or to breed successfully. Maximum longevity affected 4 out of the 5 parameters we considered. Long-lived species had higher survival after 1 week and 1 month (but not after 1 year), but were less likely to attempt breeding and were less successful at breeding. Clutch size was a predictor of all 3 survival variables, whereby species that produced larger clutches had a lower probability of survival. In contrast, clutch size was not significantly correlated with either breeding attempt or breeding success. The number of clutches per year had a positive effect on breeding success but not the other parameters (Table 2 & Supporting Information).

Table 2 contains a summary of these results, and detailed results are in Supporting Information.

Discussion

Our results document direct effects of life-history traits on specific steps of population establishment. The slow-fast continuum of life histories played a key role, as predicted by theory; taxa with slow life histories (i.e., large-bodied species with high longevity, late maturation, small clutches) were more likely to survive but less likely to breed and thus had less reproductive success (e.g., Supporting Information). In contrast, species with fast life histories (small species with short longevity, early maturation, large clutches) had lower survival but higher reproductive success. The invasion-biology literature has failed to draw clear conclusions as to the importance of the life-history buffer and population growth hypotheses (Blackburn et al. 2009; Sol et al. 2012) in determining the fate of small introduced populations. Most studies have focused on the success or failure of an introduction rather than separating the effects of survival versus breeding. We found that the same life-history parameters had contrasting effects on different steps of the settlement process (especially on survival versus breeding success), reconciling the apparent contradiction between the population-growth and life-history-buffer hypotheses (Sol & Maspons 2016).

The temporal spread of reproduction (bet hedging) also affected breeding success, which was higher in species with more clutches per year, but its effect disappeared in analyses that also included the species' position on the slow-fast life-history continuum. Environmental uncertainty thus seems less important than demographic stochasticity in determining the fate of a translocated population. This result accords with the literature on invasion success (Sol et al. 2012; Sol & Maspons 2016), but may apply more to populations

reintroduced to habitats of sufficient quality, as in the database we used, and less to invasive populations, which may arrive in habitats of low quality (Sol & Maspons 2016).

Our results have implications both for reintroduction programs and for invasion biology. In terms of reintroduction programs (e.g., Supporting Information), we suggest managers focus on priorities based on the life-history traits of the species being translocated. For species with fast life histories, the greatest risk (high rates of mortality) might be ameliorated by tactics such as local control of predator abundance or provision of additional food. For species with slow life histories, in contrast, the greatest risk (inadequate reproductive output) may be ameliorated by providing artificial nest boxes or other resources for breeding. These recommendations are additional to existing recommendations that focus on factors such as habitat quality, fit with the species usual habitat, and removal of threatening processes (e.g., predators on islands [IUCN 2013]). In short, the life-history traits of a species, as well as the local habitat and the nature of threatening processes, should be considered when framing management tactics for reintroductions.

Our results also have implications for invasion biology. Depending on which step of the introduction process is involved, such as initial survival of colonists versus subsequent reproductive output, the same life-history trait can have opposing effects on the likelihood that the population will persist and expand. Whether results from reintroduction biology can be applied directly to invasion biology remains an open question, but Blackburn and Cassey (2004) suggest introduced and reintroduced bird species are relatively similar in terms of life history. Some predictor traits will be more important in reintroductions than in invasions, such as traits favoring settlement in unfamiliar or unfavorable environments, which will likely be more favourable for invasive than for reintroduced species. However, future work could usefully explore the large database on translocations to focus on the degree to which our results remain valid for subsets of taxa in specific ecological circumstances.

More generally, we have provided a detailed empirical perspective on one of the most fundamental questions in ecology and evolutionary biology: what factors influence the fate of a small group of individuals newly arrived in a site outside their range of. This situation is central to models of speciation (Mayr 1954; Templeton 1980) and is the initial stage for natural and anthropogenically driven episodes of range expansion (Angert et al. 2011; Chuang & Peterson 2016). With rapid changes in climate, many species are expanding their ranges (Hickling et al. 2006), and the fate of such range expansions likely will depend on the life-history traits we identified.

Future work could usefully explore the contrasting roles of survival and breeding success in determining the viability of translocated populations. Population-dynamics models could clarify the interactions between these 2 demographic traits and reveal ways for managers to optimise overall population viability or to effectively extirpate small invasive populations. It would also be of interest to incorporate additional parameters (e.g., long-term survival) into such analyses and attempt to tease apart direct from indirect effects. For example, we found that rates of survival after 1 week and 1 month were higher at sites that already contained conspecifics, presumably because such sites had high-quality habitat (i.e., were a better environmental match) or because of anchoring effects (lower postrelease dispersal and associated mortality) for the species in question. Similarly, a nonintuitive result from our analyses (the number of individuals introduced had a negative effect on survival after 1 week) likely was a consequence of a bias in management effort. If managers predict high early mortality, they release large numbers of colonists in an attempt to counter that risk (Supporting Information), which causes this negative association between survival and number of released individuals. Thus, that negative relationship between propagule pressure and early survival is likely an artefact, rather than a challenge to the general importance of propagule numbers as a positive influence on invasion success (Blackburn et al. 2015). The

translocations database provides other opportunities. For example, one could explore predictors other than life-history traits (including characteristics related to ecology, behavior, genetics; reintroduction event characteristics, cf. IUCN [2013] guideline for reintroduction) to test other mechanisms of response to introduction (e.g., cognitive buffer [Sol & Maspons 2016]). More broadly, empirical results from wildlife management can illuminate fundamental questions in population biology, which in turn can facilitate conservation and invasive-species control.

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Supporting Information

Complementary methods, results, figures, and discussion (Appendix S1), the data set (Appendix S2), and photos of example species with various life histories involved in reintroduction programs (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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Table 1. Effect of life history on demographic parameters of bird species after release events for translocation.

Response variable	Explanatory variable				<i>p</i>		
		Pm ^a	Inf ^b	Sup ^b	MCMC ^c	Events ^d	Species ^e
1-week survival	fixed number of individuals released	-0.31	-0.54	-0.09	0.006*	406	58
	presence of conspecifics	0.45	0.07	0.84	0.021*		
	PC1 ^f	1.14	0.24	2.03	0.016*		
	PC2 ^f	-0.57	-1.32	0.17	0.129		
	random phylogeny	2.42	0.00	8.40	-		
	species	3.38	0.26	6.55	-		
	biogeographic region	2.85	0.00	11.57	-		
1-month survival	fixed number of individuals released	0.03	-0.16	0.23	0.725	391	54
	presence of conspecifics	0.33	0.02	0.66	0.041*		
	PC1	1.09	0.44	1.75	0.002*		
	PC2	-0.63	-1.15	-0.11	0.022*		
	random phylogeny	0.82	0.00	3.24	-		
	species	1.80	0.11	3.53	-		
	biogeographic region	4.83	0.00	20.00	-		
1-year survival	fixed number of individuals released	-0.11	-0.31	0.08	0.254	330	46
	presence of conspecifics	0.09	-0.21	0.38	0.572		
	PC1	0.33	-0.39	1.03	0.349		
	PC2	-0.45	-1.02	0.12	0.121		
	random phylogeny	2.02	0.00	4.32	-		
	species	0.90	0.00	2.27	-		
	biogeographic region	1.66	0.00	6.42	-		

		region						
Breeding attempt	fixed	number of individuals released	3.34	-13.36	19.86	0.593	587	67
		presence of conspecifics	-10.27	-26.22	3.91	0.144		
		PC1	-69.58	-	-22.25	0.002*		
				117.0				
		PC2	-2.47	-36.37	30.11	0.886		
	random	phylogeny	4856.84	0.00	22833.0	-		
		species	8547.32	0.33	20126.4	-		
		biogeographic region	1253.08	0.00	5396.12	-		
Breeding success	fixed	number of individuals released	5.61	-11.34	23.06	0.440	579	66
		presence of conspecifics	3.80	-10.57	18.98	0.595		
		PC1	-79.79	-	-24.77	0.001*		
				134.7				
		PC2	-6.37	-45.14	31.11	0.758		
	random	phylogeny	3236.41	0.00	19315.0	-		
		species	12758.4	125.0	28032.3	-		
			8	4	7			
		biogeographic region	2804.61	0.00	12563.7	-		
					2			

^aPosterior mean.

^bLower (inf) and upper (sup) bounds of the 95% CI.

^cSignificance of Markov chain Monte Carlo. Asterisk, significant principal component value.

^dTotal number of release events included in the analysis.

^eTotal number of different species included in the analyses.

^fThe PC1 and PC2 are principal components of a PCA on 5 life-history traits detailed in Fig. 1 and Table 1: PC1, slow fast life-history continuum (species with a slow lifestyle have higher PC1 value); PC2, spread of reproduction effort over time (species spreading effort at the expense of the number of eggs produced per clutch have a lower PC2 value) (asterisk, significant PC value).

Table 2. Summarized effects^a of each life-history predictor on 5 demographic parameters.

Response Variable	Life-history predictor	Pm ^b	Inf ^c	Sup ^c	<i>p</i>		
					MCMC ^d	Events ^e	Species ^f
1-week survival	body mass	1.55	0.16	2.93	0.011*	601	99
1-month survival	body mass	1.37	0.29	2.45	0.004*	631	96
1-year survival	body mass	-0.11	-0.40	0.18	0.470	550	90
Breeding attempt	body mass	-2.65	-	8.08	0.663	837	124
Breeding Success	body mass	-2.93	-	8.07	0.624	817	122
1-week survival	age at first reproduction	0.44	-0.13	1.01	0.135	540	83
1-month survival	age at first reproduction	0.25	-0.46	0.96	0.478	567	80
1-year survival	age at first reproduction	0.10	-0.35	0.55	0.651	516	71
Breeding attempt	age at first reproduction	-36.70	-	-6.89	0.002*	756	102
Breeding success	age at first reproduction	-51.95	-	-10.42	0.001*	739	100
1-week survival	longevity	0.70	0.04	1.38	0.041*	518	73
1-month	longevity	1.24	0.68	1.82	0.001*	537	68

survival							
1-year survival	longevity	0.22	-0.26	0.70	0.372	448	60
Breeding attempt	longevity	-41.48	-74.78	-9.61	0.001*	722	86
Breeding success	longevity	-41.63	-74.15	-9.13	0.001*	713	86
1-week survival	clutch size	-0.65	-1.07	-0.25	0.003*	616	106
1-month survival	clutch size	-0.69	-1.05	-0.34	0.001*	641	101
1-year survival	clutch size	-0.54	-0.92	-0.15	0.008*	559	95
Breeding Attempt	clutch size	3.18	-14.19	20.93	0.533	863	134
Breeding success	clutch size	4.70	-21.76	31.80	0.623	843	132
1-week survival	no. clutches/year	-0.36	-0.97	0.26	0.253	522	86
1-month survival	no. clutches/year	-0.19	-0.71	0.34	0.486	550	82
1-year survival	no. clutches/year	-0.21	-0.65	0.23	0.354	481	76
Breeding attempt	no. clutches/year	12.93	-3.52	33.54	0.099	765	112
Breeding success	no. clutches/year	28.34	1.92	60.73	0.018*	753	111

^aThese effects are extracted from PGLMM including other fixed and random covariables not shown here (see Supporting Information for detailed results).

^bPosterior mean.

^cLower (inf) and upper (sup) bounds of the 95% CI.

^dSignificance of Markov chain Monte Carlo. Asterisk, significant principal component value.

^eTotal number of release events included in the analysis.

^fTotal number of different species included in the analyses.

Figure 1. Association between PC1 and (a) first week survival, (b) month survival, (c) breeding attempt, and (d) breeding success in reintroduced birds in different reintroduction events of a given species (PC1, first axis in the principle component analysis on 5 life-history traits; curves, results of linear regressions on mean species values drawn for illustrative purposes). Body mass, maximum longevity, clutch size, age at first reproduction, and number of clutches per year (PC1) segregate species with a fast life history (fast reproduction but low longevity) from species with a slow life history (long-lived species with slow reproduction). Models included phylogeny, biogeographic region, and species as random factors and number of individuals released and presence of conspecifics at release site as fixed covariables.

