# Predictors of avian and mammalian translocation success: reanalysis with phylogenetically independent contrasts

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## Abstract

We use the phylogenetically based statistical method of independent contrasts to reanalyze the Wolf, C.M., Griffith, B., Reed, C., Temple, S.A. (1996. Avian and mammalian translocations: update and reanalysis of 1987 survey data. Conservation Biology 10, 1142–1154). translocation data set for 181 programs involving 17 mammalian and 28 avian species. Although still novel in conservation and wildlife biology, the incorporation of phylogenetic information into analyses of interspecific comparative data is widely accepted and routinely used in several fields. To facilitate application of independent contrasts, we converted the dichotomous (success/failure) dependent variable (Wolf et al., 1996; Griffith, B., Scott, J.M. Carpenter, J.W., Reed, C., 1989. Translocations as a species conservation tool: status and strategy. Science 245, 477–480) into a more descriptive, continuous variable with the incorporation of persistence of the translocated population beyond the last release year, relative to the species' longevity. For comparison, we present three models: nonphylogenetic multiple logistic regression with the dichotomous dependent variable (the method used by Wolf et al. 1996 and Griffith et al. 1989), nonphylogenetic multiple regression with the continuous dependent variable, and multiple regression using phylogenetically independent contrasts with the continuous dependent variable. Results of the phylogenetically based multiple regression analysis indicate statistical significance of three independent variables: habitat quality of the release area, range of the release site relative to the historical distribution of the translocated species, and number of individuals released. Evidence that omnivorous species are more successful than either herbivores or carnivores is also presented. The results of our reanalysis support several of the more important conclusions of the Wolf et al. (1996) and Griffith et al. (1989) studies and increase our confidence that the foregoing variables should be considered carefully when designing a translocation program. However, the phylogenetically based analysis does not support either the Wolf et al. (1996) or Griffith et al. (1989) findings with respect to the statistical significance of taxonomic class (bird vs mammal) and status (game vs threatened, endangered, or sensitive), or the Griffith et al. (1989) findings with respect to the significance of reproductive potential of the species and program length. © 1998 Elsevier Science Ltd. All rights reserved.

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## 1. Introduction

Numerous methodological, environmental, species-specific, and population-level factors influence whether the intentional release of wild-caught or captive-reared animals into new locations will result in the successful establishment, re-establishment, or augmentation of a wild population. Because specific causal factors and their relative importance vary widely among such release programs (herein referred to as translocations, following Griffith et al., 1989; see also Wolf et al., 1996), it is difficult to identify general trends associated with success. Nevertheless, both theoretical considerations and empirical evidence suggest that some methodological and biological factors are of general importance. For example, such methodological details as raise and release procedures, number and composition of animals released, and choice of source stock for the released animals were shown to influence translocation outcomes in single-species studies (Beck et al., 1991; Allen et al., 1993; Reed et al., 1993; Bright and Morris, 1994; Veltman et al., 1996). Environmental factors perceived as

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important to success include general habitat quality and climatic conditions (Lindenmayer, 1994; Veitch, 1994), as well as the absence of predators or competitors (Crawley, 1986; Short et al., 1992). Some species-specific and population characteristics considered favorable for successful invasion of a new location include a relatively high reproductive potential, an omnivorous diet, small body mass, and high genetic diversity (Mayr, 1965; Laycock, 1966; Berger, 1972; Smith et al., 1976; Crawley, 1986; Ehrlich, 1986; O'Connor, 1986). The question remains: how universal is the influence of such methodological and biological factors? Also, in light of substantial case-by-case variations, are generalizations across a range of taxa possible?

Griffith et al. (1989) (see also Griffith et al., 1990, 1993) used a comparative approach to test for general patterns underlying the success vs failure of translocations among species of birds and mammals. They conducted surveys of translocation programs throughout North America, Australia, and New Zealand; coded the outcomes as either a success (reported establishment of a self-sustaining population), a failure, or incomplete; and used multiple logistic regression to identify seven statistically significant predictors of success: (1) taxonomic class (bird vs mammal), (2) legal status of the translocated species (native game vs threatened, endangered, or sensitive species), (3) habitat quality of the release area (excellent, good, or fair/poor), (4) location of the release area relative to the historical range of the species (core vs periphery or outside), (5) number of animals released ($\log_{10}$ transformed), (6) program length (number of years over which releases occurred), and (7) potential productivity of the translocated species (high vs low). Wolf et al. (1996) conducted a follow-up survey, in which they up-dated the status of the translocations in the Griffith et al. study, increased the number of programs available for multiple regression analyses from 155 to 181, and tested additional variables as predictors of success. Their results, using comparable analyses, were largely consistent with the findings of Griffith et al. (1989). Wolf et al. (1996) produced a model which contained the first five of the Griffith et al. variables (as listed earlier) plus adult diet of the species in the wild (herbivorous vs omnivorous vs carnivorous).

As was abundantly demonstrated in the last decade, interspecific comparisons are potentially compromised by statistical non-independence of species values (Felsenstein, 1985; Harvey and Pagel, 1991; Garland et al., 1993; Martins and Hansen, 1996). A simplified consensus view of the problem can be summarized as follows. Species are related to greater or lesser degrees, as indicated by their phylogenetic (evolutionary) relationships. Closely related species possess many characteristics, and sometimes much of their selective regime, that were inherited from common ancestors. As

a result of such inheritance, data for a series of species may contain hierarchical resemblances (e.g. snakes look like snakes, elephants look like elephants) and cannot be assumed to represent independent data points, a key assumption of both traditional parametric and nonparametric statistical methods. Detailed discussions of why closely related species tend to be similar are available elsewhere (Grafen, 1989; Brooks and McLennan, 1991; Harvey and Pagel, 1991; Eggleton and Vane-Wright, 1994; Martins, 1996a). In general, common effects of violating the assumption of independence include an inflation of Type I error rates when hypothesis testing (claiming statistical significance when none actually exists) and poor estimation of relationships among variables (and hence diminished predictive accuracy). The reality of these adverse statistical effects was demonstrated both analytically and by computer simulation studies (Felsenstein, 1985; Grafen, 1989; Martins and Garland, 1991; Garland et al., 1992, 1993; Pagel, 1993; Purvis et al., 1994; Díaz-Uriarte and Garland, 1996, in press; Martins, 1996b).

Inclusion of phylogenetic information in statistical analyses is now routine in such fields as behavioral and physiological ecology (Miles and Dunham, 1993; Garland and Carter, 1994; Losos and Miles, 1994; Díaz et al., 1996; Martin and Clobert, 1996; Martins, 1996a; Reynolds and Lee, 1996; Ricklefs and Starck, 1996; Williams, 1996; Abouheif and Fairbairn, 1997; Bauwens and Díaz-Uriarte, 1997; Price, 1997; Clobert et al., 1998). Although an historical, evolutionary approach may not initially seem germane to questions pertaining to contemporary wildlife translocation success, *all* interspecific (and many interpopulation) comparisons are potentially subject to phylogenetic influence in statistical tests. To illustrate, one might expect a translocation of bighorn sheep in Nevada to share inherent similarities with a translocation of bighorn sheep conducted elsewhere. Part of this similarity would be caused by general capture and release methodology, whereas part of this similarity would also be caused by biological characteristics of bighorn sheep (e.g. reproductive potential, social systems, disease susceptibility). Likewise, one might expect similarities between translocations conducted with closely related species (e.g. Prairie Chicken and Sharp-tailed Grouse), as compared with translocations involving more distantly related species (e.g. Canada Goose).

Although comparative biologists have long recognized that species should not be treated as independent data points, early proposed solutions to this problem, such as averaging within genera or choosing only one species per genus, are inadequate because they ignore potentially informative variation within phylogenetic lineages (clades), ignore hierarchical relationships among clades, and diminish statistical power (review in Harvey and Pagel, 1991). State-of-the-art phylogeneti-

cally based analyses allow incorporation of phylogenetic information without loss of statistical power (Martins and Garland, 1991; Garland and Adolph, 1994; Purvis et al., 1994; Martins, 1996b).

The present study, therefore, employs phylogenetically based statistical methods to reanalyze the Wolf et al. (1996) data set (104 avian and 77 mammalian translocation programs, representing 28 avian and 17 mammalian species). Felsenstein's (1985) method of phylogenetically independent contrasts, the first fully phylogenetic method to be proposed, is the best understood of available methods (Grafen, 1989; Martins and Garland, 1991; Garland et al., 1992; Pagel, 1993; Purvis and Garland, 1993; Purvis et al., 1994; Díaz-Uriarte and Garland, 1996, in press; Martins, 1996b; Martins and Hansen, 1996). Moreover, several free computer programs are available which implement the method (e.g. Joe Felsenstein's PHYLIP package, the PDAP package (Garland et al., 1993), CAIC (Purvis and Rambaut, 1995), COMPARE (Martins and Hansen, 1996)). In brief, the method of independent contrasts uses phylogenetic information (topology and branch lengths) to transform interspecific data (i.e. estimates of mean values for a series of species) into values (standardized independent contrasts) that, in principle, are independent and identically distributed, and hence can be analyzed with standard statistical methods (see Methods section for more details).

To facilitate application of phylogenetically independent contrasts, we used a more detailed indicator of translocation outcome as a dependent variable, rather than the dichotomous measure (success vs failure) used previously (Griffith et al., 1989; Wolf et al., 1996). We developed a continuous outcome variable that was a composite (see Methods section) of the following information: (1) the translocated population persistence (in years) in the field; (2) the classification of the population as self-sustaining, declining, or gone; and (3) the maximum potential life span (years) of each species as a scaling factor. The continuous dependent variable better meets assumptions of phylogenetically independent contrasts, and the inclusion of population persistence information provides a more quantitative measure of the population's ability to persist through time. In principle, this more inclusive dependent variable should increase statistical power to detect significant predictors of 'success.'

## 2. Methods

### 2.1. The data

The up-dated avian and mammalian translocation data used by Wolf et al. (1996) in the multiple logistic regression models were also used in this study. Of the 421 targeted avian and mammalian translocations throughout North America, Australia, and New Zealand, 181 programs were used by Wolf et al. (1996) in the logistic analyses. Within the sample of 181 translocations, 122 were classified as successful and 59 as unsuccessful; 104 involved translocations of birds and 77 of mammals; and 24 programs released captive-reared animals, 141 released wild-caught animals, and 16 released a mixture of captive-reared and wild-caught animals. Ninety translocations were common to both the Griffith et al. (1989) and Wolf et al. (1996) multiple regression model-building samples.

Both the application of phylogenetically independent contrasts and ordinary multiple regression analyses generally require a continuous dependent variable (Felsenstein, 1985; Grafen, 1989; Garland et al., 1992; but see simulation results in Ridley and Grafen, 1996). We therefore developed a composite, continuous dependent variable representing the outcome of the translocation programs. Because the successful establishment of a population ultimately depends upon its ability to persist through time, the composite dependent variable incorporated the following two features of the translocated population: (1) its persistence (years) in the field since the year of the last release of animals; and (2) its classification (by the survey respondent) as self-sustaining, declining, or gone (following the criteria for the dichotomous dependent variable used by Griffith et al. (1989) and Wolf et al. (1996), with the further distinction of the unsuccessful programs into 'declining' and 'gone' categories). The persistence of a translocated population was divided by the maximum potential life span (years) of an individual of the species in the wild to scale for the wide variability (5–50 yr) in species' longevity. To be conservative in our scaling of the dependent variable, we used maximum (as opposed to mean) life expectancy in the wild to account for the longest possible time that the original released individuals could have remained in the area. Therefore, populations which persist beyond the maximum expected life span are likely sustaining through reproduction (or through ingress from other populations).

Actual construction of the outcome variable was as follows. After dividing the population persistence by the longevity estimate for the species, the resulting ratios were arranged in ascending order within each of the three status categories (self-sustaining, declining, and gone). To eliminate overlap between the three categories (e.g. self-sustaining populations could have the same persistence/longevity ratios as populations which are now gone), the highest persistence/longevity ratio in the 'gone' group was added to all of the ratios in the 'declining' group. In this way, programs with low persistence ratios and declining populations have a higher outcome score than populations that have already disappeared. Then, the highest ratio for the 'declining' group (which now includes the highest value for the 'gone' group) was added to all of the ratios in the 'self-sustaining' group.

## 2.2. Phylogenetic 'transformation'

Phylogenetically based statistical methods require specification of the topology (branching order) and branch lengths of the phylogenetic tree for the species in the study. The interspecific topology and branch lengths depicted in Fig. 1 is a composite of information drawn from a variety of studies in the literature, representing molecular, morphological, and paleontological information (predominant sources include Li et al., 1990; Sibley and Ahlquist, 1990; Wayne et al., 1991; Garland et al., 1993; see Appendix for a detailed description of the tree derivation).

In the analyses, each tip on the phylogenetic tree represented a separate translocation program (as indicated by separate questionnaires). Where more than one translocation was conducted with the same species, we represented the within-species branching order as a polytomy (multifurcation) of the distinct translocated populations. In effect, intraspecific populations were assumed to have diverged from a common ancestral population more-or-less instantaneously (termed a 'hard' polytomy; see Purvis and Garland, 1993). This is appropriate because many programs combined more than one source stock of animals. For some programs, mixing of the source stock was done intentionally in an effort to 'increase the genetic diversity' of the translocated animals.

Felsenstein's (1985) method of phylogenetically independent contrasts is intended to transform comparative data so as to make them independent and identically distributed, as is assumed by most conventional statistical methods. The method works as follows (see Felsenstein, 1985; Garland et al., 1992 for more details; and Garland and Adolph, 1994 for worked examples). Firstly, for a given variable, the datum at a given tip of the phylogenetic tree is subtracted from the value for its closest relative in the data set. For example, we might subtract the value of the outcome variable for the bird *Telespiza ultima* from the value for *T. cantans* (Fig. 1). The direction of subtraction is arbitrary (Garland et al., 1992). This difference would constitute one 'contrast'. The reason for computing contrasts is to transform the data to make them independent in the statistical sense. The rationale is that any difference between, say, *T. ultima* and *T. cantans* depends only on evolutionary events that have occurred since they diverged from their last common ancestor and is independent of other such differences (e.g. between the two *Anas* species).

Secondly, a contrast is standardized by division by the square root of the sum of its branch lengths (its standard deviation, under the assumptions that evolution was similar to a Brownian motion process and that the available branch lengths are proportional to expected variance of trait evolution). The standardization is intended to bring all contrasts to a common variance,

such that they can be considered 'identically distributed', another common assumption of most statistical procedures. The rationale for standardizing by branch lengths (i.e. computing a ratio; see Garland, 1992) is that contrasts involving relatively long divergence times (e.g. *Nyctanassa violacea* and *Puffinus puffinus*) are likely to show greater phenotypic divergence than are contrasts that involve recent divergences (e.g. *T. ultima* and *T. cantans*).

Thirdly, the foregoing computations would be repeated for all such pairs of tip species (e.g. for the two *Anas* species, for *N. violacea* and *P. puffinus*). For many of the 45 species shown as tips in Fig. 1, the species is actually represented in our data set by multiple translocation programs (e.g. two programs for the mouse *Peromyscus polionotus*, 10 programs for the otter *Lutra canadensis*, 35 programs for the wild turkey *Meleagris gallopavo*). As noted earlier, for the actual analyses, these conspecific programs were represented as polytomies (i.e. small 'stars' of equal-length branches descending from the tip node). Computations of contrasts within these 'hard' polytomies were done following Felsenstein (1985) and Purvis and Garland (1993). It is important to note that independent contrasts applied to a 'star' phylogeny result in estimates of correlations, regressions, etc., that are *exactly* the same as conventional correlations or regressions (Purvis and Garland, 1993).

Lastly, after contrasts are computed for pairs of tip species (or for programs within a given species), contrasts between internal nodes (branching points) are computed. Values at internal nodes are estimated as the weighted (by branch lengths) mean of the descendants of that node, whether they be two tip species (measured values), one tip value and one estimated nodal value, or two estimated nodal values (see Felsenstein (1985) for details). (Branches below internal nodes in the phylogenetic tree are lengthened to reflect the fact that values at nodes are estimates, not data, and so contrasts involving internal nodes should be devalued [receive lower weight] in statistical analyses; see Felsenstein, 1985). This procedure continues all the way down to the root (basal node) of the tree, and ultimately produces $n-1$ contrasts, where $n$ is the number of original tip data points (181 for the present study). Note that the contrast at the very bottom of the tree (the root or basal contrast — not shown in Fig. 1) constitutes a general comparison between the birds and mammals (Garland et al., 1993; Clobert et al., 1998). Thus, a test of its statistical significance by use of a 0–1 dummy variable is equivalent to a test comparing the mean translocation success of birds and mammals (after adjusting for other variables in the model).

The logic behind phylogenetically based analytical methods, of which independent contrasts is the best understood (review in Martins and Hansen, 1996), is

**A**



| | |
|---|---|
| 2 | *Pandion haliaetus* |
| 8 | *Haliaeetus leucocephalus* |
| 9 | *Falco peregrinus* |
| 1 | *Nyctanassa violacea* |
| 1 | *Puffinus puffinus* |
| 1 | *Himantopus novaezelandiae* |
| 2 | *Fratercula arctica* |
| 1 | *Grus canadensis* |
| 1 | *Callaeas cinerea* |
| 5 | *Creadion carunculatus* |
| 3 | *Notiomystis cincta* |
| 2 | *Atrichornis clamosus* |
| 2 | *Bowdleria punctatus* |
| 1 | *Telespiza ultima* |
| 1 | *T. cantans* |
| 2 | *Athene cunicularia* |
| 1 | *Cynanoramphus unicolor* |
| 3 | *C. novaezelandiae* |
| 1 | *Amazona vittata* |
| 1 | *Picoides borealis* |
| 1 | *Anas fulvigula* |
| 1 | *A. laysanensis* |
| 10 | *Branta canadensis* |
| 2 | *Cygnus cygnus buccinator* |
| 35 | *Meleagris gallopavo* |
| 4 | *Bonasa umbellus* |
| 2 | *Tympanuchus phasianellus* |
| 1 | *T. pallidicinctus* |

85 80   70   60   50   40   30   20   10   0
MILLIONS OF YEARS AGO

**B**

| | |
|---|---|
| 4 | *Phascolarctos cinereus* |
| 2 | *Myrmecobius fasciatus* |
| 1 | *Cynomys ludovicianus* |
| 4 | *Sciurus niger cinereus* |
| 1 | *Neotoma floridana* |
| 2 | *Peromyscus polionotus* |
| 1 | *Leontideus rosalia* |
| 10 | *Lutra canadensis* |
| 4 | *Martes americana* |
| 1 | *Canis rufus* |
| 1 | *Tayassu tajacu* |
| 3 | *Oreamnos americanus* |
| 16 | *Ovis canadensis* |
| 14 | *Antilocapra americana* |
| 6 | *Cervus elaphus* |
| 2 | *Rangifer tarandus* |
| 5 | *Odocoileus virginianus* |

110  100   90   80   70   60   50   40   30   20   10   0
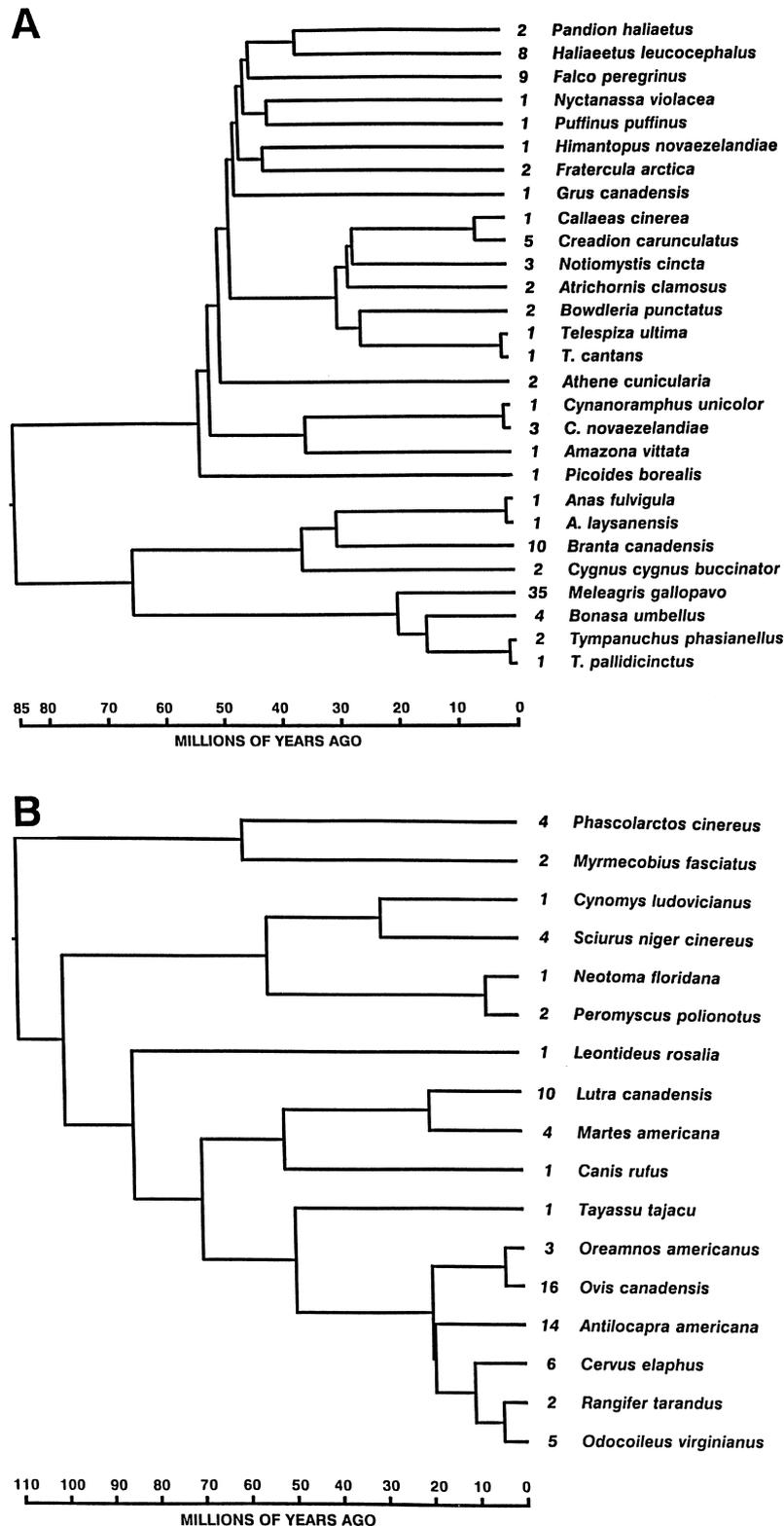MILLIONS OF YEARS AGO

Fig. 1. Composite hypothesis of phylogenetic relationships for the 28 avian and 17 mammalian species (181 translocation programs) represented in our data set. Appendix provides a description of and the sources for the compilation of this phylogeny. Numbers at tips represent the number of translocation programs in our data set for a given species. Not shown are the polytomous relationships between conspecific translocations, which, for computation of phylogenetically independent contrasts (see Methods section), were achieved by setting internodal branch lengths to zero (see Felsenstein, 1985; Purvis and Garland, 1993) and tip branch lengths equivalent to a divergence time of 1 yr. This arbitrary, small number signifies an expectation of similarity among conspecific translocations relative to programs conducted with different species. Also not shown is a connecting branch between the birds and mammals (their divergence, from ancestral reptiles, was estimated at 270 million years ago).

that species inherit genotypes, phenotypes, and to some extent habitats from their ancestors. Thus, biological variables (e.g. body mass) will tend to 'follow phylogeny'. However, many of the independent variables used in the present analysis are not biologically inherited: (1) the purpose of the translocation as either the establishment of a new population, the reestablishment of an extirpated population, or the augmentation of a critically small population; (2) the range of the release area in relation to the historical distribution of the species; (3) the status of the translocated species; (4) the number of animals released; (5) the number of separate release events; (6) the presence or absence of potential competitors on the release site; (7) the source of the translocated animals; (8) program length; (9) whether the translocated animals were released the same day as transport or some time later; (10) whether the release was 'hard' or 'soft'; (11) whether or not the release was onto an island; (12) the quality of the habitat into which the release occurred; (13) and whether or not the habitat was artificially improved prior to release. For such variables, it makes no sense to place them on a hierarchical phylogeny. Instead, for non-biological independent variables, we collapsed (by setting internal branches to zero length) the phylogenetic tree shown in Fig. 1 to create one large polytomy (a 'star' phylogeny) for all 181 translocations. Because non-species-specific variables are neither genetically based nor inherited through phylogeny, a polytomy signifies, in effect, equal-relatedness and, hence, independence among the translocations for those variables. The phylogenetic topology still exists within this polytomy (see Felsenstein, 1985; Purvis and Garland, 1993), which thus preserves contrast computation order and allows incorporation of such variables into an analysis with other variables whose contrasts were computed on a non-star, hierarchical phylogeny.

A non-star, hierarchical phylogeny was used to calculate the independent contrasts for the dependent and biologically based (phylogenetically inherited) independent variables (i.e. taxonomic class, adult diet in the wild, potential productivity, mean adult body mass, and migratory behavior). Branch lengths were checked for statistical adequacy as described by Garland et al. (1992); see also Díaz-Uriarte and Garland, 1996, in press). These graphs indicated that contrasts computed with all (non-zero) branch lengths equal to one yielded adequate standardization for each of the species-specific variables. Thus, contrasts for the dependent variable and all phylogenetically inherited variables were computed with equal-length branches, not those shown in Fig. 1.

PDTREE (Version 2) of the Phenotypic Diversity Analysis Program (PDAP, Garland et al., 1993) was used for computation of the independent contrasts. These values were then input to SPSS/PC+ version 5.0

(Norusis, 1992a,b) for subsequent statistical analyses (e.g. multiple regression through the origin).

## 2.3. Statistical analyses

To facilitate comparison with the previous study (Wolf et al., 1996) and to understand differences between the analytical modes, we emphasized three models: nonphylogenetic multiple logistic regression with the original dichotomous dependent variable, nonphylogenetic multiple regression with the new continuous dependent variable, and multiple regression using phylogenetically independent contrasts with the continuous dependent variable. Each of the models was for the entire data set (i.e. all 181 avian and mammalian programs). Eighteen candidate-independent variables were evaluated in the multiple regression analyses, including all but one of the independent variables considered by Wolf et al. (1996). (The species' potential maximum life span was not used as a candidate independent variable because this information was included in the new composite dependent variable.)

Following Wolf et al. (1996), the multiple regression models were derived using a stepwise selection procedure (forward selection with an option for removal; significance was evaluated at $p \leq 0.05$ for entry and $p \leq 0.051$ for removal). All first-order interaction terms of the model parameters were checked for statistical significance. For the phylogenetically based model, regressions were computed through the origin, as required by independent contrasts (Garland et al., 1992). Assumptions (e.g. normality, heteroscedasticity) of the multiple linear regressions were checked. Normal probability and detrended normal probability plots of the deviances were used to examine the distribution of the residuals (Draper and Smith, 1981). Plots of Cook's distance statistic and centered leverage values against case numbers allowed for identification of influential points. (Note: influential or 'leverage' points may not be identified by residual diagnostics alone (Draper and Smith, 1981)). All pairwise correlations (calculated through the origin for the independent contrasts), variance inflation factors (VIF), and eigenvalues were examined for evidence of multicolinearity (Draper and Smith, 1981; Montgomery and Peck, 1992). We also conducted tests for different slopes and mean values between the birds and mammals (see Garland et al., 1992, 1993; Clobert et al., in press). Final model selection was based on the statistical significance of model parameter estimates and whether the regression coefficients were robust following identification of influential points.

To allow direct comparisons, the three models are presented with the same independent variables; thus, we forced into each model any variable that emerged as significant in any one of the other two model types. In

general, comparisons between the two nonphylogenetic models (logistic and ordinary multiple regressions) should indicate the effects of our rescoring of the success variable, whereas comparisons of the nonphylogenetic ordinary regression and the regression using independent contrasts should indicate the effects of incorporating phylogenetic information.

In addition to the forced inclusion of two variables, the nonphylogenetic logistic regression model was modified from the combined avian and mammalian model presented by Wolf et al. (1996), their table 3) in the following ways: the golden lion tamarin translocation (a statistically influential point) was retained, indicator (as opposed to deviation) coding was used (Norusis, 1992a), and the variable for habitat quality was treated as continuous ($0 = $ poor, $1 = $ good, $2 = $ excellent). These modifications change the appearance of the model, including the presentation of the coefficients, but, with one exception, do not alter the general interpretations of the model presented in Wolf et al. (1996), their table 3). As a result of these modifications, animals with a carnivorous diet appear to be as successful as those with an omnivorous diet (the difference in the partial regression coefficients is negligible, $B_{\text{carnivorous}} - B_{\text{omnivorous}} = 0.062$), both being significantly more successful than herbivores.

## 3. Results

After converting the dichotomous dependent variable (success vs failure) into a composite, continuous variable (see Methods section), the nonphylogenetic ordinary stepwise regression produced a model with five main-effect variables and one first-order interaction term: habitat quality ($B = 0.252$, $p = 0.0176$, where $B$ equals the partial regression coefficient), migratory behavior ($B = -0.504$, $p = 0.0021$), status ($B = 0.551$, $p = 0.0002$), range ($B = 2.332$, $p < 0.0001$), number of animals ($B = 0.954$, $p < 0.0001$), and range × number of animals ($B = -0.920$, $p = 0.0003$) (model $r^2 = 0.31$, $F = 12.911$, $p < 0.0001$). Thus, this model contained four of the six variables included in the multiple logistic regression model of Wolf et al. (1996). Although taxonomic class (bird vs mammal) and diet were not included in the initial model using the stepwise algorithm, they had statistically significant coefficients when forced into the model (Table 1, second column; combined $p$ for the two diet dummy variables was determined using the TEST subcommand in SPSS/PC+). Migratory behavior had a negative coefficient sign, suggesting that nonmigratory animals were more likely to establish self-sustaining populations when translocated; however, this variable was statistically nonsignificant with diet and class forced into the model (Table 1, second column). Thus, the two nonphylogenetic models, one with a dichotomous and the other with a continuous dependent variable, were highly consistent.

The initial phylogenetically based model, derived from ordinary stepwise regression (through the origin) with the independent contrasts, contained three main-effect variables and one first-order interaction term: omnivory ($B = 0.857$, $p = 0.0332$), range ($B = 0.450$, $p = 0.0008$), number of animals ($B = 0.226$, $p = 0.0191$), and range × number of animals ($B = 0.382$, $p = 0.0347$) (model $r^2 = 0.13$, $F = 6.688$, $p < 0.0001$). For comparability with the derivation of the logistic regression model (where the SPSS/PC+ procedure automatically codes indicator variables and assesses their fit as a unit), the indicator variable for carnivory was then forced into the model. With both the omnivory and carnivory indicator variables in the phylogenetically based model, the combined influence of diet was no longer statistically significant ($p = 0.0756$, as determined using the TEST subcommand in SPSS/PC+). With the subsequent removal of both diet indicator variables from the model, habitat quality entered into the model as a statistically significant predictor, producing the model: habitat quality ($B = 0.184$, $p = 0.0421$), range ($B = 0.418$, $p = 0.0020$), number of animals ($B = 0.214$, $p = 0.0266$), and range × number of animals ($B = 0.474$, $p = 0.0094$).

The foregoing indicates that three variables entered by stepwise model-building procedures into all three multiple regression models (logistic, ordinary, phylogenetically independent contrasts): the number of animals released, the range of the release area, and habitat quality. For more direct comparison of the three models, they are presented in Table 1 containing the same eight independent variables. Forcing variables into the models alters the partial regression coefficients, $p$ values, and model-fit statistics; however, this enables comparison of the relative size of the $p$ values for specific independent variables and, to a certain degree, permits interpretation of the relative importance of variables across the different models. Notable differences between the two nonphylogenetic models and the phylogenetic model are the lack of significance of taxonomic class, diet, and status (Table 1). (Although omnivory alone was initially significant in the phylogenetically based model, the combined influence of omnivory plus carnivory was statistically nonsignificant.)

Of the 45 species represented in our data set (see Fig. 1), five were represented by a sufficient number of programs ($\geq 10$) to evaluate intraspecific correlations of translocation success. Of those five species, however, only two exhibited sufficient variation for both independent and dependent variables. In the logistic regression model for bighorn sheep ($n = 16$ programs), type of release was a significant predictor of translocation success ($B = -5.804$, $p = 0.0032$); that is, 'hard' releases (no provisioning of food or water) were more successful for this species. For pronghorn ($n = 14$ programs), logistic

Table 1
Model coefficients and statistics of combined avian and mammalian translocations using nonphylogenetic multiple logistic regression, nonphylogenetic ordinary multiple regression (with a composite, continuous dependent variable), and ordinary multiple regression with phylogenetically independent contrasts[a]

| Variable | Nonphylogenetic | | | | Regression of Phylogenetically Independent Contrasts[c] | |
| | Logistic Regression[b] | | Ordinary Regression[c] | | | |
| | $B$ | $p$ | $B$ | $p$ | $B$ | $p$ |
|---|---|---|---|---|---|---|
| Taxonomic Class | 1.181 | 0.0231 | 0.413[d] | 0.0262 | 0.028[d] | 0.9735 |
| Diet | | 0.0003 | | 0.0414 | | 0.1135 |
|   Carnivorous | 2.070 | | 0.275[d] | | −0.558[d] | |
|   Omnivorous | 2.008 | | 0.551[d] | | 0.539[d] | |
| Migratory | −0.532[d] | 0.2936 | −0.332 | 0.0746 | −0.140[d] | 0.5360 |
| Status | 1.967 | 0.0001 | 0.513 | 0.0055 | 0.093[d] | 0.4651 |
| Habitat Quality | 0.817 | 0.0098 | 0.209 | 0.0500 | 0.176 | 0.0570 |
| # Animals ($\log_{10}$) | 2.512 | 0.0001 | 1.018 | <0.0001 | 0.190 | 0.0592 |
| Range | 3.847 | 0.0119 | 2.269 | <0.0001 | 0.400 | 0.0033 |
| Range × # Animals | −1.415[d] | 0.1023 | −0.907 | 0.0003 | 0.415 | 0.0296 |
| Constant | −7.777 | | −0.413 | | — | |
| **Model Statistics** | | | | | | |
| $X^2$ | 74.637 (9df) | | | | | |
| $p$ value | <0.0001 | | | | | |
| $r^2$ | | | 0.3365 | | 0.1599[e] | |
| $F$ | | | 9.638 | | 3.617 | |
| $p$ value | | | <0.0001 | | 0.0004 | |

[a] $n = 181$ translocation programs or 180 phylogenetically independent contrasts.
[b] Compare with Wolf et al. (1996); regression coefficients and statistics differ for reasons discussed in text.
[c] Produced with a composite, continuous dependent variable.
[d] Not an original variable for this model; forced into the model for comparison with the other two models. Parameter estimates without footnote were statistically significant ($p \leq 0.05$) prior to the forced inclusion of additional variables.
[e] Regression of independent contrasts is computed through the origin; therefore, the $r^2$ is not comparable with the nonphylogenetic model $r^2$.

regression indicated that habitat improvement was negatively associated with success ($B = -10.491$, $p = 0.0073$). These intraspecific results appear to be nonintuitive and suggest that further investigations are necessary to understand the relationship between the dependent and independent variables. Hence, although it is possible to identify general predictors of translocation success, practitioners are cautioned that such results may or may not apply to any particular species.

## 4. Discussion

Complicated biological questions and associated data sets can be analyzed in many different ways. Often, little consensus exists as to the 'best' way to analyze a particular type of data. The application of different analytical methods to a single data set is, therefore, prudent. To the extent that different analytical techniques lead to similar conclusions, then we may have enhanced confidence in those conclusions.

With respect to interspecific comparative studies, a flurry of research activity since Felsenstein's (Felsenstein, 1985) seminal paper has led to a consensus that

phylogenetic information should be incorporated into analyses (Brooks and McLennan, 1991; Harvey and Pagel, 1991; Eggleton and Vane-Wright, 1994; Martins, 1996a). We have, therefore, reanalyzed the data set of Wolf et al. (1996) with the method of phylogenetically independent contrasts. Our reanalysis supports several of the more important conclusions of Wolf et al. (1996), and of the original paper by Griffith et al. (1989), but also indicates some important differences.

Table 1 shows that habitat quality at the release site, the number of animals released, and release into an area within the core of the species' historical distribution were positively associated with success in avian and mammalian translocation programs, irrespective of the type of multiple regression analysis employed. All three of these independent variables are under the control of translocation practitioners. Thus, our phylogenetic analysis increases our confidence that these variables should indeed be considered carefully when designing an avian or mammalian translocation program.

Habitat quality was emphasized as an essential component of translocation success by innumerable other authors (Dodd and Seigel, 1991; Jackson, 1994; Lindenmayer, 1994; Wilson and Stanley Price, 1994;

Armstrong and McLean, 1995; Veltman et al., 1996). Indeed, suitable habitat quality (and quantity) relative to the requirements of the translocated species was the factor most often cited as influencing translocation outcome by our survey respondents (Wolf et al., 1996, their table 4). In contrast, 64% of the Wolf et al. (1996) survey respondents reported that they based their evaluation of the habitat quality on their subjective opinion alone. (The remaining 36% of the respondents incorporated some quantitative assessment of the habitat quality.) Nevertheless, given the consistency of habitat quality as an important correlate of successful translocations, we agree with Lindenmayer (1994), Armstrong and McLean (1995), and others who recommend that translocation protocols should incorporate rigorous, quantitative assessments of habitat quality.

The total number of animals released over the duration of a translocation program also remained a consistent predictor of translocation success, irrespective of analytical technique (Griffith et al., 1989; Wolf et al., 1996; this study). Although populations were established with an extremely small number of individuals (see examples in Copley, 1994), the consistency of our results supports the notion that adverse demographic and environmental stochastic effects are more prevalent in small populations. As discussed by Wolf et al. (1996), however, determination of some minimum viable number of animals to release will depend on the unique circumstances of each translocation. Computer programs that analyze population viability under diverse conditions may provide helpful minimum population size estimates. One admonition to translocation practitioners is not to mistake a high density of animals present as necessarily indicating a self-sustaining population. By including duration of a population's persistence in our outcome variable, we presumably have reduced potential effects of over-reporting of self-sustaining translocation populations by respondents. This is an important consideration because the average population of translocated animals reported on by survey respondents had not persisted (since the last release) longer than the maximum expected life span of the translocated species in the wild.

Release of translocated animals into the core of the species' historical range was the third consistent predictor of success in both nonphylogenetic and phylogenetic analyses. As noted in Wolf et al. (1996), our findings appear to contradict Lomolino and Channell (1995) recommendations, which were derived from their observation that declining terrestrial mammals tend to persist on the periphery of their historical range. However, our findings do support a study by Nathan et al. (1996), in which they conclude that peripheral bird populations are more vulnerable to extinction. With all else held equal (e.g. habitat quality), our results suggest that animals released into the core of their historical

distribution should have a greater chance of persisting and establishing a self-sustaining population.

Unlike the previous analyses (Griffith et al., 1989; Wolf et al., 1996), the phylogenetically based statistical model indicated that translocations involving mammals did not have statistically higher average success rates than those which involved birds. This difference cannot be attributed to our recoding of success into a composite, continuous variable, because the conventional multiple regression (Table 1, second column) also indicated taxonomic class as a significant predictor of success. Instead, the difference was likely caused by the fact that mammals and birds constitute two distinct clades, and hence all of the information pertaining to a possible difference in mean value was encapsulated in a single independent contrast connecting the roots of the mammalian and avian phylogenetic trees (Garland et al., 1993). The drastic difference in $p$ values between the nonphylogenetic and phylogenetic analyses with respect to taxonomic class (Table 1) is consistent with a methodological paper in which home range areas of mammalian Carnivora and ungulates were compared (Garland et al., 1993; and see Reynolds and Lee, 1996, for a similar example). Whenever single evolutionary events are involved (e.g. the ancient divergence between birds and mammals), it may be exceedingly difficult to demonstrate statistically significant effects (see Garland and Adolph, 1994; Martins and Hansen, 1996; Ricklefs and Starck, 1996).

Also, unlike the previous nonphylogenetic analysis (Wolf et al., 1996 and Table 1, first column), neither diet nor status was a statistically significant predictor of translocation success in the phylogenetic model. However, the omnivory indicator variable exhibited statistical significance $(p < 0.05)$ in an early-stage phylogenetic model without the complementary carnivory indicator variable, thus providing some evidence that omnivores were generally more successful than animals of the other two diet categories. Moreover, the significance level for diet in the phylogenetic model $(p = 0.1135)$ was not that much different from the ordinary regression $(p = 0.0414)$. The difference between the nonphylogenetic logistic regression and the phylogenetically based regression with respect to status again cannot be attributed to our recoding of success, because the conventional multiple regression also indicated statistical significance (Table 1).

Significant model parameters in the Griffith et al. (1989) study, program length (number of years over which releases occurred) and species' reproductive potential were not found to be significant predictors of translocation outcome in either the phylogenetic or nonphylogenetic multiple regressions in Wolf et al. (1996) or this study (see Wolf et al. (1996) for further discussion).

We close by noting an important caveat concerning the present data set: it is not necessarily representative

of birds and/or mammals in general. Extant birds and mammals comprise over 9 000 and 4 000 recognized species, yet were represented here by only 28 (0.3%) and 17 (0.4%) species, respectively. Many major lineages were entirely absent, such as hummingbirds, flycatchers, bats, cats, and whales. Moreover, some species were represented by multiple programs, most notably the wild turkey, which accounted for 19% of the 181 data points. These 35 data points can have a considerable impact on the statistical models. For example, when turkey programs were omitted from the non-phylogenetic ordinary multiple regression analysis (Table 1, second column), both diet ($p = 0.4198$) and status ($p = 0.1383$) became statistically nonsignificant. In the logistic regression (Table 1, first column), both variables also became less significant (diet $p = 0.0170$; status $p = 0.0553$). Because we were constrained for reasons of comparability with Griffith et al. (1989) and Wolf et al. (1996) and because many translocations in the original surveys had undetermined outcomes, many species were not included in our model building data set. Future comparative papers on translocations should, therefore, focus on improving the phylogenetic 'evenness' of species represented.

## 5. Conclusion

Although routinely employed in other disciplines, phylogenetically based statistical analyses are virtually nonexistent within such fields as conservation biology and wildlife management. Yet conservation and wildlife biologists often make interspecific comparisons. The same resemblances among closely related species that are often exploited by wildlife biologists for guidance in developing methodological protocols can confound traditional correlational and regression analyses of multi-species data sets. Species are related to greater or lesser degrees, depending on their phylogeny, and so do not necessarily offer independent or identically distributed data points, both of which are assumptions of conventional statistical analyses. Although conventional statistical analyses can be used to suggest important predictor variables in an interspecific comparative data set (Griffith et al., 1989; Wolf et al., 1996), phylogenetically based procedures are theoretically more reliable in terms of both hypothesis testing and parameter estimation. In any case, the different statistical methods presented in this study yielded congruent results (see also Ricklefs and Starck, 1996; Price, 1997) with respect to three variables associated with translocation success: the habitat quality of the release location, the number of individuals released, and the range of the release area relative to the historical distribution of the species.

Although still somewhat experimental, phylogenetic methods are continually being developed and refined,

and our understanding of comparative statistical methods has risen dramatically in the past decade. We strongly encourage conservation and wildlife professionals to consider application of phylogenetically based statistical methods in future analyses of comparative data sets.

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# Appendix

Table A1
Sources used to derive the topology and divergence times of the phylogenetic tree in Fig. 1[1]

| Lineage Divergence | Date (MYA) | Source[1] |
|---|---|---|
| Aves/Mammalia | 270 | Li et al., 1990 |
| Avian Taxa | | |
| *Callaeas/Creadion* | 5 | (arbitrary date) |
| *Telespiza ultima/T. cantans* | 1 | (arbitrary date) |
| *Cynanoramphus unicolor/C. novaezelandiae* | 1 | (arbitrary date) |
| *Anas fulvigula/A. laysanensis* | 1 | (arbitrary date) |
| *Meleagris/Bonasa, Tympanuchus* | 20 | (arbitrary date) topology, Johnsgard, 1973 |
| *Bonasa/Tympanuchus* | 15 | Johnsgard, 1973 (mid-Miocene for earliest fossil of *Tympanuchus*) |
| *Tympanuchus pallidicinctus/T. phasianellus* | 1 | (arbitrary date) |
| Mammalian Taxa | | |
| Marsupialia/Eutheria | 110 | J.A.W. Kirsch, pers. comm. (100–110 MYA) Novacek, 1992b (130 MYA) Rowe, 1993 (95–100 MYA) |
| Phascolaretidae/Myrmecobiidae | 60 | J.A.W. Kirsch, pers. comm. |
| Rodentia/Primates,Carnivora,Artiodactyla[2] | 100 | Li et al., 1990 (81–100 MYA) Easteal, 1990 (topology) Janke et al., 1994 (114 ± 15 MYA) |
| Sciuridae/Muridae | 55 | Sarich, 1985 |
| *Peromyscus/Neotoma* | 7.3 | Catzeflis et al., 1993 |
| *Cynomys/Sciurus* | 30 | Hafner, 1984 (near the end of the Oligocene) |
| Primates/Carnivora,Artiodactyla | 85 | Li et al., 1990 (65–85 MYA) Janke et al., 1994 (93 ± 12 MYA) |
| *Lutra/Martes* | 20 | Kurtén and Anderson, 1980 (lower Miocene for earliest occurance of *Martes*) |

[1] Sources reported are those other than Sibley and Ahlquist (1990) and Garland et al. (1993). The DNA–DNA hybridization study of Sibley and Ahlquist (1990) served as the primary source for the avian taxa. Branch lengths were based on the mean $\Delta T_{50}H$ values provided by Sibley and Ahlquist (1990); each $\Delta T_{50}H$ value was multiplied by a calibration constant between 2 and 4.5 for conversion to an estimated divergence time. Calibration constants vary because the rate of DNA evolution differs among lineages; those used for Fig. 1 were approximated to accommodate the $\Delta T_{50}H$ branching order and the tentative rates of evolution for specific lineages and the fossil record as discussed by Sibley and Ahlquist (1990). Bleiweiss et al. (1994, 1995) supported our use of the Sibley and Ahlquist phylogeny for the branching order between the Passeriformes, Strigi-formes, Piciformes, Anseriformes, and Galliformes. Although Livezey (1986) hypothesized a conflicting phylogenetic tree for the Anseriform genera based on 120 morphological characters (showing *Branta* more closely related to *Cygnus* than with *Anas*), we chose to use the molecularly-based analyses of Sibley and Ahlquist (1990). Garland et al. (1993) and sources therein as the primary source for the mammalian taxa. If divergence times were not available from the literature, we assigned arbitrary divergence times of 1 MYA (million years ago) between congeneric species and 5 or 20 MYA between species within the same family. The estimated divergence times were used to test for the adequacy of the branch lengths for statistical analyses (see Garland et al., 1992). The virgule (/) represents the tree node separating the taxon (a) on its right and left (refer to Fig. 1).
[2] For contradicting branching order, see also Novacek, 1992a,b and Johnson et al. (1994).