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Phylogenetic effects on morphological, life-history, behavioural and ecological traits of birds

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ABSTRACT

The aim of this study was to assess the influence of phylogenetic history on 21 avian morphological, life-history, behavioural and ecological traits using Mantel permutation tests. The results demonstrated that, for 13 of 21 traits, closely related species were significantly more similar than distantly related species. For diet and for all morphological and life-history traits except number of clutches per year, phylogeny accounted for a notable amount of variation in trait values. However, for most behavioural and ecological traits, relatedness explained less than 1% of the variation among species. Because phylogenetic effects were weak in traits traditionally associated with the niche of a species, we conclude that phylogenetic effects do not reflect phylogenetic niche conservatism. When tested at different phylogenetic levels (complete phylogeny, within families, among families, among orders), phylogenetic effects were very variable. Only two traits had consistently strong phylogenetic effects at all phylogenetic levels and only two traits had consistently weak phylogenetic effects at all phylogenetic levels. Phylogenetic effects tended to be positive but relatively weak within families, positive and strong among families, and negative and weak among orders. Methods that intend to control for phylogenetic effects by working solely within families, among families, or among orders are not reliable in removing phylogenetic effects.

Keywords: avian traits, behaviour, ecology, life history, Mantel permutation tests, morphology, phylogenetic effects, phylogenetic relatedness.

INTRODUCTION

Recently, the study of diversity in biological systems has led to the realization that current patterns might not only be adaptations to present-day selective forces acting on the organism, but that they may also result from the phylogenetic history of the lineage (Stearns, 1983; Harvey and Pagel, 1991; Edwards and Naeem, 1993; Miles and Dunham, 1993). Closely related species tend to share similar morphologies and life-history strategies. Thus, a comparative analysis among species in which species are treated as independent sampling units might inflate the degrees of freedom in the analysis because

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species are not really independent (Felsenstein, 1985). In comparative studies, therefore, it is important to know whether and at which taxonomic level phylogenetic effects are found.

Phylogenetic effects have been detected for a variety of morphological, physiological, life-history and behavioural traits (Harvey and Pagel, 1991; Miles and Dunham, 1993). They have been identified using a variety of methods, ranging from nested analyses of variance (Harvey and Mace, 1982; Stearns, 1983), phylogenetic autocorrelation (Cheverud *et al.*, 1985; Gittleman and Kot, 1990; Miles and Dunham, 1992) and phylogenetic regression (Grafen, 1989, 1992), to permutational phylogenetic regression (Lapointe and Legendre, 1990, 1991, 1992; Legendre *et al.*, 1994) and phylogenetic independent contrasts (Felsenstein, 1985; Harvey and Pagel, 1991; Garland *et al.*, 1992). Furthermore, phylogenetic effects have been found at different phylogenetic levels, such as among species within genera (Richman and Price, 1992) and among genera within subfamilies (Miles and Dunham, 1992).

However, even within well-studied groups of organisms such as birds, little is known about phylogenetic effects on ecological and behavioural characteristics of species, such as abundance, range size, choice of breeding habitat, migratory status, diet, nest type and seasonal start of the breeding period (but see Edwards and Naeem, 1993). Little is known about the *relative* importance of phylogenetic effects on different morphological and life-history characteristics (but see Gittleman *et al.*, 1996). Additionally, we do not know at which phylogenetic level (within genera, within families, within orders) phylogenetic effects are strongest. Thus, the aim of this study was to compare the relative importance of phylogenetic effects for a wide variety of avian morphological, life-history, behavioural and ecological traits. Phylogenetic effects were studied at different phylogenetic levels (complete phylogeny, within families, among families and among orders).

METHODS

Species traits

To conduct the study with a biologically meaningful group of organisms, we used 151 bird species co-existing in a regional bird community. All these species are recorded for the Lake Constance region in central Europe (Schuster *et al.*, 1983; Bauer and Heine, 1992; Böhning-Gaese and Bauer, 1996). The 151 species represent 12 of the 23 orders classified by Sibley and Ahlquist (1990).

The species traits used in the analysis were 10 morphological and life-history traits (body weight, wing length, age at maturity, egg weight, clutch size, number of clutches per year, number of eggs per year, incubation period, fledging time, maximum age), and 11 ecological and behavioural traits (migratory status, breeding habitat, diet, nest type, seasonal start of breeding period; and local abundance, regional abundance and range size at the landscape and regional scales). Although abundance and range size are usually not considered species traits, we will nevertheless use the term ‘trait’ for simplification of terminology. All data were taken from Bezzel (1985, 1993) except in cases explicitly noted. The seasonal start of the breeding period was classified based on time intervals of 10 days (beginning, middle or end of March, April, May, etc.). Nest type was classified as one of three categories: open (cup or saucer nest), half-open (niche, half-cavity) and closed (cavity in tree or mud wall). Diet was classified as one of three categories: vertebrates (small mammals, birds, reptiles, amphibians, fish or carrion), invertebrates (land or water invertebrates, such as insects, spiders, molluscs and earthworms) and herbs (land or aquatic plants, fruits, berries, seeds).

Breeding habitat was classified as one of four categories by three regional ornithologists (Böhning-Gaese and Bauer, 1996): wetland (open water, reed, water edge), farmland (fields, dry and damp meadows, pasture, natural orchard, hedgerows), forest (forest, forest clearings) and urban (city, suburbs, cemeteries, parks, farm houses). Migratory status was classified as one of three categories by the same ornithologists: long-distance migrant (wintering south of the Sahara), short-distance migrant (wintering in the Mediterranean region) and resident (Böhning-Gaese and Bauer, 1996).

Abundance and range size data on a landscape scale were taken from the semi-quantitative breeding bird atlas 'Lake Constance' (Schuster *et al.*, 1983; Bauer and Heine, 1992; Böhning-Gaese and Bauer, 1996). The atlas covers the landscapes surrounding Lake Constance in central Europe and consists of 303 grid squares of 2×2 km, covering 1212 km^2 in total. Abundance and range size data on a regional scale were extracted from a semi-quantitative German breeding bird atlas (Rheinwald, 1993). The German atlas consists of 625 squares of 25×25 km, covering 390,625 km^2 in total. For both data sets, we defined range size as the number of squares occupied and local abundance as the mean abundance in squares occupied. Regional abundance was the product of local abundance and range size. Note that regional and local abundance are relative terms within a data set. In absolute terms, the 'local abundance' of a species at the German scale is similar to the 'regional abundance' of the species at the Lake Constance scale. In the following, LC refers to the landscape scale (Lake Constance) and G refers to the regional scale (Germany).

Statistical analysis

Permutational phylogenetic regression

To assess and quantify phylogenetic effects for different traits at different phylogenetic levels, we used permutational phylogenetic regressions working with plain dissimilarity matrices (Lapointe and Legendre, 1992; Legendre *et al.*, 1994). Using this method, for each pair of species their dissimilarity in a certain trait is compared with their phylogenetic distance. Thus, for each trait the bird community is characterized by two matrices: one matrix describes the dissimilarity in the trait and the other the phylogenetic distance among the species. The trait dissimilarity matrix is then regressed on the phylogenetic distance matrix 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 regression coefficient b, the t-value and the R^2-value (Smouse *et al.*, 1986; Legendre *et al.*, 1994). The significance of the t-value is tested against a null distribution of t-values constructed by Monte Carlo randomizations, whereby the phylogenetic distance matrix is held constant and the species in the trait matrix are randomly permuted (Legendre *et al.*, 1994). This approach keeps the phylogenetic tree fixed while randomly reshuffling the traits, an approved null model for tests of phylogenetic inertia (Maddison and Slatkin, 1991). To construct the null distribution of t-values in the present study, we used 2000 randomizations. A computer program to conduct these simulations written in IDL (Version 4.0, Research Systems, Inc.) is available from the authors.

Similarity in traits and phylogeny among species

To compare the dissimilarity in traits between two species, the same procedure was used for all continuous traits besides start of the breeding period. A trait dissimilarity index, d, was calculated by dividing the species with the higher value by the species with the lower value. This procedure is based on the assumption that the similarity between two species weighing 100 g and 10 g, for example, is the same as between two species weighing 1000 g and 100 g. The dissimilarity values were log-transformed to improve fit to the linear regression. For the seasonal start of the breeding period, the trait dissimilarity index, *d*, between two species was calculated as the difference in the start of breeding in number of 10-day periods. If species *a* began breeding at the beginning of April, species *b* at the end of April and species *c* at the beginning of May, the dissimilarity between species *a* and *b* was 2 and between species *a* and *c* it was 3.

With respect to migratory status, breeding habitat, diet and nest type, the dissimilarity index, *d*, ranged between 0 and 2. For migratory status, the dissimilarity between two species having the same migratory status was set at 0, that between a resident and a short-distance migrant at 1, that between a short-distance migrant and a long-distance migrant at 1, and that between a resident and a long-distance migrant at 2. For breeding habitat, the dissimilarity between two species using the same habitat type was set at 0; the dissimilarity between two species using different habitat types was set at 1. For diet, the dissimilarity between two species having the same diet was set at 0, that between a vertebrate-eating and an invertebrate-eating species was set at 1, that between an invertebrate- and a herb-eating species at 1, and that between a vertebrate- and a herb-eating species at 2. For nest type, the dissimilarity between two species with the same type of nest was set at 0, that between a closed-nest species and a half-open-nest species at 1, that between a half-open-nest species and an open-nest species at 1, and that between a closed-nest species and an open-nest species at 2.

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). Sibley and Ahlquist's phylogeny is based on DNA–DNA hybridization with $\Delta T_{50}H$ the temperature when 50% of hybridizable DNA has melted. Although Sibley and Ahlquist's phylogeny is controversial, several recent studies have supported it and have suggested that it is generally valid, especially when conducting large-scale analyses (Mooers and Cotgreave, 1994). Furthermore, it is widely applied in the comparative analysis of ecological and evolutionary patterns (e.g. Cotgreave and Harvey, 1991; Nee *et al.*, 1991; Fjeldså, 1994; Mönkkönen, 1995; Blackburn *et al.*, 1996). Note that by defining phylogenetic distance as genetic distance, we do not compare the similarity between two species in a certain trait with the true phylogenetic distance of these species but with their genetic distance. However, as long as there is a linear relationship between true phylogenetic distance and genetic distance, this does not confound the results. Some of the species and genera we used in the present study are not represented in the phylogeny of Sibley and Ahlquist (1990). We estimated the genetic distance values for these species by calculating the average distance value of the other species or genera in the same genus or tribe, respectively.

RESULTS

Phylogenetic effects at the level of the complete phylogeny

Figure 1 displays the maximum, mean and minimum dissimilarity of a trait as a function of phylogenetic distance. To make the figure easier to read and to interpret, phylogenetic distance was classified in discrete classes following Sibley and Ahlquist (1990, p. 254)

(Table 1). For example, class 1 is the dissimilarity between congeneric species, class 5 the dissimilarity between species that belong in different families, and class 10 the dissimilarity between species that are from different orders. Discrete classes hardly change the optical impression of the figure because class size varies only between 2.0 and 2.5 (Table 1). Note that class 7 has low sample size (Table 1).

Generally, for diet and for all morphological and life-history traits except number of clutches per year, phylogenetic effects were strong or moderate (Table 2). The strongest phylogenetic effect was found for incubation period, with 25.2% of the variation between species explained by phylogeny. Strong phylogenetic effects were also found for egg weight, body weight, clutch size, fledging time and wing length, with 13.7–19.3% of the variation explained by phylogeny. Moderate phylogenetic effects were noted for diet, age at maturity, eggs per year and maximum age. For these traits, phylogeny explained 4.4–7.2% of the variation.

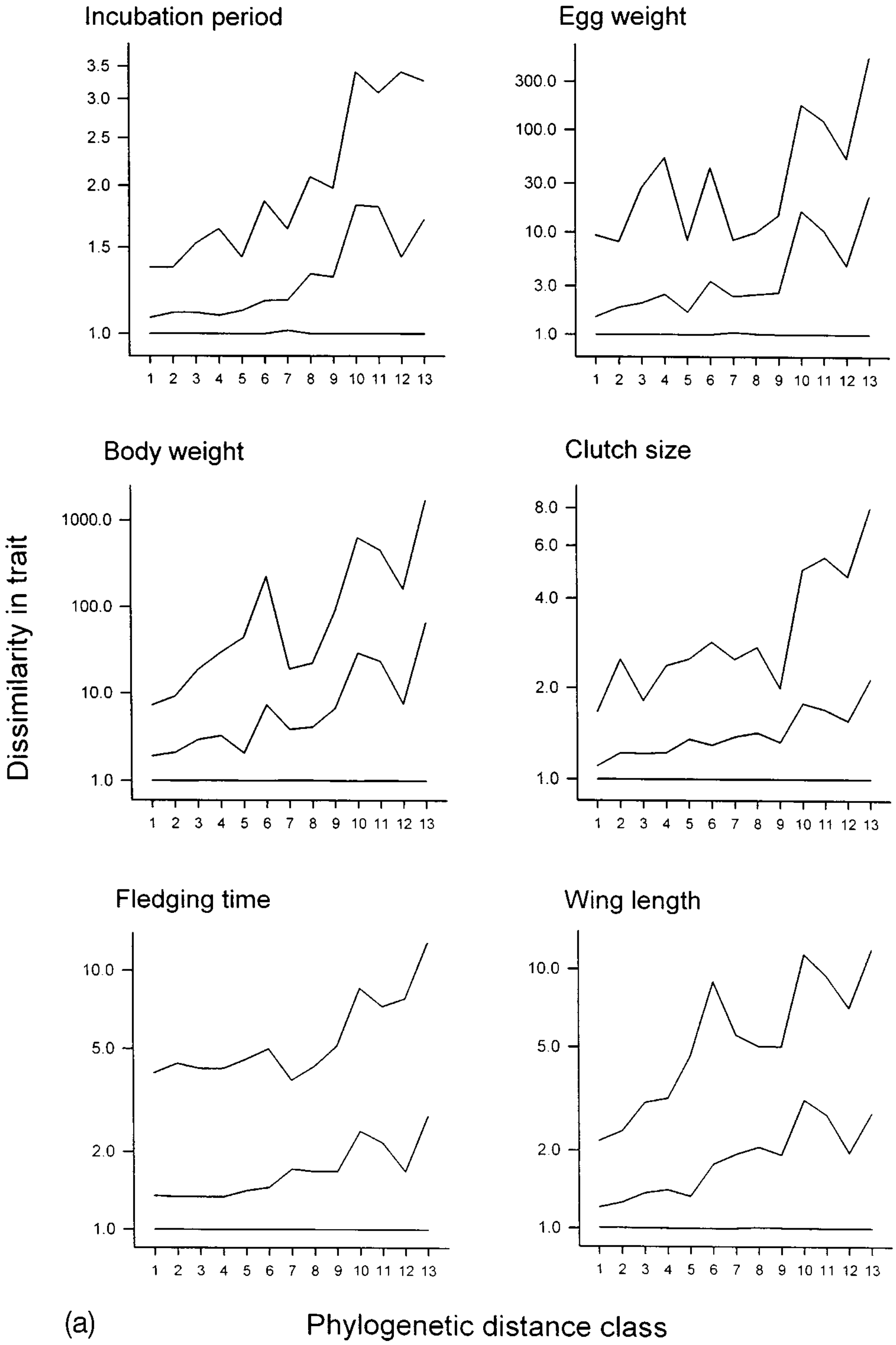
For number of clutches per year and for all behavioural and ecological traits except diet, phylogenetic effects were weak or non-significant (Table 2). Weak but significant effects were found for range size (LC), breeding habitat and local abundance (G). Only 0.6–0.8% of the variation in these traits was explained by phylogeny. No significant phylogenetic effects were found for range size (G), regional abundance (G), nest type, seasonal start of breeding season, regional abundance (LC), migratory status, local abundance (LC) or number of clutches per year.

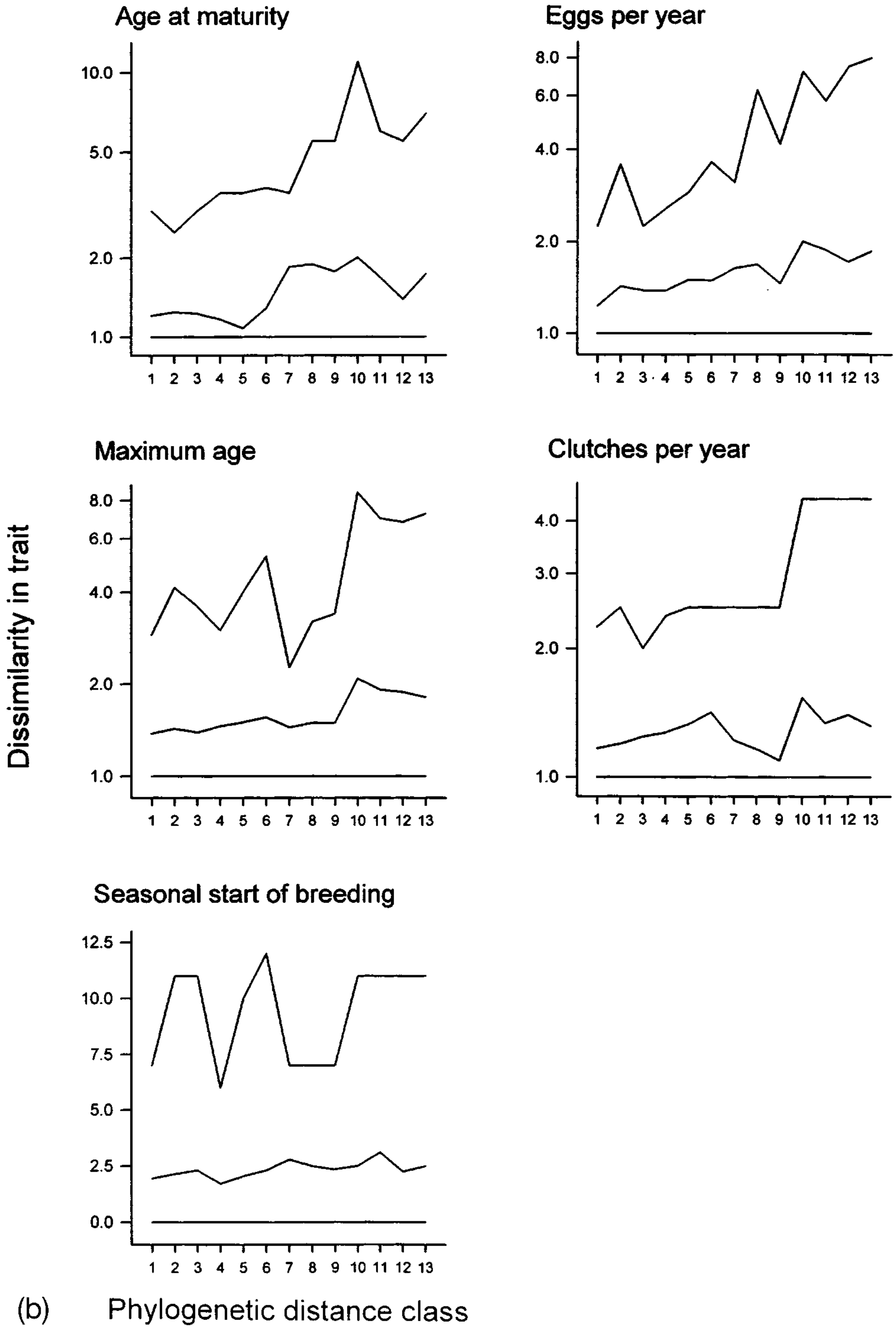
Some of the trait values varied continuously and over a wide range, whereas others took only a small number of values. To test whether these differences among traits influenced the

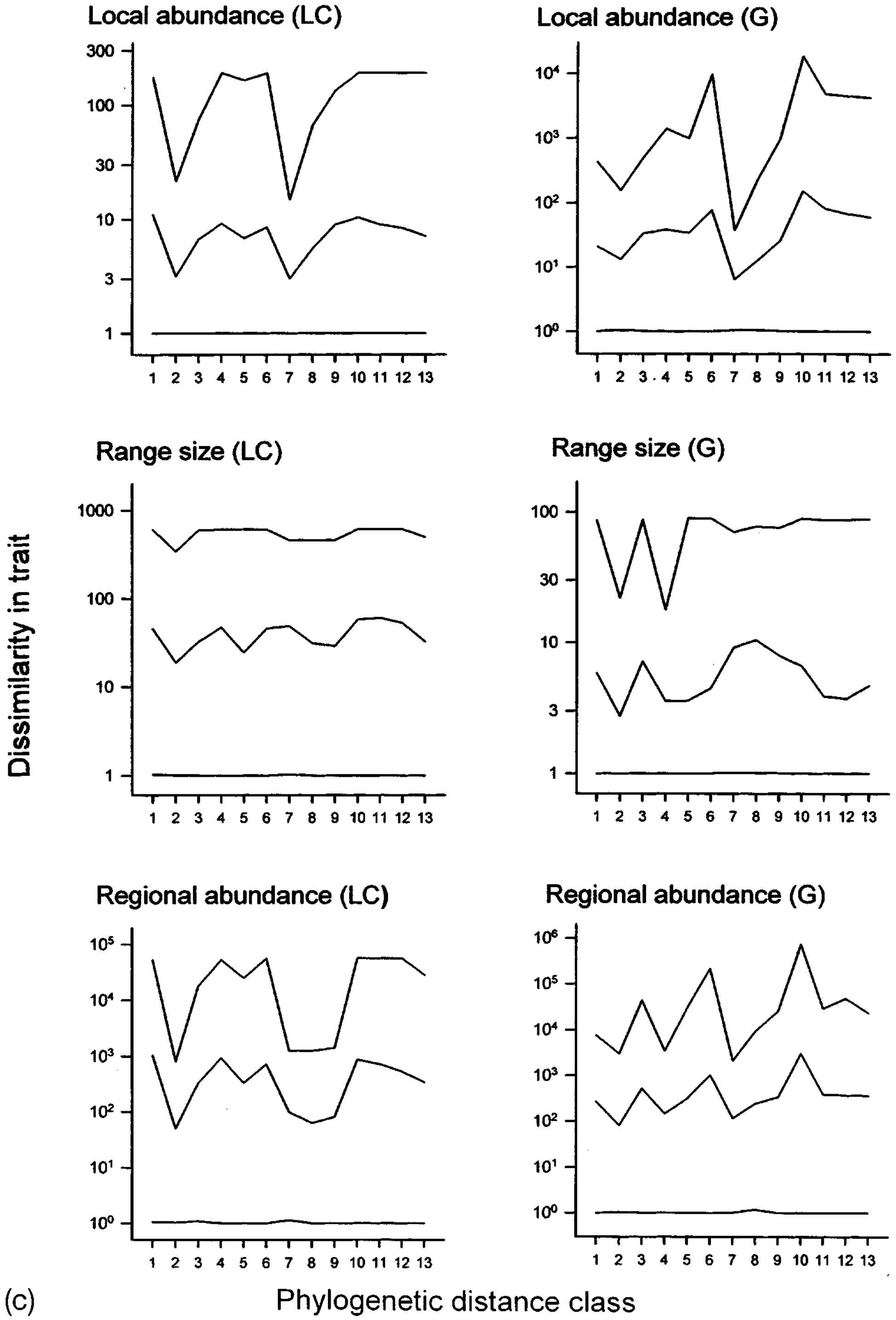
Table 1. Classes of phylogenetic distance used in Fig. 1 following Sibley and Ahlquist (1990)[a]

	Class	$\Delta T_{50}H$ (range)	Number of species–species comparisons
1	Congeneric spp.	0.0–2.2	84
2	Subtribe	2.2–4.5	108
3	Tribe	4.5–7.0	152
4	Subfamily	7.0–9.0	187
5	Family	9.0–11.0	590
6	Superfamily	11.0–13.0	2 447
7	Parvorder	13.0–15.5	37
8	Infraorder	15.5–18.0	98
9	Suborder	18.0–20.0	187
10	Order	20.0–22.0	3 464
11	Superorder	22.0–24.5	887
12	Parvclass	24.5–27.0	1 166
13	Infraclass	27.0–29.0	1 918
Total			11 325

[a] Sibley and Ahlquist's phylogeny is based on DNA–DNA hybridization with $\Delta T_{50}H$ the temperature when 50% of hybridizable DNA has melted.


Incubation period
3.5
3.0
2.5
2.0
1.5
1.0
Egg weight
300.0
100.0
30.0
10.0
3.0
1.0
Body weight
1000.0
100.0
10.0
1.0
Clutch size
8.0
6.0
4.0
2.0
1.0
Fledging time
10.0
5.0
2.0
1.0
Wing length
10.0
5.0
2.0
1.0
1 2 3 4 5 6 7 8 9 10 11 12 13
Dissimilarity in trait
(a)
Phylogenetic distance class


Age at maturity
10.0
5.0
2.0
1.0
1 2 3 4 5 6 7 8 9 10 11 12 13
Eggs per year
8.0
6.0
4.0
2.0
1.0
1 2 3 4 5 6 7 8 9 10 11 12 13
Maximum age
8.0
6.0
4.0
2.0
1.0
1 2 3 4 5 6 7 8 9 10 11 12 13
Clutches per year
4.0
3.0
2.0
1.0
1 2 3 4 5 6 7 8 9 10 11 12 13
Seasonal start of breeding
12.5
10.0
7.5
5.0
2.5
0.0
1 2 3 4 5 6 7 8 9 10 11 12 13
Dissimilarity in trait
(b)
Phylogenetic distance class


Local abundance (LC)
300
100
30
10
3
1
1 2 3 4 5 6 7 8 9 10 11 12 13
Local abundance (G)
10^4
10^3
10^2
10^1
10^0
1 2 3 4 5 6 7 8 9 10 11 12 13
Range size (LC)
1000
100
10
1
1 2 3 4 5 6 7 8 9 10 11 12 13
Range size (G)
100
30
10
3
1
1 2 3 4 5 6 7 8 9 10 11 12 13
Regional abundance (LC)
10^5
10^4
10^3
10^2
10^1
10^0
1 2 3 4 5 6 7 8 9 10 11 12 13
Regional abundance (G)
10^6
10^5
10^4
10^3
10^2
10^1
10^0
1 2 3 4 5 6 7 8 9 10 11 12 13
Dissimilarity in trait
(c)
Phylogenetic distance class

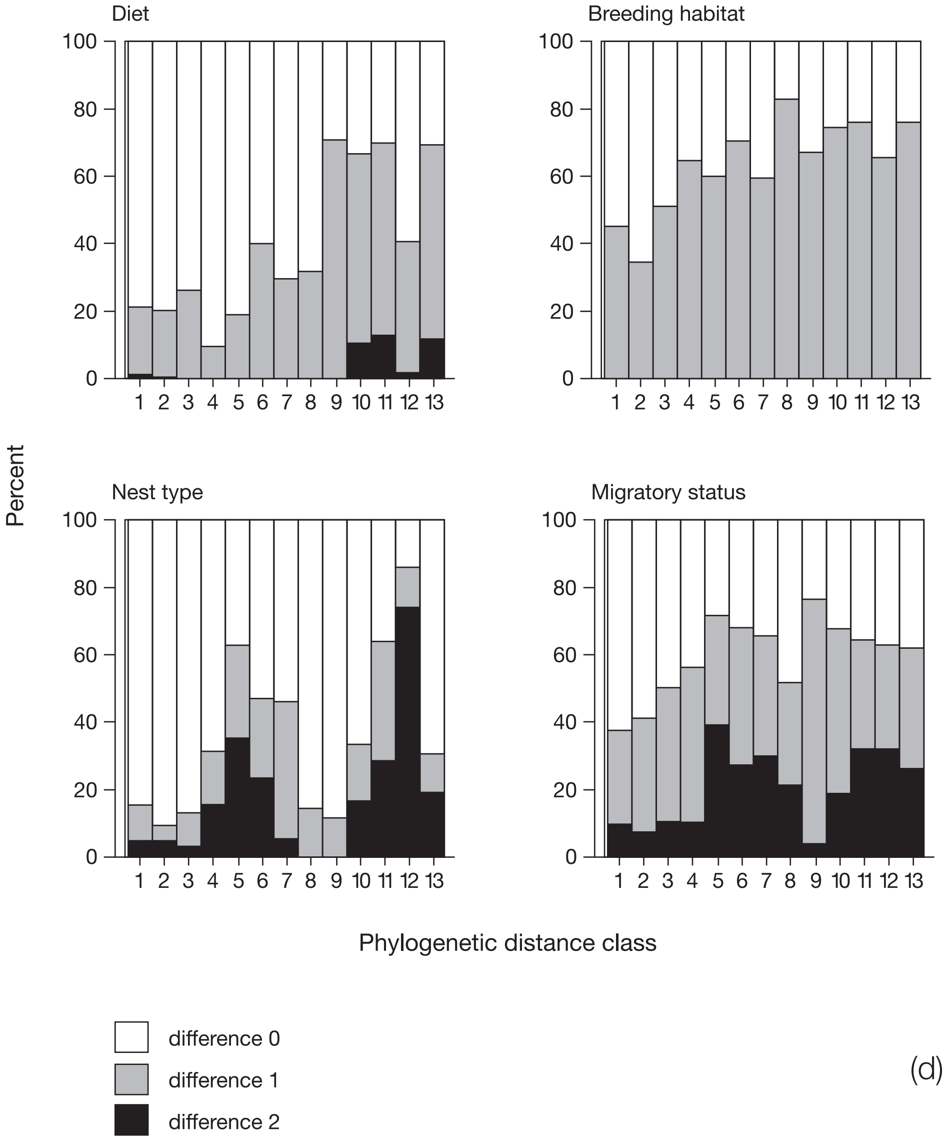


Fig. 1. Maximum, mean and minimum dissimilarity among 151 bird species as a function of phylogenetic distance for 21 morphological, life-history, behavioural and ecological traits. Minimum dissimilarity in each class was zero (identical trait values) or very close to zero. For breeding habitat, migratory status, nest type and diet, the percentage of species pairs with difference 0, difference 1 and difference 2 is displayed. For classes, see Table 1; for statistics, see Table 2.

results, we correlated the range of values each trait covered with its R^2-value (Table 2). There was no significant correlation (Spearman correlation analysis: rho = –0.049, $P = 0.83$). Furthermore, there was no difference in the R^2-values for traits that varied continuously and traits that took only two or three values (Wilcoxon test: $n_1 = 17$, $n_2 = 4$;

Table 2. Regression analysis of the influence of phylogenetic distance on dissimilarity among 151 bird species for 21 morphological, life-history, behavioural and ecological traits using the complete phylogeny[a]

Trait	Number of species–species comparisons	*b*	*t*	*P*	R^2 (%)
Incubation period	11 175	0.0097	61.4	<0.001	25.2
Egg weight	11 175	0.0335	51.8	<0.001	19.3
Body weight	11 175	0.0407	51.2	<0.001	19.0
Clutch size	11 026	0.0093	47.5	<0.001	17.0
Fledging time	10 731	0.0122	46.2	<0.001	16.6
Wing length	11 325	0.0129	42.4	<0.001	13.7
Diet	11 325	0.0243	29.6	<0.001	7.2
Age at maturity	11 026	0.0073	27.6	<0.001	6.4
Eggs per year	10 878	0.0054	25.2	<0.001	5.5
Maximum age	9 870	0.0051	21.3	<0.001	4.4
Range size (LC)	11 325	0.0102	9.6	0.021	0.8
Range size (G)	11 325	0.0058	9.5	n.s.	0.8
Breeding habitat	10 585	0.0060	9.2	<0.001	0.8
Regional abundance (G)	11 325	0.0119	8.4	n.s.	0.6
Local abundance (G)	11 325	0.0088	8.2	0.049	0.6
Nest type	11 175	0.0091	7.7	n.s.	0.5
Seasonal start of breeding	11 175	0.0185	7.0	n.s.	0.4
Regional abundance (LC)	11 325	0.0052	3.6	n.s.	0.1
Migratory status	11 325	0.0009	0.9	n.s.	0.0
Local abundance (LC)	11 325	–0.0007	–1.1	n.s.	0.0
Clutches per year	11 175	–0.0002	–1.2	n.s.	0.0

[a] Significance was evaluated based on Mantel tests with 2000 randomizations.

$z = -0.94$, $P = 0.34$). Thus, differences among variables in their pattern of variation did not influence the results.

Phylogenetic effects within families, among families and among orders

Because orders and families are traditionally used as 'break points' in the evolutionary process, we split the phylogeny in three sections and tested for phylogenetic effects within families (classes 1–4), among families (classes 5–9) and among orders (classes 10–13). Thus, we tested whether species that belonged, for example, to closely related families were more similar in traits than species from distantly related families. These tests involved separate regression analyses for the three subsets of the trait dissimilarity and phylogenetic distance matrices.

The results revealed a strong but variable phylogenetic effect for different traits at different phylogenetic levels (Tables 3–5). For six of the eight traits that did not have overall phylogenetic effects, significant phylogenetic effects were found on at least one of the three smaller phylogenetic levels. For example, for migratory status, phylogenetic effects were not significant over the complete phylogeny but were so within and among families (Tables 3 and 4). In contrast, 8 of the 10 traits that had moderate or strong overall phylogenetic effects (variation explained > 10%) had only weak phylogenetic effects (variation explained < 1%) at some phylogenetic level. For example, phylogeny explained 25.2% of the variation in incubation period for the complete phylogeny, but was not significant within families (Table 3).

Furthermore, 12 of the 21 traits had significant negative phylogenetic effects on at least one phylogenetic level. For example, egg weight had significantly positive phylogenetic effects for the overall phylogeny, within families and among families (Tables 3 and 4), but significantly negative phylogenetic effects among orders (Table 5). This means that species belonging to closely related orders were more dissimilar in egg weight than species from distantly related orders.

Overall, within families, phylogenetic effects appeared to be weak, as they accounted for only an average of 1.4% and a maximum of 4.3% of the variation in trait values (Table 3).

Table 3. Within-family relationship between phylogenetic distance and dissimilarity for avian morphological, life-history, behavioural and ecological traits[a]

Trait	Number of species–species comparisons	b	t	P	R^2 (%)
Egg weight	521	0.0169	4.8	0.003	4.3
Wing length	531	0.0077	4.7	0.003	4.0
Body weight	530	0.0201	4.5	0.001	3.7
Breeding habitat	487	0.0357	4.3	0.001	3.7
Clutch size	522	0.0043	3.7	0.013	2.6
Nest type	531	0.0329	3.5	0.030	2.2
Clutches per year	531	0.0044	2.8	n.s.	1.5
Migratory status	531	0.0277	2.6	0.036	1.3
Local abundance (G)	531	0.0253	2.5	n.s.	1.2
Local abundance (LC)	531	0.0175	2.5	n.s.	1.1
Eggs per year	522	0.0038	2.4	n.s.	1.1
Regional abundance (G)	531	0.0249	1.8	n.s.	0.6
Maximum age	476	0.0028	1.5	n.s.	0.5
Regional abundance (LC)	531	0.0174	1.1	n.s.	0.2
Range size (G)	531	0.0037	0.6	n.s.	0.1
Range size (LC)	531	0.0040	0.3	n.s.	0.0
Incubation period	531	−0.0004	−0.6	n.s.	0.1
Fledging time	489	−0.0016	−0.8	n.s.	0.1
Seasonal start of breeding	527	−0.0446	−1.5	n.s.	0.4
Age at maturity	525	−0.0035	−1.8	n.s.	0.6
Diet	531	−0.0150	−2.4	n.s.	1.0

[a] Significance was evaluated based on Mantel tests with 2000 randomizations.

Table 4. Among-family relationship between phylogenetic distance and dissimilarity for avian morphological, life-history, behavioural and ecological traits[a]

Trait	Number of species–species comparisons	*b*	*t*	*P*	R^2 (%)
Age at maturity	3338	0.0331	29.2	<0.001	20.4
Incubation period	3359	0.0111	26.1	<0.001	16.9
Wing length	3359	0.0263	18.6	<0.001	9.3
Body weight	3278	0.0534	15.1	<0.001	6.5
Range size (G)	3359	0.0496	13.8	0.004	5.4
Fledging time	3158	0.0128	11.4	0.001	4.0
Egg weight	3359	0.0278	11.3	<0.001	3.7
Diet	3359	0.0332	7.9	0.032	1.8
Range size (LC)	3359	0.0351	5.3	N.S.	0.8
Seasonal start of breeding	3336	0.0615	3.9	N.S.	0.4
Maximum age	2804	0.0035	3.0	N.S.	0.3
Eggs per year	3358	0.0017	1.7	N.S.	0.1
Clutch size	3358	0.0010	1.3	N.S.	0.0
Breeding habitat	3081	0.0029	0.7	N.S.	0.0
Regional abundance (G)	3359	0.0023	0.3	N.S.	0.0
Local abundance (G)	3359	–0.0054	–0.9	N.S.	0.0
Regional abundance (LC)	3359	–0.0099	–1.1	N.S.	0.0
Local abundance (LC)	3359	–0.0111	–2.8	N.S.	0.2
Migratory status	3359	–0.0272	–4.1	0.030	0.5
Clutches per year	3359	–0.0125	–13.5	<0.001	5.1
Nest type	3359	–0.0941	–13.7	<0.001	5.3

[a] Significance was evaluated based on Mantel tests with 2000 randomizations.

Seven traits had significantly positive phylogenetic effects and no trait had significantly negative phylogenetic effects. Among families, phylogenetic effects were relatively strong, with an average of 3.8% and a maximum of 20.4% of the variation explained by relatedness (Table 4); 8 of the 11 significant traits were positive and three were negative. Among orders, phylogenetic effects were relatively weak, explaining only an average of 1.2% and a maximum of 3.0% of the variation (Table 5); however, among orders, all 10 of the significant phylogenetic effects were negative.

DISCUSSION

Phylogenetic effects on morphological and life-history versus behavioural and ecological traits

Significant phylogenetic effects were found for diet and for all morphological and life-history traits except number of clutches per year (Table 6). Thus, closely related species tended to be more similar in these traits than distantly related species. In comparative

Table 5. Among-order relationship between phylogenetic distance and dissimilarity for avian morphological, life-history, behavioural and ecological traits[a]

Trait	Number of species–species comparisons	*b*	*t*	*P*	R^2 (%)
Clutch size	7146	0.0072	10.9	n.s.	1.6
Nest type	7285	0.0353	9.9	n.s.	1.3
Body weight	7367	0.0040	1.6	n.s.	0.0
Migratory status	7435	0.0040	1.3	n.s.	0.0
Fledging time	7084	0.0008	1.0	n.s.	0.0
Breeding habitat	7017	−0.0017	−0.9	n.s.	0.0
Seasonal start of breeding	7312	−0.0274	−3.4	n.s.	0.2
Range size (G)	7435	−0.0066	−3.7	n.s.	0.2
Diet	7435	−0.0146	−5.7	n.s.	0.4
Range size (LC)	7435	−0.0213	−6.9	n.s.	0.6
Regional abundance (G)	7435	−0.0351	−8.4	n.s.	0.9
Regional abundance (LC)	7435	−0.0372	−8.9	0.026	1.1
Local abundance (G)	7435	−0.0301	−9.4	0.022	1.2
Egg weight	7295	−0.0208	−9.9	0.002	1.3
Local abundance (LC)	7435	−0.0202	−10.3	0.017	1.4
Eggs per year	6998	−0.0075	−11.0	0.006	1.7
Maximum age	6590	−0.0082	−11.0	0.005	1.8
Wing length	7435	−0.0123	−13.0	<0.001	2.2
Incubation period	7285	−0.0071	−14.0	<0.001	2.6
Clutches per year	7285	−0.0087	−14.9	<0.001	3.0
Age at maturity	7163	−0.0136	−16.1	0.001	3.5

[a] Significance was evaluated based on Mantel tests with 2000 randomizations.

studies that involve those traits, species cannot be considered as independent sampling units. In contrast, for number of clutches per year and for all behavioural and ecological traits except diet, the phylogenetic effect was very weak (Table 6). Phylogenetic distance explained less than 1% of the variation in dissimilarity among species. Furthermore, no phylogenetic effects were found for regional abundance at the regional and landscape scales, for range size at the regional scale, for local abundance at the landscape scale, for nest type, migratory status, seasonal start of the breeding period and for number of clutches per year. Thus, our results suggest that, for most behavioural and ecological traits examined here, phylogenetic effects may not compromise comparative analysis of large species assemblages to a great extent.

Phylogenetic effects were especially strong in morphological traits such as body weight, but also in life-history traits correlated with body weight, such as egg weight, clutch size, incubation period and fledging time (Table 6). Moderate phylogenetic effects were found in age variables such as age at maturity and maximum age, and for number of eggs per year (which was a combination of strong phylogenetic clutch size effects and weak phylogenetic

Table 6. Differences in phylogenetic effects on 10 morphological and life-history traits and on 11 ecological and behavioural traits of 151 bird species using the complete phylogeny (data from Table 2)

	Variation explained (R^2)		
	<1%	1–10%	>10%
Morphological and life-history traits			
Body weight			√
Wing length			√
Egg weight			√
Clutch size			√
Incubation period			√
Fledging time			√
Age at maturity		√	
Maximum age		√	
Eggs per year		√	
Clutches per year	√		
Ecological and behavioural traits			
Diet		√	
Breeding habitat	√		
Nest type	√		
Migratory status	√		
Seasonal start of breeding	√		
Regional abundance (LC)	√		
Regional abundance (G)	√		
Local abundance (LC)	√		
Local abundance (G)	√		
Range size (LC)	√		
Range size (G)	√		

clutches per year effects). The reason why seasonal start of the breeding period and number of clutches per year did not have phylogenetic effects might be that these traits are strongly influenced by migratory behaviour (Kipp, 1943; von Haartman, 1968; O'Connor, 1990), which itself did not have phylogenetic effects.

The results of the present study are very similar to those obtained by analysing the evolutionary lability of morphological, life-history and behavioural traits of mammals (Gittleman *et al.*, 1996). Also for mammals, morphological and life-history traits – such as brain weight, body weight, gestation length and birth weight – had lower phylogenetic flexibility than behavioural traits, such as home-range size and group size. But in the study of Gittleman *et al.*, morphological traits showed generally stronger phylogenetic effects than life-history traits.

These results can be used to investigate possible mechanisms that produce phylogenetic effects. Three reasons why closely related species tend to be more similar than distantly related species have been suggested: phylogenetic niche conservatism, phylogenetic time lags and different adaptive responses (Harvey and Pagel, 1991). The results of the present study suggest that phylogenetic niche conservatism might not play an important role in phylogenetic effects. Phylogenetic niche conservatism assumes that past and present phenotypes of a lineage are likely to have occupied similar niches (Grafen, 1989; Wanntorp *et al.*, 1990; Harvey and Pagel, 1991). The niches of birds are usually defined by ecological and behavioural variables such as breeding habitat, diet, foraging mode, migratory behaviour and nest type (Wiens, 1989). All niche variables that have been addressed in the present study had weak, or at most moderate, phylogenetic effects. All niche variables except diet had smaller phylogenetic effects than morphological and life-history traits. Closely related species tended to be similar in morphological and life-history traits but they were not similar in breeding habitat, migratory behaviour and nest type. Obviously, species changed their niche much faster than they changed, for example, body weight. This suggests that niche conservatism did not cause phylogenetic effects. Consequently, phylogenetic effects must be produced by phylogenetic time lags or by different adaptive responses (Harvey and Pagel, 1991).

Variability of phylogenetic effects at different phylogenetic levels

An important result of this study was that phylogenetic effects were strong but very variable when tested at different phylogenetic levels. To work with an ecologically and evolutionary similar group of species, many studies are conducted within families. Phylogenetic effects can appear or disappear within families. Some traits – for example, migratory status – which had no overall phylogenetic effects had significant phylogenetic effects within families. Other traits – for example, incubation period – which had strong phylogenetic effects over the complete phylogeny had no phylogenetic effects within families. One possible reason for the lack of phylogenetic effects on incubation period within families is that incubation period was on average similar within families (Fig. 1). There was, however, variation. Even within the same genus (e.g. *Podiceps*) we find species such as the Great-crested Grebe (*P. cristatus*) with an incubation period of 28 days and the Black-necked Grebe (*P. nigricollis*) with an incubation period of 20–21 days (Bezzel, 1985). The crucial point is that the variation in incubation period within families could not be explained by phylogenetic relatedness. It is important to note that we quantified phylogenetic effects on incubation period within families by pooling all 34 families in the data set. From the variance found among different phylogenetic levels, we expect that some families do nevertheless show phylogenetic effects for incubation period.

To control for phylogenetic effects, some ecological and evolutionary studies have been conducted at higher phylogenetic levels comparing, for example, different families (Krebs *et al.*, 1989; Sherry *et al.*, 1989). The present study demonstrated, however, that strong phylogenetic effects are also found among families and even among orders. For most traits, closely related families tended to be more similar than distantly related families and closely related orders tended to be more *dis*similar than distantly related orders. Thus, analyses at the family and order level do not control for phylogenetic effects. Phylogenetic effects among families were even stronger than those within families. One possible reason for strong phylogenetic effects among families is that the variation in most traits is much higher among than within families (Bell, 1989; Harvey and Pagel, 1991). This increase in variation with phylogenetic distance is why researchers have tried to control for phylogenetic effects by conducting comparative studies at the family or order level. Again, however, the important point is that a relatively large amount of variation among families is, unfortunately, related to phylogeny.

These results are again similar to those obtained by analysing the evolutionary lability of morphological, life-history and behavioural traits of mammals (Gittleman *et al.*, 1996). Also, for mammals, phylogenetic effects were variable at different phylogenetic levels, with significantly negative phylogenetic effects occurring in the deeper parts of the phylogeny. Thus far, it is difficult to explain which micro-evolutionary processes cause this variability of phylogenetic effects and particularly the large number of significantly negative phylogenetic effects. It remains to be tested whether simple models of micro-evolutionary processes such as Brownian motion are sufficient to account for these patterns.

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