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Factors influencing the clutch size, number of broods and annual fecundity of North American and European land birds

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ABSTRACT

We conducted a comparative analysis of 373 North American and 252 European land bird species to determine whether clutch size, annual number of broods and annual fecundity (clutch size × annual number of broods) are influenced by body size, diet, nest type, nest location, nestling development, migratory behaviour, habitat, latitude, continent and the phylogenetic relatedness among the species. The most significant factors influencing the three life-history traits were body size, nestling development, migratory behaviour and latitude. Body size had a negative effect on clutch size, number of broods and annual fecundity. Precocial species had larger clutches, fewer broods and higher annual fecundity than altricial birds. Long-distance migrants had smaller clutches, fewer broods and lower annual fecundity than short-distance migrants and residents. With increasing latitude, there was a significant increase in clutch size and a similarly strong decrease in number of broods, but no latitudinal gradient in annual fecundity. Thus, birds breeding at high latitudes had, on average, the same annual fecundity as species breeding at low latitudes (within North America and Europe). Phylogenetic effects were strong, particularly in clutch size. However, controlling for phylogenetic effects using permutational phylogenetic regression had only a minor influence on the results. Comparing the present results with those of previous studies on the three life-history traits demonstrates that results differ considerably and depend mainly on the diversity of bird species included in the study.

Keywords: body size, broods, clutch size, fecundity, land birds, latitude, migratory behaviour, nestling development.

INTRODUCTION

An important challenge in the study of life histories is understanding the factors that influence the enormous interspecific variation in life-history traits (Roff, 1992; Stearns, 1992). Some of the most important life-history traits in birds are clutch size, annual number of broods and annual fecundity (clutch size × annual number of broods; Martin, 1995).

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Annual fecundity of North American and European land birds can vary from as little as one egg and one brood per year in the Black Vulture (*Aegypius monachus*) to 20 eggs per brood in the Grey Partridge (*Perdix perdix*) and six broods per year in the Collared Dove (*Streptopelia decaocto*; Ehrlich *et al.*, 1994).

Many factors have been suggested to influence clutch size and number of broods. Clutch size and number of broods are correlated with body weight (Sæther, 1987; Bennett and Harvey, 1988). Diet has an effect on clutch size, with herbivores having smaller clutches than other trophic groups (Lack, 1954). Clutch size and number of broods vary with the degree of nest predation, which itself is influenced by nest type and nest location (Lack, 1968; Martin and Li, 1992; Martin, 1995; Owens and Bennett, 1995). Species that suffer higher nest predation tend to have smaller clutches, more broods and higher annual fecundity than species with low nest predation (Martin, 1995). Nestling development has an effect on both clutch size and number of broods. Precocial birds have larger clutches because parents might invest the same amount of energy to raise a larger clutch of precocial young than a smaller clutch of altricial offspring (Case, 1978a,b). In contrast, altricial birds grow faster and have shorter nestling periods, which can lead to more broods (Ricklefs, 1969, 1984).

Migratory behaviour appears to influence clutch size and number of broods (Kipp, 1943; Whitcomb *et al.*, 1981; Mönkkönen, 1992). Long-distance migrants have been shown to have both smaller clutches and fewer broods than residents and short-distance migrants. Clutch size is affected by habitat, with savanna species having larger clutches than forest species (Lack and Moreau, 1965). Furthermore, clutch size increases with latitude (Lack, 1947; Klomp, 1970; Ricklefs, 1980). Clutch size is larger in Europe than in North America (Martin and Clobert, 1996). Finally, phylogenetic effects may play an important role. Closely related species tend to have similar clutch sizes and similar numbers of broods. For example, most pigeon species have clutch sizes of two and comparatively many broods per year (Ehrlich *et al.*, 1988, 1994).

Despite these studies, two limitations prevent a thorough understanding of the factors that influence clutch size, number of broods and annual fecundity. First, in many studies, only clutch size was investigated. This limits our understanding, especially of latitudinal variation in the three life-history traits. The latitudinal increase in clutch size has been well known since the work of Stresemann (1927–34). However, it is not known how latitude influences the annual number of broods and whether there is a latitudinal increase in annual fecundity. Secondly, many of the above factors are intercorrelated. This makes it difficult to understand how migratory behaviour in particular influences the three life-history traits. Migratory behaviour is correlated with nest type and habitat. Migrants are less frequently cavity nesters than residents (von Haartman, 1968). North American long-distance migrants are found more frequently in forested habitat types than short-distance migrants and residents (Mönkkönen *et al.*, 1992). Thus, the small clutch size of long-distance migrants might be a consequence of their open nests or their preference for forest habitats (Martin, 1995).

To address these limitations, the aim of the present study was to determine the combined effect of body size, diet, nest type, nest location, nestling development, migratory behaviour, habitat, latitude and continent on clutch size, number of broods and annual fecundity. The analysis includes data for 373 North American and 252 European land bird species and was conducted both with and without controlling for the phylogenetic relatedness among the species using permutational phylogenetic regression.

METHODS

Species and their traits

We restricted our analyses to all North American and European bird species that live in and obtain their resources from terrestrial habitats. We excluded all species that use marine, coastal, freshwater and wetland habitats, such as ducks, geese, gulls, storks, cranes, waders and rails, because they have distinctly different ecological requirements. North American birds were defined as all species represented by range maps in the field guide of the National Geographic Society (1987). European birds were all species whose ranges covered Europe according to Heinzel *et al.* (1995), with Europe defined as including the British Isles and continental Europe eastward to 30° longitude (Peterson *et al.*, 1993).

The dependent variables used in the analysis were clutch size, annual number of broods and annual fecundity (clutch size × annual number of broods following Martin, 1995). To use a consistent source of data for both North American and European birds, all data for North American species were taken from Ehrlich *et al.* (1988) and for European species from Ehrlich *et al.* (1994) if not otherwise stated. We did not include data about yearling or adult survivorship for two reasons. First, estimation of survival is much more difficult than estimation of fecundity. Estimates of survival are largely based on recapture rates, which can be a biased estimator of survival because it includes both survival and probability of recapturing birds. For example, comparisons of survivorship between migrants and residents might be biased because migrants exhibit lower natal philopatry than residents and, therefore, have a lower probability of being recaptured (Weatherhead and Forbes, 1992). Secondly, comparatively reliable data about yearling or adult survivorship can be obtained only from a limited number of species, which reduces the sample size of bird species. Because the aim of this study was to assess the combined effect of a multitude of factors, we wished to keep the sample size as high as possible.

As independent variables, we used body size, diet, nest type, nest location, nestling development, migratory behaviour, habitat, latitude and continent. Body size was defined as body length from tip of bill to tip of tail (National Geographic Society, 1987; Heinzel *et al.*, 1995). Diet was classified in four categories: primarily carnivore (mammals, birds, fish, carrion), insectivore (insects, aquatic invertebrates), herbivore (greens, fruits, seeds, nectar) and omnivore (Ehrlich *et al.*, 1988, 1994). Nest type was classified in three categories: open (scrape, cup, saucer, platform), half-open (pendant, sphere, crevice) and closed (cavity) (Ehrlich *et al.*, 1988, 1994). Nest location was classified in three categories: primarily ground, intermediate (shrub) and high (tree, cliff) (Ehrlich *et al.*, 1988, 1994). And nestling development was classified in two categories: precocial (precocial 2, 3, 4, semi-precocial) and altricial (semi-altricial 1, 2, altricial) (Ehrlich *et al.*, 1988, 1994).

Migratory behaviour was classified in three categories: primarily resident, short-distance migrant (regularly wintering south of the breeding range, centre of the winter range for North American species north of the Tropic of Cancer, for European species north of the Sahara) and long-distance migrants (centre of the winter range for North American species south of the Tropic of Cancer, for European species south of the Sahara). Range maps were taken from the field guide of the National Geographic Society (1987) and from Heinzel *et al.* (1995) using additional information from Stotz *et al.* (1996) and Bezzel (1985, 1993). Habitat was defined as a continuous variable that covered a gradient from forest to open country with values of 1 (forest/woodland), 2 (open forest/woodland), 3 (forest/woodland edge), 4 (savanna, orchards, gardens), 5 (bushland, shrubland), 6 (open country with some bushes/trees) and 7 (open country) (Ehrlich *et al.*, 1988, 1994). Latitude was defined as the mean of the northern and southern edge of the range within North America and Europe, respectively (National Geographic Society, 1987; Heinzel *et al.*, 1995).

In all analyses that did not control for phylogeny, the relationship between the dependent and independent variables was tested using analysis of covariance (ANCOVA) (SAS, 1995). Note that some of the independent variables were intercorrelated (Table 1). However, 86% of the correlation coefficients (r) were smaller than 0.30; the highest correlation coefficient was 0.45 (correlation between latitude and continent). It would be interesting to test for interactions between the independent variables. However, as nine independent variables were assessed, we would have to consider 36 two-way interactions and many more higher-order interactions. Because it is extremely difficult to interpret that many interaction terms, we omitted them from our analysis.

The relationship between the dependent and independent variables was also tested using multiple regression (SAS, 1995). For the traits that did not have numerical values, dummy values were assigned. For nest type, open was given a value of 1, half-open a value of 2 and closed a value of 3. For nest location, ground was given a value of 1, intermediate a value of 2 and high a value of 3. For nestling development, precocial was given a value of 1 and altricial a value of 2. For migratory status, residents were given a value of 1, short-distance migrants a value of 2 and long-distance migrants a value of 3. For continent, Europe was given a value of 1 and North America a value of 2. Diet was omitted from this analysis because it could not be transformed to a meaningful numerical dummy variable. Multiple regression yielded very similar results to the ANCOVA. Therefore, only the results of the ANCOVA are presented.

The results are displayed in figures that present leverage plots for continuous variables and least squares means for categorical variables. Leverage plots are constructed such that the distance from a point to the line of fit shows the actual residual. The distance from that point to the horizontal line of the mean shows what the residual error would

Table 1. Correlations between eight of the nine independent variables (Pearson correlation coefficients, r, that are significant at $P < 0.05$)

	Nest type	Nest location	Nestling development	Migratory behaviour	Habitat	Latitude	Continent
Body size	–0.11*	0.14*	–0.26*	–0.29*	0.08	N.S.	N.S.
Nest type		0.35*	0.15*	–0.24*	–0.16*	N.S.	N.S.
Nest location			0.38*	–0.11*	–0.36*	–0.17*	N.S.
Nestling development				0.19*	–0.08	N.S.	N.S.
Migratory behaviour					N.S.	N.S.	N.S.
Habitat						N.S.	–0.21*
Latitude							–0.45*

* Significance after sequential Bonferroni adjustment (Rice, 1989). Body size was log-transformed. Because nest type, nest location, nestling development and continent are class variables that cannot be used for correlation analysis, these variables were transformed using numerical dummy values (see Methods).

be without the factor in the model (Sall, 1990; SAS, 1995). Thus, the plot shows for each point what the residual would be both with and without that factor in the model. Least squares means are predicted values from the specified model across the levels of a categorical variable holding the other variables in the model constant (SAS, 1995). Both methods allow the effect of a variable to be displayed after controlling for the other variables in the model.

Test for phylogenetic effects

Permutational phylogenetic regression

When analysing statistical patterns across species, one has to bear in mind that species might not represent independent data points because some of them are more closely related than others (Felsenstein, 1985; Harvey and Pagel, 1991). To control for these possible phylogenetic effects, we used permutational phylogenetic regression (PPR), working with plain dissimilarity matrices (Lapointe and Legendre, 1990, 1991, 1992; Legendre *et al.*, 1994; Taylor and Gotelli, 1994; Thorpe *et al.*, 1996; Böhning-Gaese and Oberrath, 1999). With this method, for each pair of species their dissimilarity in the dependent variable is compared with their phylogenetic distance and with their dissimilarity in a number of other independent variables. Thus, for a statistical test, the bird community is characterized by a number of matrices. The Y-matrix describes the dissimilarity in the dependent variable, the X_1-matrix the phylogenetic distance among the species and the $X_{2,\ldots,n}$-matrices the dissimilarity in the other independent variables among the species.

The Y-matrix is then regressed on the X-matrices and tested for significance using Mantel tests (Mantel, 1967; Smouse *et al.*, 1986; Legendre *et al.*, 1994). With Mantel tests, the regression of the individual values in the matrices yields the partial regression coefficients b_1 to b_n, and the respective t-values (Smouse *et al.*, 1986; Legendre *et al.*, 1994). The significance of the t-values is tested against a null distribution of t-values constructed by Monte Carlo randomizations, whereby the X-matrices are held constant and the species in the Y-matrix are randomly permuted (Smouse *et al.*, 1986; Legendre *et al.*, 1994). To construct the null distribution of t-values, we used 2000 randomizations in the present study.

This method allows a statistical approach to testing the effect of phylogeny on the dependent variable and on the relationship between the dependent and the independent variables. The influence of phylogenetic effects on the results is tested by calculating partial regression coefficients for a number of independent variables controlling for phylogenetic distance. This is comparable to analyses in which the influence of allometric effects on the results is tested by calculating partial regression coefficients for independent variables controlling for body size. Permutational phylogenetic regression does not assume any particular micro-evolutionary process besides that the relationship between the mean dissimilarity of the species in the dependent variable is a linear function of their phylogenetic distance. This linear relationship was investigated and proved to be the case. One of the advantages of this method is that the analysis is not limited to the level of species; the analysis can also be conducted at the level of populations within species. In the present study, the North American and European populations of species that occur on both continents were treated as two different sampling points. In the PPR-analysis, the two populations were given the genetic distance value, $\Delta T_{50}H = 0.0$ (see below).

Construction of the dissimilarity matrices

Before being able to apply PPR, the trait values of the species have to be transformed into trait dissimilarity values (contrasts) for each pair of species. The phylogenetic distance between each pair of species was defined as their genetic distance, $\Delta T_{50}H$, according to the molecular phylogeny of Sibley and Ahlquist (1990) and Sibley and Monroe (1990). Although this phylogeny is controversial, several new studies support it and suggest that it is generally valid, especially when conducting large-scale analyses (Mooers and Cotgreave, 1994). The $\Delta T_{50}H$ values were classified in discrete classes following Sibley and Ahlquist (1990) and Sibley and Monroe (1990). For example, the genetic distance $\Delta T_{50}H = 0.0$ was given to the North American and European population within the same species, $\Delta T_{50}H = 1.1$ to different species within the same genus, $\Delta T_{50}H = 4.6$ to species in different genera but in the same tribe, and $\Delta T_{50}H = 8.0$ to species in different tribes but in the same subfamily, and so on.

To construct the dissimilarity matrix for nest type, nest location, nestling development, migratory behaviour, habitat, latitude and continent, a trait dissimilarity index, *d*, was calculated by subtracting the trait value of the one species from the value of the other species. For this purpose, dummy numerical values were assigned for nest type, nest location, nestling development, migratory status and continent (see above). For clutch size, number of broods, annual fecundity and body size, the trait dissimilarity index, *d*, was calculated by dividing the trait value of the one species by the value of the other species. This procedure is based on the assumption that the dissimilarity between two species with lengths of 8 and 10 cm, respectively, is the same as between two species with lengths of 80 and 100 cm, respectively. The dissimilarity values were log-transformed to improve the fit to the linear regression. With respect to diet, species with the same diet were given a dissimilarity index $d = 0$; for species with different diets the dissimilarity index was $d = 1$. A computer program designed to construct the dissimilarity matrices from the original trait values and to perform the Mantel tests, written in IDL (Version 4.0, Research Systems, Inc.), is available from the authors.

Test for phylogenetic effects

To assess the influence phylogenetic effects had on the results, we compared three types of analyses.

1. The original ANCOVA in which species were treated as independent data points.
2. The PPR-analysis *not* including the phylogenetic distance matrix.
3. The PPR-analysis *including* the phylogenetic distance matrix.

By comparing the results of analyses 1 and 2, we can determine whether the transformation of the original trait values to dissimilarity indices (contrasts) preserves the results of the original ANCOVA. By comparing the results of analyses 2 and 3, we can assess whether phylogenetic effects influence the relationship between the dependent and the independent variables. One of the most significant advantages of this method is that we can judge whether different results between the original ANCOVA (analysis 1) and the analysis controlling for phylogenetic effects (analysis 3) are due to transformations of the original trait values into contrasts or due to phylogenetic effects. If different results are caused by transformations of the original trait values, we will find differences between analyses 1 and 2, but

Table 2. Multivariate analysis of the influence of nine independent variables on the clutch size, annual number of broods and annual fecundity of North American and European land bird species (*F*-values from an ANCOVA)

	d.f.	Log(clutch size)	Log(# broods)	Log(annual fecundity)
Number of species		620	519	519
Log(body size)	1	51.5***	7.5**	69.5***
Diet	3	10.3***	7.7***	5.4***
Nest type	2	22.2***	2.5	6.7**
Nest location	2	3.8*	1.4	2.7
Nestling development	1	60.7***	13.8***	27.3***
Migratory behaviour	2	15.0***	31.3***	40.5***
Habitat	1	0.0	2.7	2.4
Latitude	1	82.6***	44.6***	1.1
Continent	1	0.1	2.7	1.0
Explained variance, R^2		41.6%	35.1%	43.7%

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Fig. 1. Influence of body size on the clutch size, number of broods and annual fecundity of 625 North American and European land bird species. Leverage plot after controlling for diet, nest type, nest location, nestling development, migratory behaviour, habitat, latitude and continent (SAS, 1995). For a more detailed description of leverage plots, see the Methods section. For statistical analysis, see Table 2.

not between 2 and 3. If different results are caused by phylogenetic effects, we might or might not find differences between analyses 1 and 2, but we will definitely find differences between analyses 2 and 3.

RESULTS

Not taking phylogeny into account

Body size had a negative effect on clutch size, number of broods and annual fecundity (Fig. 1, Table 2). Diet influenced all three life-history traits (Table 2). Omnivores had larger clutches than carnivores, insectivores and herbivores. Insectivores and herbivores had more broods than carnivores and omnivores, and omnivores and insectivores had higher annual fecundity than carnivores and herbivores (Fig. 2). Nest type had an effect on clutch size and annual fecundity. Species which build cavity and half-open nests had larger clutches and higher annual fecundity than species with open nests (Fig. 3, Table 2). Nest location had a small but significant influence on clutch size. Species with nests on the ground had larger clutches than species with nests at intermediate and high heights (Fig. 4, Table 2). Combining nest type and location in one variable, thereby distinguishing between pure excavators and non-excavators following Martin (1995), led to less significant results than coding nest type and nest location as two separate variables. Nestling development had a strong influence on all three life-history traits (Table 2). Precocial species had larger clutches, fewer broods and higher annual fecundity than altricial birds (Fig. 5).

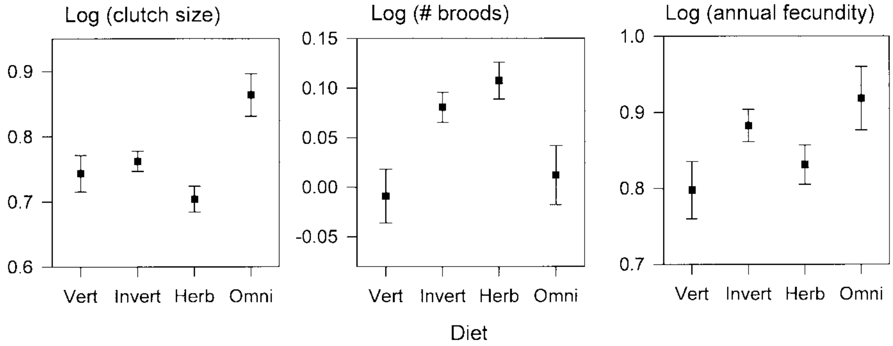

Fig. 2. Influence of diet on the clutch size, number of broods and annual fecundity of 625 North American and European land bird species. Displayed are least squares means (± 1 standard error) after controlling for body size, nest type, nest location, nestling development, migratory behaviour, habitat, latitude and continent (SAS, 1995). For statistical analysis, see Table 2.

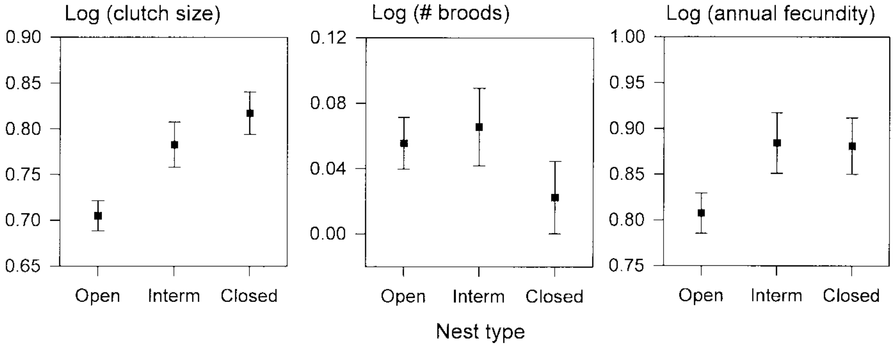

Fig. 3. Influence of nest type on the clutch size, number of broods and annual fecundity of 625 North American and European land bird species. Displayed are least squares means (± 1 standard error) after controlling for body size, diet, nest location, nestling development, migratory behaviour, habitat, latitude and continent (SAS, 1995). For statistical analysis, see Table 2.

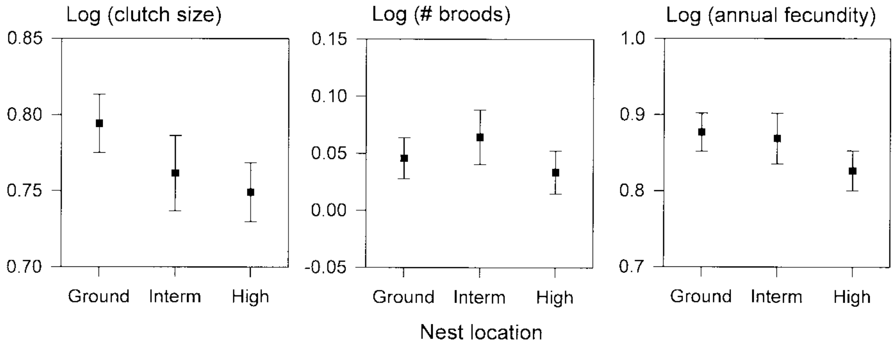

Fig. 4. Influence of nest location on the clutch size, number of broods and annual fecundity of 625 North American and European land bird species. Displayed are least squares means (± 1 standard error) after controlling for body size, diet, nest type, nestling development, migratory behaviour, habitat, latitude and continent (SAS, 1995). For statistical analysis, see Table 2.

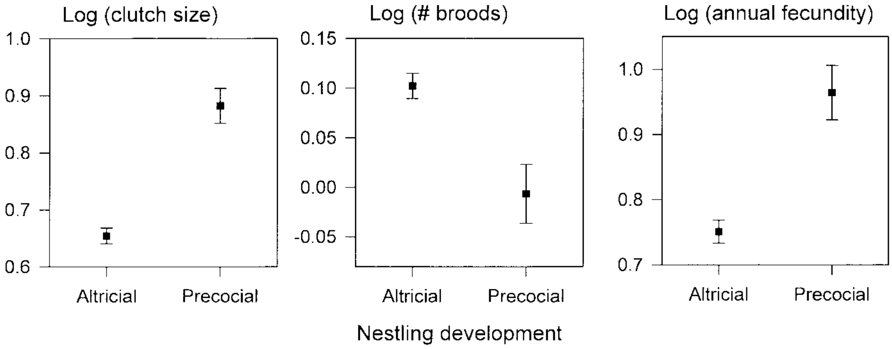

Fig. 5. Influence of nestling development on the clutch size, number of broods and annual fecundity of 625 North American and European land bird species. Displayed are least squares means (± 1 standard error) after controlling for body size, diet, nest type, nest location, migratory behaviour, habitat, latitude and continent (SAS, 1995). For statistical analysis, see Table 2.

Migratory behaviour was strongly correlated with clutch size, number of broods and annual fecundity (Table 2). Short-distance migrants had smaller clutches but more broods than residents, leading to short-distance migrants and residents having the same annual fecundity (Fig. 6). Long-distance migrants had both smaller clutches and fewer broods per year, resulting in lower annual fecundity, than short-distance migrants and residents. Habitat did not have an effect on the three life-history traits (Table 2). Latitude was strongly correlated with both clutch size and number of broods (Table 2). Clutch size increased with latitude, whereas number of broods decreased with latitude (Fig. 7). Annual fecundity, however, had no latitude effect. Obviously, the increase in clutch size and the decrease in number of broods with latitude compensated each other exactly. The effect of continent on clutch size, number of broods and annual fecundity was not significant once latitude was entered into the model. Removing latitude from the model led to European species having significantly larger clutches than North American species

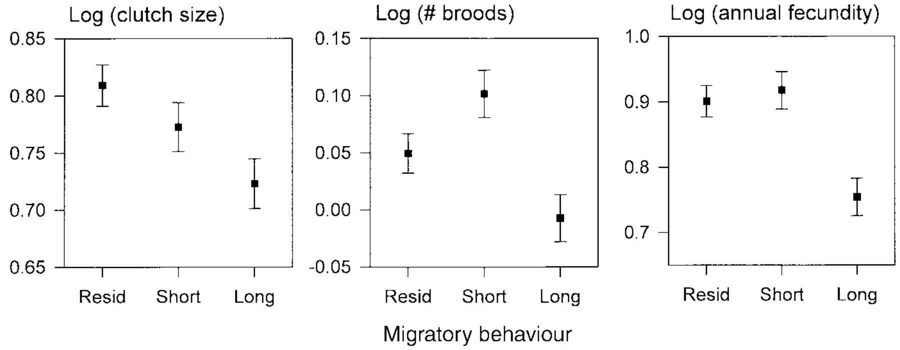

Fig. 6. Influence of migratory behaviour on the clutch size, number of broods and annual fecundity of 625 North American and European land bird species. Displayed are least squares means (± 1 standard error) after controlling for body size, diet, nest type, nest location, nestling development, habitat, latitude and continent (SAS, 1995). For statistical analysis, see Table 2.

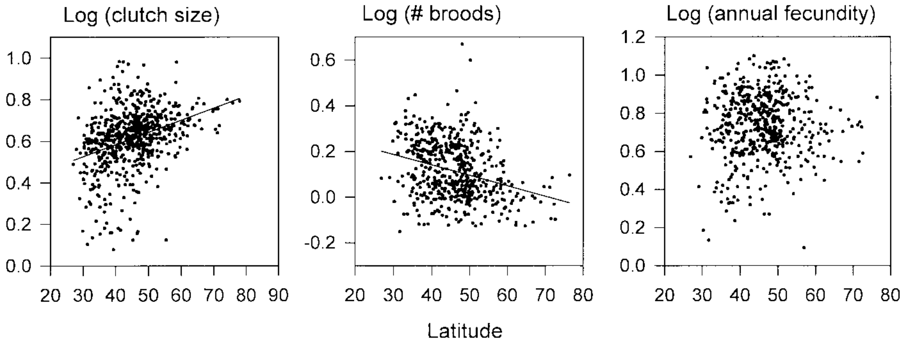

Fig. 7. Influence of the mean latitude of the breeding range on the clutch size, number of broods and annual fecundity of 625 North American and European land bird species. Leverage plot after controlling for body size, diet, nest type, nest location, nestling development, migratory behaviour, habitat and continent (SAS, 1995). For a more detailed description of leverage plots, see the Methods section. For statistical analysis, see Table 2.

($F_{1,608} = 16.7$, $P < 0.0001$). However, even in the absence of latitude, continent was not significantly correlated with number of broods ($F_{1,505} = 3.0$, $P = 0.083$) or annual fecundity ($F_{1,505} = 3.0$, $P = 0.086$).

In summary, the most influential factors on clutch size were latitude, nestling development, body size and nest type. The most influential factors on number of broods were latitude, migratory behaviour, nestling development and diet. Finally, annual fecundity was most influenced by body size, migratory behaviour, nestling development and diet.

Transformation of the trait values

In the PPR-analysis *not* including the phylogenetic distance matrix, the most influential factors on clutch size were body size, nestling development, migratory behaviour and latitude (Table 3). Number of broods was most influenced by migratory behaviour, body size, latitude and nestling development. The most significant determinants of annual fecundity were body size, migratory behaviour, nestling development and latitude.

The transformation of the original trait values into dissimilarity indices (contrasts) had substantial effects on the analysis. Comparing the original ANCOVA (Table 2) with the PPR-analysis not including phylogenetic distance (Table 3) demonstrates a change in the influence of nest type on number of broods, of nest location on annual fecundity, of habitat on number of broods and annual fecundity, and of latitude on annual fecundity. The original ANCOVA explained a greater proportion of the variation in the three life-history traits (35.1–43.7%; Table 2) than the PPR-analysis (5.2–20.6%; Table 3).

Taking phylogeny into account

The PPR-analysis *including* the phylogenetic distance matrix demonstrates that phylogeny had a very strong influence on clutch size, a weak influence on number of broods and a strong influence on annual fecundity (Table 4). For all three traits, closely related species were significantly more similar than distantly related species. Phylogeny was the most influential factor on the clutch size of North American and European land bird species. Besides phylogeny, the most influential factors on clutch size in this analysis were body size, nestling development, latitude and migratory behaviour (Table 4). Number of broods was most influenced by migratory behaviour, latitude, body size and nest type. The most significant determinants of annual fecundity were body size, migratory behaviour, nestling development and nest type.

In spite of strong phylogenetic effects, the presence of the phylogenetic distance matrix had only minor effects on the significance of the other independent variables. Comparing the PPR-analysis not including phylogenetic distance (Table 3) with the PPR-analysis

Table 3. Multivariate permutational phylogenetic regression analysis *not* including phylogenetic distance, testing the influence of nine independent variables on the clutch size, annual number of broods and annual fecundity of North American and European land bird species (*t*-values)

	d.f.	Log(clutch size)	Log(# broods)	Log(annual fecundity)
Number of species		620	519	519
Number of species–species contrasts		175 607	78 045	129 921
Log(body size)	1	–112.9***	–30.8***	–147.0***
Diet	1	74.2***	15.3*	21.5**
Nest type	1	58.3***	–22.0***	30.2***
Nest location	1	–31.5***	2.4	–20.0**
Nestling development	1	–93.2***	22.5***	–49.4***
Migratory behaviour	1	–82.8***	–32.3***	–75.0***
Habitat	1	–5.7	20.7***	19.9**
Latitude	1	78.1***	–28.7***	31.2***
Continent	1	9.9	–4.0	6.8
Explained variance, R^2		20.6%	5.2%	20.6%

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

including phylogenetic distance (Table 4) demonstrates that the only relationship that lost its significance in the presence of the phylogenetic distance matrix was the influence of diet on number of broods and especially on annual fecundity. For the other independent variables, only minor changes in the *t*-values and in the levels of significance were noted.

DISCUSSION

Before examining the implications of our results, we consider how to interpret different results obtained with different types of analysis. One of the advantages of permutational phylogenetic regression is that one can judge whether different results between the original ANCOVA (Table 2) and the analysis controlling for phylogenetic effects (Table 4) are due to transformations of the original trait values or due to real phylogenetic effects. If we find differences between the original ANCOVA (Table 2) and the PPR-analysis not including phylogeny (Table 3), these differences are caused by transformations of the original trait values. Differences between the PPR-analysis not including phylogeny (Table 3) and the PPR-analysis including phylogeny (Table 4) are caused by phylogenetic effects.

The presence or absence of the phylogenetic distance matrix had only minor effects on the significance of the other independent variables. Comparing the PPR-analysis with and without phylogeny revealed that the only relationship that lost its significance in the presence of the phylogenetic distance matrix was the influence of diet on number of broods and especially on annual fecundity. Therefore, in the present study, effects of diet in analyses that did *not* control for phylogeny (e.g. the original ANCOVA; Table 2) probably have to be dismissed as phylogenetic effects. This is consistent with previous studies (Garland *et al.*, 1993; Ricklefs and Starck, 1996).

Table 4. Multivariate permutational phylogenetic regression analysis *including* phylogenetic distance, testing the influence of ten independent variables on the clutch size, annual number of broods and annual fecundity of North American and European land bird species (*t*-values)

	d.f.	Log(clutch size)	Log(# broods)	Log(annual fecundity)
Number of species		620	519	519
Number of species–species contrasts		175 607	78 045	129 921
Phylogeny	1	133.9***	18.8*	52.2***
Log(body size)	1	−116.3***	−25.2***	−142.4***
Diet	1	35.1***	10.7	4.7
Nest type	1	59.9***	−19.0**	32.1***
Nest location	1	−21.5**	2.0	−17.7**
Nestling development	1	−87.9***	17.8***	−43.8***
Migratory behaviour	1	−68.8***	−32.4***	−71.4***
Habitat	1	−6.2	20.5***	20.1***
Latitude	1	77.8***	−29.2***	27.0***
Continent	1	5.7	−4.0	5.3
Explained variance, R^2		28.0%	5.6%	22.3%

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Most differences between the original ANCOVA and the analysis controlling for phylogeny could be attributed to transformations of the original trait values. Four variables altered their significance between the original ANCOVA (Table 2) and the PPR-analysis not including phylogeny (Table 3). Possible reasons for these changes include distortions of the original trait values by calculating dissimilarity indices (contrasts), corresponding distortions in the intercorrelations among the independent variables, changes in the type of significance testing (ANCOVA *vs* Mantel tests), changes in the degrees of freedom and changes in the statistical power of the tests. These changes (e.g. in the statistical power of the tests) are similar to those seen in other methods that control for phylogenetic effects, such as phylogenetic independent contrasts (see discussion in Rosenzweig, 1996). The results of the present study suggest that differences between an analysis in which species are treated as independent data points and an analysis controlling for phylogenetic effects are just as likely to be caused by data transformations and differences in the type and statistical power of the test as by real phylogenetic effects.

Which method should be preferred for independent variables that did not show phylogenetic effects, the original ANCOVA (Table 2) or the PPR-analysis not including phylogeny? (Table 3). The original ANCOVA has the advantage that it used the original trait values and well-known statistics. Additionally, it explains a substantially higher proportion of variation in the dependent variables (mean = 40.1% *vs* mean = 15.5%). Therefore, in the case of differing results, we base the interpretation of the results on the original ANCOVA (Table 2) for all variables that did not change their significance with phylogeny (body size, nest type, nest location, nestling development, migratory behaviour, habitat, latitude and continent).

The results demonstrate that the most influential factors on the clutch size, number of broods and annual fecundity of North American and European land bird species are body size, nestling development, migratory behaviour and latitude. These factors were the most significant in all types of analyses. Body size had a negative effect on clutch size, number of broods and annual fecundity. Precocial species had larger clutches, fewer broods and higher annual fecundity than altricial birds. Long-distance migrants had smaller clutches, fewer broods and lower annual fecundity than short-distance migrants and residents. Finally, with increasing latitude, we found a significant increase in clutch size and a similarly strong decrease in number of broods, with no latitudinal gradient in annual fecundity.

Note that, in this analysis, we focused on the mean effects of the factors. Although the factors explain between 35.1 and 43.7% of the variance in clutch size, numbers of broods and annual fecundity, considerable variation is left unexplained and outliers exist that are particularly interesting. For example, four relatively large bodied species have an especially high number of broods (Fig. 1). All four species are pigeons: Rock Dove (*Columba livia*), 5 broods; Collared Dove (*Streptopelia decaocto*), 3–6 broods; Stock Dove (*C. oenas*), 2–5 broods; and Turtle Dove (*S. turtur*), 2–3 broods (Ehrlich *et al.*, 1994). However, all four species have relatively small clutches, and thus their annual fecundity is not larger than average in relation to their body size.

An important result of this study is that migratory behaviour had a strong influence on clutch size, number of broods and annual fecundity. Interestingly, short-distance migrants had smaller clutches but more broods per year than residents, resulting in short-distance migrants and residents having the same annual fecundity (Fig. 6). This pattern is counter-intuitive to what is expected from the timing of the breeding season in the two groups of species. European short-distance migrants start breeding on average 2 weeks later than residents (K. Böhning-Gaese, unpublished data). Therefore, we would expect short-distance migrants to have fewer broods than residents, which might be compensated by larger clutch sizes. Instead, smaller clutch sizes appear to be compensated by larger numbers of broods per year.

Long-distance migrants had both smaller clutches and fewer broods, resulting in lower annual fecundity, than short-distance migrants and residents. Thus, an analysis including a larger number of bird species than used, for example, by Martin (1995), revealed a significantly lower annual fecundity of long-distance migrants compared to short-distance migrants and residents controlling for nest type, habitat and a large number of other variables. European long-distance migrants start breeding on average 2 weeks later than short-distance migrants (K. Böhning-Gaese, unpublished data). Thus, the smaller number of broods per year might be caused by the short breeding season. Yet, this smaller number of broods is not compensated by larger clutch sizes (Kipp, 1943). Life-history theory would predict that the low annual fecundity of long-distance migrants is caused by high winter survival of yearling or adult birds (for eastern North American birds, see Mönkkönen, 1992). It would be interesting to test this hypothesis. However, before conducting a comparative study of survival rates at a similar large scale as the present study, much more information regarding survival rates of yearling and adult birds has to be collected (see Methods).

Another important result of the present study is the lack of latitudinal gradients in annual fecundity (at least within North America and Europe). Obviously, the latitudinal increase in clutch size was compensated by a decrease in the number of broods. Species at high and low latitudes appeared to lay exactly the same number of eggs. They differed, however, in the amount of effort put into clutch size versus number of broods. The latitudinal increase in clutch size has been explained by longer daylength, the spring flush of food resources, low population sizes caused by high winter mortality, and lower predation pressure at high latitudes (Lack, 1947, 1968; Skutch, 1949; Ashmole, 1963; Klomp, 1970). The latitudinal decrease in number of broods is probably caused by a latitudinal reduction in the length of the breeding season. There is no straightforward explanation why annual fecundity shows no latitudinal gradient. Life-history theory, however, would predict that no latitudinal gradient in annual fecundity is connected with no latitudinal gradient in survival rates. Thus, for birds breeding and wintering within North America or Europe, survival rates appear not to vary with latitude. This is consistent with the fact that short-distance migrants and residents have the same annual fecundity and, possibly, also the same survival rate.

In general, comparing the results of this study with those of other studies on factors influencing clutch size or annual fecundity demonstrates that they depend strongly on the scale of the analysis – that is, the number and diversity of species included in the analysis. The present study was conducted with 625 North American and European land bird species and covered a wide range of body sizes, foraging behaviours, nesting strategies and the two developmental modes altricial and precocial. In similar large-scale studies, body size was also found to influence clutch size, number of broods and annual fecundity (Sæther, 1987; Bennett and Harvey, 1988). In contrast, in a thorough analysis of factors influencing the annual fecundity of 123 North American Passeriformes and Piciformes birds, nest type and nest location were found to be the most important variables (Martin, 1995). In this more homogeneous group of birds, body size and food hardly influenced the results. In studies conducted at the intraspecific scale, food appears to be an important predictor of clutch size (Lack, 1968; Martin, 1987). For example, spatial and temporal variation in the clutch size of a bird species is often strongly correlated with spatial and temporal variation in food availability (Martin, 1987). Thus, when comparing different studies of factors influencing life-history traits, it is essential to take into account the scale of the studies.

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