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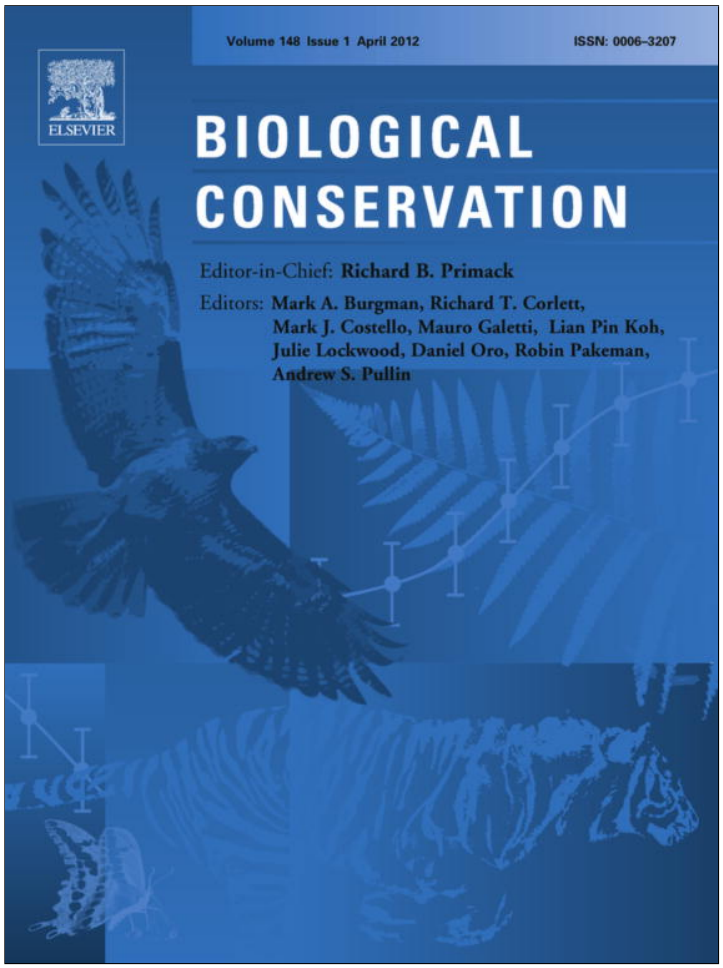

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Psittacine reintroductions: Common denominators of success

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ABSTRACT

With 28% of the 350 species of parrots considered threatened, numerous conservation efforts have been initiated for these species. Among these, the restoration or establishment of new populations has increasingly relied on reintroductions as a conservation strategy, often with mixed or uncertain results. We reviewed the results and methodologies of 47 distinct releases and reintroductions of psittacines in nine different countries worldwide over the past 25 years to identify common denominators of successful efforts. To do so, we established a uniform and objective definition of reintroduction success (first-year survival >0.50 and released birds breeding with conspecifics, either captive-reared or wild), and applied generalized linear models and information-theoretic model selection to multiple datasets to identify important predictor variables. We identified several likely predictors of successful psittacine reintroductions, relating to predation mitigation, habitat quality, and post-release supplementation that may provide guidance for future efforts. We also advocate SWOT analysis for objectively evaluating the suitability of potential reintroduction sites.

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1. Introduction

The family Psittacidae comprises nearly 350 species worldwide, of which approximately 28% are considered threatened (IUCN, 2010), making this one of the most endangered avian groups in the world. Further, because of their colorful plumage and sociability, psittacines are also highly charismatic fauna, a trait which ironically has contributed to their current endangered status due, in part, to the perennially high demand for psittacines in aviculture and the pet trade (Collar and Juniper, 1992; Wright et al., 2001; Carrete and Tella, 2008; ProFauna, 2008). These demands, coupled with progressive and widespread habitat loss, are generally considered the primary threats to these birds worldwide (Snyder et al., 2000; Wright et al., 2001; Wiley et al., 2004). Consequently, numerous conservation efforts on behalf of these species have been initiated. Among these, the restoration or establishment of new populations of psittacines, and the bolstering of existing ones, has increasingly relied on reintroductions and supplementations as a conservation strategy (e.g., Clubb and Clubb, 1992; Snyder et al., 1994; Sanz and Grajal, 1998; Oehler et al., 2001; Collazo et al., 2003; Ziembicki et al., 2003; Brightsmith et al., 2005; Collar, 2006; Adams and Cash, 2010). The existence of numerous captive breeding programmes and often substantial captive populations has made reintroductions potentially viable for numerous psittacines (Clubb, 1992; Derrickson and Snyder, 1992; Wiley et al., 1992; Wilson and Stanley Price, 1994; Smales et al., 2000a; Woolaver et al., 2000; USFWS, 2009). Frequently, both captive-bred and wild-caught stocks are available for release (Cassey et al., 2004). It is not just a matter of availability; often there is also pressure from government officials attempting to find appropriate solutions for birds confiscated from illegal traders and trappers (ProFauna, 2008). Thus, modern psittacine conservation reflects a general shift from the early, almost exclusive focus on very seriously threatened species to a broader agenda of reestablishing or securing local or national populations of species whose global conservation status is likely to be of less concern.

Nevertheless, even for these latter species reintroduction and supplementation are not straightforward procedures, and officials seeking to dispose of confiscated birds quickly are likely to be disappointed by the conservationist response (see IUCN, 2002; Carrete and Tella, 2008). On the other hand, there remain a few very rare species of psittacines (e.g., Puerto Rican parrot *Amazona vittata*; Spix's macaw *Cyanopsitta spixii*) for which reintroduction or supplementation remains the only option. For all species involved, the minimization of the risk of failure is important; but

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for very rare species, whose fate exclusively depends on these techniques, it is absolutely crucial. So how much do we know about psittacine reintroduction and supplementation, and how can we put this knowledge to best use to ensure that future reintroductions and supplementations will be successful?

The crucial document on reintroductions and associated conservation techniques is IUCN (1998), which defines *reintroduction* as 'an attempt to establish a species in an area which was once part of its historical range, but from which it has been extirpated or become extinct'. It further defines *translocation* as 'deliberate and mediated movement of wild animals to an existing population of conspecifics', and *supplementation* as the 'addition of individuals to an existing population of conspecifics', while *conservation introduction* or *benign introduction* is defined as 'an attempt to establish a species, for the purpose of conservation, outside its recorded distribution but within an appropriate habitat and eco-geographical area'. These terms are important, as they help distinguish the types of activities that have characterized such work on psittacines over the past 25 years (see Collar, 2006). Accordingly, herein we use the term 'reintroduction' in its broadest sense, inclusive of the aforementioned definitions.

Regardless of the definitions of these techniques, methodological prescriptions have varied widely. For example, Snyder et al. (2000) described eight general conditions for parrot reintroductions, most of which restated certain key criteria in IUCN (1998) including correction of the original cause(s) of endangerment or extirpation (e.g., habitat loss, hunting, chick harvesting), thorough evaluation of potential release sites, release of sufficient numbers of birds, pre-release conditioning (e.g., flight training, socialization, local acclimatization, experience with local foods) and the allocation of adequate resources for monitoring results. Grajal (2002) expanded on these recommendations by including use of captive-bred and confiscated birds for releases (but see Snyder et al., 1994; Carrete and Tella, 2008). However, his analysis was explicitly limited to supplementations, although he believed his recommendations were equally valid for reintroductions (see Collar, 2006). Various other techniques have also been suggested, such as lengthy periods of post-release supplementary feeding (e.g., Brightsmith et al., 2005), releasing only within historic range of species (e.g., Snyder et al., 1994; Enkerlin-Hoeflich, 2002), use of only juvenile birds for releases (e.g., Collazo et al., 2003), and pre-release exposure to predators (e.g., Sanz and Grajal, 1998; White et al., 2005a).

It is not surprising, therefore, that previous deliberate reintroductions of psittacines have frequently met with mixed or uncertain results. For example, attempts at reestablishing the thick-billed parrot (*Rhynchopsitta pachyrhyncha*) in the USA were plagued with low survival of released birds, resulting in failure of these efforts (Snyder et al., 1994). Translocations of the Uvea horned parakeet (*Eunymphicus uvaeensis*) among islands of the Loyalty Island chain also failed (Wiley et al., 1992), allegedly due to the birds' ability to return to site of origin. Similar attempts to reintroduce the Tahitian lorikeet (*Vini peruviana*) to Tahiti were also unsuccessful (Wiley et al., 1992), as were attempts to introduce the Vasa parrot (*Coracopsis vasa*) to Reunion Island (Forshaw, 1989). Additionally, results of past reintroductions of military macaws (*Ara militaris*) in Guatemala have proven inconclusive (Collar, 2006).

Nevertheless, viable populations of numerous species of psittacines have become successfully established or reestablished worldwide, albeit often inadvertently (Cassey et al., 2004; Carrete and Tella, 2008). Examples include the eastern rosella (*Platycercus eximius*), introduced in New Zealand, which has reportedly thrived and increased in numbers and range (Robertson et al., 2007). The green-rumped parrotlet (*Forpus passerinus*) was introduced to Jamaica in 1918 (Wiley et al., 1992) and is now common in lowland forests of that island (Forshaw, 1989). A range expansion of Malherbe's parakeets (*Cyanoramphus malherbi*) in New Zealand was also reported as result of a successful reintroduction of captive-reared birds on Maud Island (Ortiz-Catedral et al., 2010a). Furthermore, feral populations of monk parakeets (*Myiopsitta monachus*) have become established in southern Europe and elsewhere through both deliberate and accidental introductions (Lever, 2005; Carrete and Tella, 2008).

Regardless of the methods employed, however, factors which frequently compound the problem of objectively assessing results of reintroductions include poorly documented or inconsistent methodologies, insufficient post-release monitoring, and widely differing definitions – or no definition – of 'success' (see Scott and Carpenter, 1987; MacMillan, 1990; Snyder et al., 1994; IUCN, 1998; Seddon, 1999a, 1999b; Fischer and Lindenmayer, 2000; Soorae, 2010; Sutherland et al., 2010). For example, in a recent compendium of 72 reintroduction case-studies worldwide (only three of which were psittacines), each study reported a variety of different metrics for and levels of 'success' (Soorae, 2010). Indeed, the whole question of determining success in reintroductions has been the subject of inconclusive debate. Seddon (1999b) proposed four distinct criteria for measuring success: (1) breeding by the first wild-born generation; (2) a three-year breeding population with recruitment exceeding adult mortality; (3) an unsupported wild population of at least 500 individuals; or (4) the establishment of a 'self-sustaining' population – each obviously requiring extensive, long-term post-release monitoring (see Seddon and Cade, 1999; Moseby et al., 2011).

Thus, substantial variation exists in methodologies for, and assessments of, reintroductions worldwide. This inherent variation confounds efforts not only to assess results of reintroductions objectively, but also to prescribe optimal methodologies. Meanwhile, given the increasing use and importance of reintroductions in psittacine conservation worldwide, an assessment of results to date is long overdue. The purpose of our study therefore is to evaluate recent psittacine reintroductions quantitatively and, using a standardized metric, identify those factors which contribute most to reintroduction success. Knowledge of such factors may inform future efforts, and spur further investigation into how these and other factors influence success. Based on our results, we also offer specific suggestions for improving not only the success of future psittacine reintroduction efforts, but also their broader conservation value.

2. Methods

2.1. Data acquisition

We obtained data from a total of 100 individual releases or reintroductions of nine species of psittacines – ranging from the echo parakeet (*Psittacula eques echo*; 160 g) to the world's heaviest psittacine, the kakapo (*Strigops habroptila*; 3000 g) – in nine countries worldwide during primarily the past 25 years, and for which extensive and detailed data were available (Table 1). Data were obtained from both published accounts and questionnaires sent to practitioners. The questionnaire solicited information regarding 57 aspects – both quantitative and qualitative – of the specific release(s), which yielded 14 independent variables for analyses (Table 2). Variables were selected based on their importance in several previous studies (e.g., Snyder et al., 1994; Wolf et al., 1996; Sanz and Grajal, 1998; Fischer and Lindenmayer, 2000; O'Connor, 2000; Duncan et al., 2003; Brightsmith et al., 2005; Collar, 2006), their relevance to psittacine ecology, and for which reliable data existed for each reintroduction. This approach allowed us to maximize the heuristic value of available information while simultaneously establishing a useful and comprehensive baseline for future comparisons (sensu Wolf et al., 1996). Some variables were

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Table 1
Sources of data for analyses of factors relating to psittacine reintroduction success.

Species	Location	Years	Events[a]	Source(s)
Rhynchopsitta pachyrhyncha	Arizona, USA	1986–1993	5 (5)	Snyder et al. (1994)
Amazona ventralis	Dominican Rep.	1997–1999	2 (7)	Collazo et al. (2000, 2003) White et al. (2005b)
Amazona vittata	Puerto Rico	2000–2009	9 (12)	White et al. (2005a) PRDNER[b], unpubl. data USFWS[c], unpubl. data
Amazona barbadensis	Venezuela	1993–1997	2 (2)	Sanz and Grajal (1998) Grajal (2002)
Psittacula eques echo	Maritius	1997–1999	1 (6)	Woolaver et al. (2000)
Ara ararauna	Trinidad	1999–2004	2 (4)	Oehler et al. (2001) and Plair et al. (2008)
Ara macao	Costa Rica	1999–2001	7 (7)	Brightsmith et al. (2003, 2005)
Ara macao	Peru	1991–1994	4 (4)	Brightsmith et al. (2003, 2005)
Strigops habroptila	New Zealand	1974–2005	10 (48)	Lloyd and Powlesland (1994) Elliot et al. (2001); NKT[d] unpubl. data
Nestor meridionalis	New Zealand	1999–2007	5 (5)	RJ Moorhouse, unpubl. data R. Empson, unpubl. data
TOTAL			47 (100)	

[a] Total independent reintroduction events; numbers in parentheses are total individual releases.
[b] Puerto Rico Department of Natural & Environmental Resources.
[c] United States Fish & Wildlife Service.
[d] National Kakapo Team.

Table 2
Predictor variables used for analyses of factors relating to psittacine reintroduction success.

Variable acronym	Variable description (levels)
PredThreat	Predation threat (1 = low-none; 2 = medium; 3 = high)
HabQual	Habitat quality (1 = fair-poor; 2 = good; 3 = excellent)
FoodTrain	Pre-release wild food training? (yes/no)
Releases	Number of individual releases
TotalReleased	Total number of individuals released
SupFeed	Post-release supplementary feeding (months)
HistRange	Released within historic range? (1 = outside; 2 = periphery; 3 = core)
ConsPresent	Conspecifics present at release site? (yes/no)
RelWild%	Percent of wild birds in release cohort
Juvenile%	Percent of juvenile birds in release cohort
HandReared%	Percent of hand-reared birds in release cohort
PreAccltime	Time birds were acclimated at/near release site prior to release (months)
PredExpPre	Birds exposed to predators or training prior to release? (yes/no)
OrigCauseFixed	Was original cause(s) of population decline/loss corrected? (yes/no)

expressed in three categorical levels (Table 2) which were assessed by the respective practitioners, either via the questionnaire or previously published accounts. Such levels were chosen because: (1) they were broad enough to accommodate individual variation in categorical assessments without loss of precision, (2) they were discrete enough to retain discriminatory value, and (3) they were directly comparable with those of previous similar studies (e.g., Griffith et al., 1989; Wolf et al., 1996). Further, categorical assessments were both species- and site-specific, thereby facilitating comparisons among reintroductions. For instance, although the specific predation threats differed for Puerto Rican parrots and kakapo, the use of relative threat levels (low, medium, high) established a common metric of comparative risk, independent of species. In such cases, relative threat levels were functionally equivalent, regardless of the specific threat mechanisms (e.g., raptors, mammals, reptiles).

From the 100 releases examined, we identified 47 distinct and independent reintroduction 'events' for subsequent analyses. Reintroduction events consisted of one or more individual releases of a species per country (Table 1). For any given species, events were considered independent if they complied with *at least two* of the following conditions: (1) they occurred in different years and/or seasons (temporal variation), (2) they occurred in different regions or habitat types (spatial variation), or (3) they varied in one or more predictor variables (methodological variation). Individual releases which were replicates within an overall reintroduction effort (e.g., Woolaver et al., 2000; Collazo et al., 2003) were not treated as independent events in our analyses. We recognise that there have been other releases of psittacines during the past 25 years (see, e.g., Collar, 2006; Soorae, 2010); however, not all have had sufficient documentation of methods and results to have been used in our analyses. We evaluated all variables for evidence of influence on reintroduction success. For analytical purposes, we defined 'success' as those reintroductions in which first-year survival was >0.50 (i.e., each individual's probability of survival > probability of mortality) *and* in which released birds later bred with conspecifics, either captive-reared or wild. This definition is important in this context as it establishes an empirically-based and objective benchmark combining the two most fundamental parameters in terms of population establishment and persistence: survival and reproduction (Seddon, 1999b; Teixiera et al., 2007; Armstrong and Seddon, 2008; Tavecchia et al., 2009). However, we also examined separately the first of these parameters – first-year survival – in order to evaluate specific factors influencing this important and commonly reported metric of success. Fischer and Lindenmayer (2000) suggested that analyses based on published accounts of reintroductions may over-estimate 'success', as many failed efforts and their associated insights go unreported (but see Snyder et al., 1994; Bell et al., 2010; Moseby et al., 2011). By establishing an independent metric for success, however, we objectively re-evaluated such accounts, thereby reducing any potential reporting bias. For example, although White et al. (2005a) reported that captive-reared Puerto Rican parrots were 'successfully' released, those results did not meet our stated criteria for success, and were not classified as such in our analyses.

2.2. Data analysis and inference

Our goal in analysing patterns of successful psittacine reintroductions among those studied was to identify covariates associated with successful reintroductions, and also those associated with lower success. We focused on two response variables which quantified the success of psittacine reintroductions. The first was

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a continuous response variable measuring the proportion of individuals released that survived to one year. This variable was used as the response in general linear models, with a set of predictor variables measuring attributes of the reintroductions (Table 2). These models were formulated as generalized linear models with an identity link and Gaussian random component, and are referred to as linear regression models hereafter. The second response variable treated the outcome of reintroductions as a binary variable (successful or not) based on our criteria for success. These models were formulated as generalized linear models with a logit link and binomial random component, and are referred to as logistic regression models hereafter. We did not apply phylogenetically independent contrasts (see Wolf et al., 1998) because our primary response variable (success) was binary, and because our data (i.e., number of genera) were insufficient for such analyses. However, our total observations (i.e., number of reintroduction events) equally represented three of the principal IUCN global regions and associated psittacine lineages (see Soorae, 2010); namely, North American/Caribbean (34%), Oceania (34%), and Meso/South American (32%). Hence, our inferences and recommendations are appropriate for, and limited to, the family Psittacidae.

For each analysis, we first formulated an a priori set of statistical models representing alternative explanations of how the covariates influenced the response variable. Because our analyses were of a more exploratory than confirmatory nature, we included all single variable models and models with two-way interactions that represented potentially meaningful ecological relationships between factors. To access the evidence in support of each hypothesis, we used information-theoretic model selection based on the expected relative Kullback–Leibler information (Burnham and Anderson, 2002). In this approach, alternative hypotheses are ranked according to the degree of support given by the data. The key scientific step is deciding on the a priori model set. Evidence evaluating support for models in the a priori set were evaluated based on the relative adjusted Akaike weight (Δ_i), model weight (w_i), and evidence ratios, based on Burnham and Anderson (2002) and calculated as follows:

(1) $\text{AICc}_i = -2 * \log_e(\text{Likelihood of model } i \text{ given the data}) + 2 * K + 2 * K * (K+1)/(n-K-1)$, where K = the number of parameters estimated and n = the sample size.
(2) $\text{AICc}_{\min} = \text{AICc}$ for the model with the lowest AICc value.
(3) $\Delta\text{AICc} = \text{AICc}_i - \text{AICc}_{\min}$.
(4) $w_i = \exp(-1/2 * \Delta_i)/\sum_{r=1}^{n} \exp(-1/2 * \Delta_r)$.
(5) Evidence ratio of model i to model $j = w_i/w_j$.

Model weights (w_i) can be interpreted as the likelihood that model i is the best model in the a priori set, and evidence ratios (w_i/w_j) can be interpreted as the relative support of the data for model i compared with model j (Anderson, 2008). The statistical models were fitted using R version 2.12.2 (R Development Core Team, 2011). Within each analysis, models were considered for interpretation of their parameters if they: (1) had ΔAICc of less than 10.0, (2) were included in the set of best supported models with combined Akaike weights of 0.80 (80% confidence set) and (3) had an evidence ratio relative to the best supported model greater than 0.135 (Burnham and Anderson, 2002). Following model selection, model fitting diagnostics were performed on the full model (i.e., a model with all main effects and interaction terms included in any of the a priori) and all models considered for further interpretation, following recommendations in Zuur et al. (2009) for linear regressions models, and Hosmer and Lemeshow (2000) for logistic regression models. Only models without significant departures of model fit or numerical problems were retained in the set of models considered for interpretation.

We initially attempted to include interactions between HabQual (see Table 2 for variable acronyms and descriptions) and three other variables (HistRange, ConsPresent and SupFeed); however, these interactions resulted in two-way classifications of reintroductions with zero observations in some categories. Such zero counts create numerical problems with maximum likelihood estimation algorithms in logistic regression, a problem referred to as quasi-complete separation (Hosmer and Lemeshow, 2000). Thus, these interactions were dropped from the analysis, as the data would not support fitting these parameters. This was also the case for the interaction between RelWild% and FoodTrain, so this model was also dropped. We also had quasi-complete separation for the variable PredThreat (none of the reintroductions with the highest PredThreat level was successful). However, there was strong evidence from the data that PredThreat was an important variable for predicting success of reintroduction, so to proceed we treated PredThreat as a continuous variable, thereby allowing generation of parameter estimates and the model maximum likelihood, which was necessary for model selection.

3. Results

3.1. First-year survival

The best-supported linear regression model had PredThreat as the only explanatory variable, while the next best supported model had both PredThreat and PredExpPre as additive effects. These two models had nearly all of the support among the models considered, with a combined Akaike weight of 0.93 (Table 3). In fact, the first four models accounted for 98% of all support (Table 3). Examination of the beta estimates for the best supported model indicated that there was a measurable negative impact on the proportion of individuals surviving to one year when PredThreat was at the highest level (Table 4). PredThreat also had a negative effect at its highest level in the second best supported model, but this

Table 3
Information-theoretic model selection results for linear regression models relating predictor variables with the proportion of individuals surviving to one year in psittacine reintroductions.

Model	k	neg2LL[a]	ΔAICc[b]	w_i
PredThreat	4	3.38	0.00	0.69
PredThreat + PredExpPre	5	2.99	2.12	0.24
PredThreat * PredExpPre	7	1.22	5.76	0.04
HabQual + ConsPresent	5	10.52	9.65	0.01
HabQual	4	13.55	10.17	0.00
HabQual + SupFeed	7	5.70	10.24	0.00
Releases	3	16.44	10.66	0.00
HabQual * ConsPresent	7	6.21	10.75	0.00
RelWild + PredExpPre	4	14.30	10.92	0.00
PreAccItime	3	17.42	11.64	0.00
ConsPresent	3	17.79	12.01	0.00
Juvenile.p	3	18.12	12.34	0.00
RelWild	3	18.28	12.50	0.00
OrigCauseFixed	3	18.77	13.00	0.00
HabQual + HistRange	6	11.38	13.14	0.00
RelWild * FoodTrain	5	14.21	13.34	0.00
RelWild * PredExpPre	5	14.23	13.36	0.00
RelWild + FoodTrain	4	16.87	13.49	0.00
Intercept only	2	21.58	13.52	0.00
Total.rel	3	19.42	13.65	0.00
PredExpPre	3	19.83	14.06	0.00
FoodTrain	3	20.23	14.46	0.00
HandRear.p	3	21.58	15.80	0.00
HistRange	4	19.21	15.83	0.00
HabQual * SupFeed	13	−4.35	16.35	0.00
SupFeed	5	17.22	16.35	0.00
SupFeed + FoodTrain	6	16.16	17.93	0.00
HabQual * HistRange	10	6.37	18.15	0.00
SupFeed * FoodTrain	9	16.16	20.69	0.00

[a] Table entry gives −2 * ln(Likelihood of model$_i$ given the data).
[b] Lowest model AICc = 12.33.

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Table 4
Parameter estimates for the best-supported linear regression models for first-year survival in psittacine reintroductions. Also shown are the post hoc models with two categories for PredThreat (levels 1 and 2 merged).

Model/β	Estimate	SE
SurvYearOne ~ PredThreat		
(Intercept)	0.75	0.05
PredThreat (=2)	−0.07	0.09
PredThreat (=3)	−0.44	0.10
SurvYearOne ~ PredThreat + PredExpPre		
(Intercept)	0.79	0.08
PredThreat (=2)	−0.06	0.10
PredThreat (=3)	−0.42	0.10
PredExpPre (=1)	−0.05	0.09
*SurvYearOne ~ PredThreat * PredExpPre*		
(Intercept)	0.81	0.09
PredThreat (=2)	−0.27	0.21
PredThreat (=3)	−0.31	0.28
PredExpPre (=1)	−0.09	0.11
PredThreat (=2) * PredExpPre (=1)	0.26	0.23
PredThreat (=3) * PredExpPre (=1)	−0.12	0.30
SurvYearOne ~ PredThreat2		
(Intercept)	0.73	0.04
PredThreat (=3)	−0.42	0.09
SurvYearOne ~ PredThreat2 + PredExpPre		
(Intercept)	0.77	0.08
PredThreat (=3)	−0.40	0.09
PredExpPre (=1)	−0.06	0.09

model also included a negative effect when PredExpPre = 1 (previous predator exposure). However, the precision of the effect size estimate for PredExpPre in this model was poor (large standard errors resulting in 95% confidence intervals overlapping zero) and thus no definitive conclusion about the effect of PredExpPre can be drawn from this model. Because the parameter estimate for the second level of PredThreat was small and poorly estimated (large standard error) we fitted a post hoc model with PredThreat coded as a two-category variable by combining levels 1 and 2. This model had an AICc = 10.5 (AIC = 10.0), making it superior to all models in the set. The predicted effect of PredThreat from this model was nearly identical with that of the best supported a priori model (Table 4). We also fitted a post hoc model with the additive effects of both PredThreat as a two-category variable, and PredExpPre. This model had AICc = 12.4 (AIC = 10.9), making it tied for second place among all models considered. The model with the interaction between PredThreat and PredExpPre estimated a change in the magnitude of the effect of the level of predator threat, depending on whether or not there was previous exposure to predators (Table 4). However, the precision with which this parameter was estimated was also poor, and this model was not considered further.

The response variable (proportion of individuals surviving to one year) was somewhat discrete due to the small sample size. There were also several observations at either end of the range (five cases with none surviving and eight cases with all surviving). Both factors are of concern in ensuring that we met the basic assumptions for the general linear models used. Although the fit of the best models appeared adequate based on standard diagnostics, our results should be interpreted with these considerations in mind. Thus, our analyses were better suited to exploring the relative importance of factors than to predicting precise magnitudes of effect sizes.

3.2. Reintroduction success

Based on our success criteria, 26 (55%) of the 47 releases and reintroductions were categorized as 'successful' for analytical purposes. Model selection resulted in the logistic regression model with PredThreat having virtually all of the support (Table 5). A useful and intuitive way to interpret the beta parameters from a logistic regression is to examine the predicted probability of success for each level of the predictor variable. Using this approach, the predicted probability of a successful psittacine reintroduction was more than four times lower when PredThreat was at the highest level versus the lowest level (Table 6). Another way to look at these results is to recognise that categorical logistic regression models are essentially contingency tables. Thus, we can examine the cell counts and standardized residuals from a contingency table analysis, to gain insight into patterns between the explanatory and response variables. This was particularly useful for PredThreat, because we treated it as a continuous variable in the logistic regression to avoid numerical problems. The contingency table analysis of PredThreat indicated that cell counts were lower than expected for successful reintroductions when PredThreat was at the highest level, and higher than expected for successful reintroductions when PredThreat was at the lowest level (Table 7).

Based on our model selection criteria, we would ordinarily not consider any of the other models as having much support from the data. However, because we treated PredThreat as a continuous variable to overcome numerical problems, we may have given this model an advantage in model selection (because a continuous variable uses only 1 df while the categorical variable would have required 2). Thus, we also examined results from the next three models in the a priori set; namely, the models with FoodTrain, HabQual and SupFeed (Table 5). The model with FoodTrain had low precision on its estimated effect size (Table 6), and the

Table 5
Information-theoretic model selection results for models relating predictor variables with the probability of successful reintroduction of psittacines.

Model	k	neg2LL[a]	ΔAICc[b]	w_i
PredThreat	2	52.88	0.00	0.89
FoodTrain	2	60.07	7.18	0.02
HabQual	3	57.81	7.22	0.02
SupFeed	4	56.00	7.80	0.02
Intercept only	1	64.62	9.56	0.01
ConsPresent	2	62.44	9.56	0.01
Releases	2	62.63	9.74	0.01
OrigCauseFixed	2	63.04	10.15	0.01
HandRear.p	2	63.70	10.82	0.00
PreAccltime	2	63.71	10.83	0.00
PredExpPre	2	63.77	10.88	0.00
Total.rel	2	64.45	11.57	0.00
Juvenile.p	2	64.47	11.58	0.00
RelWild	2	64.60	11.71	0.00
HistRange	3	63.07	12.47	0.00

[a] Table entry gives −2 * ln(Likelihood of model$_i$ given the data).
[b] Lowest model AICc = 57.16.

Table 6
Parameter estimates for the best supported logistic regression models relating predictor variables with the probability of successful reintroduction of parrots.

Model	Pr(Success|treat)	Pr(Success|no treat)	β	se(β)	Nag. R^{2e}
PredThreat[a]	0.16	0.75	−1.39	0.46	0.30
FoodTrain[b]	0.49	0.88	−2.00	1.12	0.12
HabQual[c]	0.73	0.25	2.11	0.89	0.18
SupFeed[d]	0.77	0.33	1.92	0.71	0.22

[a] Estimates for PredThreat = high versus PredThreat = low-none.
[b] Estimates for FoodTrain = "yes" versus FoodTrain = "no".
[c] Estimates for HabQual = "excellent" versus HabQual = "fair-poor".
[d] Estimates for SupFeed ⩾ 12 months versus SupFeed < 1 month.
[e] Analog of regression multiple R^2 proposed by Nagelkerke (1991).

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Table 7
Contingency table analysis for the top four logistic regression models relating predictor variables with the probability of successful reintroduction of psittacines.

Factor	Outcome		Standardized residuals[a]		χ^2	df	p[b]
	Not successful	Successful	Not successful	Successful			
PredThreat = low	8	18	−2.13	2.13	15.77	2	<0.001
PredThreat = med	3	8	−1.33	1.33			
PredThreat = high	10	0	3.97	−3.97			
FoodTrain = no	1	7	−2.01	2.01	2.62	1	0.11
FoodTrain = yes	20	19	2.01	−2.01			
HabQual = fair-poor	9	3	2.45	−2.45	6.61	2	0.04
HabQual = good	8	12	−0.56	0.56			
HabQual = excellent	4	11	−1.70	1.70			
SupFeed < 1 mo	12	6	2.39	−2.39	8.31	3	0.04
SupFeed = 1–6 mo	3	2	0.73	−0.73			
SupFeed = 6–12 mo	1	1	0.15	−0.15			
SupFeed ⩾ 12 mo	5	17	−2.84	2.84			

[a] Residuals calculated following Agresti (2007).
[b] p-Value calculated using continuity correction (Agresti, 2007).

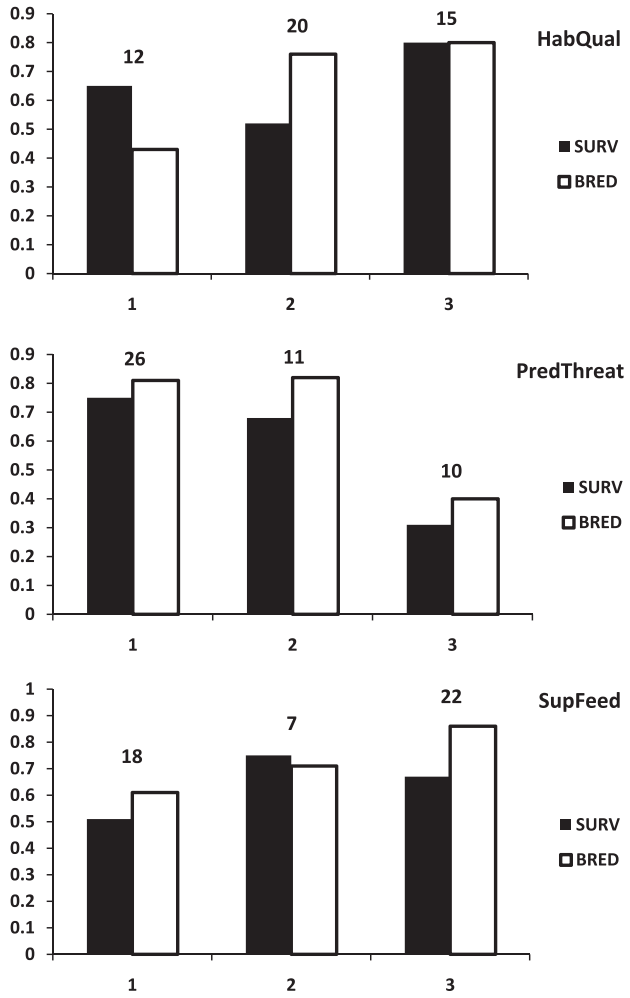

Fig. 1. Differential effects of varying levels of habitat quality (HabQual), predation threat (PredThreat) and supplementary feeding (SupFeed) on first-year survival of released psittacines and the proportion of reintroductions in which released psittacines later bred. Levels for HabQual: 1 = fair-poor; 2 = good; 3 = excellent. Levels for PredThreat: 1 = low-none; 2 = medium; 3 = high. Levels for SupFeed: 1 = <1 month; 2 = 1–12 months; 3 = ⩾12 months. Numbers above bar pairs denote sample sizes.

contingency table analysis did not indicate any evidence for a relationship between FoodTrain and reintroduction success (Table 7).

In contrast, HabQual showed a strong positive effect on the probability of success, with a successful reintroduction predicted to be nearly three times more likely when HabQual was at the highest versus the lowest level (Table 6). The contingency table analysis indicated that the number of successes and failures when HabQual was at the lowest level was the main reason for the association (Table 7). Deconstructing 'success' into its component parameters (survival, breeding) reveals that the greatest contribution of habitat quality to reintroduction success was its positive influence on subsequent breeding by released birds (Fig. 1), in contrast to predation threat, which at its highest level adversely affected both components of success equally. SupFeed also showed a strong positive effect with more than twice the probability of success when supplementary feeding was administered the longest versus the shortest time (Table 6). The contingency table analysis indicated that the relative difference in successes and failures when SupFeed was at the lowest and highest levels was the main reason for the association (Table 7). As with habitat quality, increased supplementary feeding contributed proportionately more to subsequent breeding by released birds than to post-release survival (Fig. 1).

4. Discussion and conclusions

As parsimony lends itself to heurism, we applied a statistical equivalent of 'Occam's razor' to a broad array of potential explanatory variables and identified factors important for initial survival of released parrots and success of psittacine reintroduction efforts. Foremost among these factors was predation. High predation threat significantly reduced overall success rates by reducing both post-release survival and probability of subsequent breeding by released birds. Fischer and Lindenmayer (2000) and Moseby et al. (2011) also reported predation as a major factor influencing reintroduction success of birds, mammals and reptiles. Indeed, predation was cited as the primary cause of failure of reintroduction efforts for the thick-billed parrot in the USA (Snyder et al., 1994), as well as for the apparent failure of efforts to reintroduce the ultramarine lorikeet (*Vini ultramarina*) on Fatu Iva (Ziembicki et al., 2003). Moreover, significant post-release losses of Puerto Rican parrots to raptor predation, and gains in survival following implementation of pre-release predator aversion training, have been reported (White et al., 2005a), as have benefits from predator aversion training involving non-psittacine species (McLean et al., 1999; van Heezik et al., 1999; Griffin et al., 2000). In this study, although we were unable to assess conclusively the overall value of pre-release predator exposure to the survival of released birds,

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results indicated some positive effects at moderate, but not high, levels of predation threat (Table 4). This suggests that in some cases, high levels of predation pressure may potentially override any putative survival gains accrued from pre-release predator exposure. It is noteworthy that high survival and success rates have been attained for reintroductions of the kakapo and kaka (*Nestor meridionalis*) as well as the kakariki (*Cyanoramphus novaezelandiae*) in New Zealand, and have been primarily attributed to releases on predator-free islands or in areas with otherwise high-quality habitat and low numbers of introduced mammalian predators (e.g., Elliot et al., 2001; Powlesland et al., 2006; Ortiz-Catedral et al., 2010b; RJM, unpubl. data). Similarly, Brightsmith et al. (2005) attributed high survival of scarlet macaws (*Ara macao*) released in Costa Rica, in part, to the virtual absence of large avian predators in the vicinity of the releases. Clearly, the threat of predation must be taken seriously in psittacine reintroductions, and in those areas with high predation threat, either efforts to control or otherwise mitigate this danger should be implemented (e.g., trapping and translocation or lethal control of predators, aversion training of the potential prey), or alternative release sites should be chosen in areas with less predation threat.

For most reintroduced animals – particularly if captive-reared – the post-release provisioning of food (i.e., supplementary feeding) tends to aid transition to the new environment (e.g., Heath et al., 2008), and psittacines apparently are no exception. In this study, longer supplementary feeding times were associated with higher success. In Peru and Costa Rica, Brightsmith et al. (2005) credited extended periods of supplementary feeding with promoting site fidelity of released birds, increased social interactions, and accelerated integration of subsequently released birds into previously established flocks. In Puerto Rico, extended (i.e., >1 year) supplementary feeding of reintroduced Puerto Rican parrots resulted in increasingly higher survival of successive release cohorts, rapid formation of breeding pairs, and greater effectiveness of project personnel in monitoring released parrots (PRDNER, unpubl. data; THW, pers. obs.). In Australia, supplementary feeding greatly facilitated post-release monitoring of reintroduced orange-bellied parrots (*Neophema chrysogaster*), owing to the near impossibility of accurately observing colored leg bands on these diminutive (40–50 g) birds except at feeding stations (Smales et al., 2000b). In New Zealand, supplementary feeding of reintroduced kaka promoted site fidelity and facilitated post-release monitoring (Adams, 2005), and has improved survival and breeding success of reintroduced kakapo during short-term natural food scarcities (Elliot et al., 2006; but see Elliot et al. (2001) and Clout et al. (2002) for some caveats). Notwithstanding, high survival and subsequent success of released blue-and-yellow macaws (*Ara ararauna*) were attributed to habitat quality and low predation rather than to any effects of (minimal, e.g., 1 week) supplementary feeding (Plair et al., 2008). In this study, supplementary feeding was notably not a significant predictor of initial post-release survival, per se, but rather of the ultimate success of the reintroduction effort (see Tables 3, 6 and 7). This is because with highly social species, such as psittacines, supplementary feeding apparently promotes and facilitates site fidelity and flock cohesion, both of which contribute to the social interactions necessary for pair formation and subsequent breeding efforts, a key component of reintroduction success. Moreover, the establishment and maintenance of a resident flock may also promote higher long-term survival via increased antipredator vigilance (Westcott and Cockburn, 1988; Brightsmith et al., 2005; Caro, 2005; Beauchamp, 2008). When releasing parrots to augment existing wild populations however, supplementary feeding duration should be balanced with the need to optimize integration of released birds into wild flocks (see Sanz and Grajal, 1998; Collazo et al., 2000), and diligent monitoring of post-release behavioural interactions should be used to determine when and how such feeding should be curtailed.

Pre-release wild food training of psittacines is believed to facilitate recognition of appropriate food items, thereby improving post-release survival and adaptation to the release environment (e.g., Sanz and Grajal, 1998; White et al., 2005b). Of those reintroductions that utilized pre-release wild food training, about half were successful and half were not, suggesting that such training may be beneficial or necessary for some – but not all – efforts. However, we had no data on potential differences in the quality (e.g., number of wild food species and frequency provided) and/or total duration of food training amongst individual releases. For example, the flowers, fruits and seeds of 31 plant species were provided to captive-reared yellow-shouldered parrots (*Amazona barbadensis*) prior to release in Venezuela (Sanz and Grajal, 1998), whereas food training for thick-billed parrots consisted of providing the cones of five locally-occurring pines (*Pinus* spp.; Snyder et al., 1994). Interestingly, although no significant interactions were detected between FoodTrain and SupFeed (Table 3), successful reintroductions that used wild food training also tended to use longer supplementary feeding (19.5 ± 4.8 mos.), as opposed to that of unsuccessful efforts (7.9 ± 3.6 mos.), although this difference was not significant ($t = 1.95$; $df = 33$; $p = 0.06$). Therefore, it is possible that in some cases supplementary feeding may have mitigated potential deficiencies in pre-release food training. Thus, additional data are needed before definitive conclusions can be drawn on the effects of pre-release wild food training on psittacine reintroduction success.

Many previous assessments or reports of reintroductions have also attributed success to releases conducted within the core of the historic range of the species (e.g., Griffith et al., 1989; Wolf et al., 1996; Plair et al., 2008). This pattern did not hold true in our study. We found no relation between whether birds were released outside, on the periphery or in the core of their respective historic ranges. This finding is probably related to the innate adaptability of psittacines in general. Numerous psittacines – particularly those in the genera *Amazona* and *Aratinga* – have proven adept at establishing large feral populations in areas far removed from their native ranges (Cassey et al., 2004; Lever, 2005). In the case of the threatened red-crowned parrot (*Amazona viridigenalis*), the current feral populations in areas such as southern California and Florida, USA, now apparently exceed those within its native range in Mexico (BirdLife International, 2011). Thus, contrary to previous studies with other taxa, whether or not a release site is within the core of the historic range does not appear a significant predictor of psittacine reintroduction success.

Historically, most psittacine reintroduction plans have focused more on selection of the birds themselves and the actual process of preparing and releasing them than on selection of what is arguably the most important underlying component: the release site itself. Moreover, it is often assumed that the last known area occupied by a species or population prior to extirpation represented the 'best' habitat – and thus the 'best' site for reintroduction – when in fact such areas may simply have been by default the sole remaining refugium, as in the case of the El Yunque population of the Puerto Rican parrot (see Snyder et al., 1987; Trujillo, 2005; USFWS, 2009). Reintroduction of captive-reared Puerto Rican parrots in the higher-quality habitat of the karst forest region resulted not only in greater post-release survival, but also in greater numbers of breeding pairs than the relict wild population in the montane rainforests of El Yunque (USFWS, 2009; PRDNER, unpubl. data). In New Zealand, differences in breeding success of reintroduced kakapo have likewise been linked to local differences in habitat quality, with females being more successful in higher-qareas (Elliot et al., 2006; Whitehead et al., 2012). Indeed, the importance of habitat quality to reintroduction success has been a recurring theme in

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the literature (e.g., Griffith et al., 1989; Armstrong and McLean, 1995; Veltman et al., 1996; Wolf et al., 1996; Moorhouse et al., 2009; Ewen et al., 2012), yet current IUCN reintroduction guidelines (IUCN, 1998) place substantially more emphasis on selection and treatment of release stock, policy and legal issues and post-release monitoring than on selection of release sites. Based on our results, however, selection of high-quality release sites is a significant factor in psittacine reintroduction success, and the selection of inadequate sites may effectively undermine otherwise well-planned efforts. So, how does one objectively assess relative 'quality' of reintroduction sites?

An instructive and useful example of site quality assessment can be found in the recent selection of optimal reintroduction sites for a second and third population of Puerto Rican parrots (Trujillo, 2005; White et al., 2010). These sites were evaluated using SWOT ('Strengths, Weaknesses, Opportunities and Threats') analysis. SWOT analysis is an empirical method for evaluating risk in the environmental units of interest and allows predictions of future opportunities and threats. Originally developed for the business field (Martínez and Casas, 2002), SWOT analysis is only beginning to be applied to ecological problems (e.g., Ndenecho, 2009). The method is based on internal and external analyses of an environmental unit (e.g., release site), in which strengths are the inherent attributes or qualities of a site that justify its use for reintroduction. Weaknesses are the risks of losing these attributes to natural causes such as predation or environmental catastrophes (e.g., hurricanes, droughts). Threats are a measure of the decline in qualities by inadequate management or adverse surrounding conditions (e.g., resource extraction, urbanization), while opportunities include the potential for sustainable management of the area according to its strengths, weaknesses and threats (Trujillo, 2005). This analytical method has the advantages of simplicity, precision, broad applicability, and effective use of empirical data in conjunction with expert opinion. Importantly, it also provides an a priori mechanism for quantitatively evaluating management options in terms of their potential impact on release site quality (see White et al., 2010), and can be used for this purpose even if only one site is available for a given reintroduction. Such capability can be invaluable for properly and efficiently allocating scarce financial or biological resources, a common situation in psittacine reintroductions. Moreover, accurately identifying potential threats and weaknesses of a release site can provide valuable insights for prescribing appropriate pre-release treatments (e.g., aversion training, food training, nest boxes). Therefore, we recommend that future psittacine reintroductions use SWOT analysis to conduct thorough and comprehensive evaluations of potential release sites.

An implicit and important assumption of our study was that parrots were released in good physical condition and were disease-free. Although we were unable to rigorously test this assumption, we believe it is intuitively obvious that reintroductions should use only individuals that are healthy and in optimal physical condition. Releasing animals that are physically or immunologically compromised may undermine reintroduction efforts just as effectively as the selection of inadequate release sites. For example, Maloney and Murray (2000) reported that pre-release dietary deficiencies substantially reduced post-release survival of reintroduced black stilts (*Himantopus novaezelandiae*) in New Zealand. Also, although Snyder et al. (1994) reported predation as the primary cause of failed efforts to reintroduce thick-billed parrots, they also reported presence of pathogens (e.g., *Pastuerella* sp.) in release stock and suggested that disease may have also contributed to post-release mortality. Conversely, Hispaniolan parrots (*Amazona ventralis*) released in the Dominican Republic were subjected to systematic pre-release screening for potential avian pathogens, and no diseases were detected prior to release or documented as contributing to post-release losses (Collazo et al., 2000, 2003).

Finally, as acknowledged earlier, there have been more than 47 reintroductions of psittacines worldwide over the past 25 years. For a variety of reasons, however, many have been poorly documented either methodologically and/or regarding long-term results. This hampers efforts to rigorously assess relationships between treatments (i.e., methods) and outcomes (see Fischer and Lindenmayer, 2000; Sutherland et al., 2010; Ewen et al., 2012). Therefore, we strongly recommend that future psittacine reintroductions include not only a systematic and detailed documentation of all methods, but also a practical and effective plan for post-release monitoring (e.g., radio-telemetry, banding, standardized counts/surveys) that will provide the necessary information for accurately assessing both short- and long-term results. At a minimum, the collection of comparable data relative to the variables examined in this study will provide an invaluable route to more robust future assessments of psittacine reintroductions. Further, the dissemination of such information, either as formal, peer-reviewed publications or reports posted on stable websites, will also greatly enhance the value of future reintroductions to the conservation of psittacines worldwide.

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