Sources of distinctness of juvenile plumage in Western Palearctic passerines

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Juveniles of many avian species possess a spotted or mottled body plumage that is visually distinct from the plumage of adults. In other species, however, juveniles fledge with a body plumage that is just a pale representation of adult female plumage. The reasons for this variation are poorly understood. Several hypotheses concerning social (parent–offspring, adult–juvenile, juvenile–juvenile), ecological (predation risk) and physiological (costs of plumage development) implications of juvenile body plumage are presented in relation to predictions concerning associations with certain ecological and life-history attributes of avian species. In the present study, we conduct a phylogenetically corrected comparative analysis of Western Palearctic passerines looking for sources of variation in the incidence of distinct and adult-like juvenile body plumages. We scored plumages based on plates in the *Handbook of the Birds of the Western Palearctic* (Cramp & Perrins, 1988–1994; Oxford University Press) (*HBWP*) and entered body mass, migratory habits, habitat, nestling diet, breeding dispersion, gregariousness, duration of the nestling period, type of nest, conspicuousness of female plumage, and sexual dimorphism as explanatory variables, as presented in *HBWP*, in phylogenetic generalized least square regression analyses. One-third of the species presented distinct juvenile body plumages, which lasted on average for the first 2 months of life. Body mass, conspicuousness of female plumage, migratory habits, and habitat were significantly associated with interspecific variation in distinctness of juvenile plumage, with smaller species, more conspicuous species, migrants, and species from forested habitats showing distinct juvenile plumages with higher frequency. The phylogenetic signal was moderately high. Assuming that conspicuous adult plumage is costlier to produce than distinct juvenile body plumage (pigments, conspicuousness), the need to acquire social status among juveniles before the winter may explain the more adult-like plumage in resident species because juveniles will probably compete with individuals that they may have known during their first months of life. On the other hand, migrant juveniles may compete with a different set of individuals in winter quarters and can use savings in resources necessary for developing adult-like plumages to improve migration capacity by allocating resources to other functions. The association with habitat could be related to juveniles in open habitats participating in more extended interactions with other juveniles than in forested habitats where lower visibility may reduce the capacity to detect or respond to signals from juvenile conspecifics. More studies on this possibly crucial life stage are needed. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, **102**, 440–454.

ADDITIONAL KEYWORDS: nestling diet – nonbreeding season – phylogeny – predation – social status.

INTRODUCTION

The juveniles of many animals show typical colorations that differ from those exhibited by adults and whose function is poorly understood (Guiasu & Win-terbottom, 1998; Creer, 2005; Kraus & Allison, 2009). Thus, juveniles of many avian species possess spotted or mottled body plumage that is clearly distinct from the plumage of adults. In other species, however, juveniles fledge with a body plumage that is just a pale representation of adult plumage. In sexually dimorphic species, this adult-like juvenile plumage is

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most often more similar to female plumage than to male plumage. In a few species, juveniles are already dichromatic when leaving the nest (Edelaar, Phillips & Knop, 2005; Siefferman et al., 2008). Juvenile body plumage developed in the nest has poor structural integrity compared to subsequent plumages, and this has probably favoured replacement with a structurally stronger first basic plumage as soon as possible after fledging (Butler, Rohwer & Speidel, 2008). Accordingly, juvenile body plumage is normally moulted some months after hatching. Its pattern and coloration must therefore be related to life as nestling, dependent fledgling, and recently independent juvenile. The question of the distinctness of juvenile body plumage is not related to the issue of delayed plumage maturation (Berggren, Armstrong & Lewis, 2004), which concerns variation in moults subsequent to the first body moult. We are also not concerned with flight feathers for which moult strategies are affected by selection pressures related exclusively to flight (Jenni & Winkler, 1994). One interpretation of variation in juvenile body plumage, which is challenged in the present study, is that it is merely an expression of phylogenetic origins of adult plumage (Graber, 1955), a version of the 'ontogeny recapitulates phylogeny' argument. However, this interpretation does not explain the variation in colour and pattern among closely-related taxa (Maley & Winker, 2007; Ligon & Hill, 2009). Moreover, if distinctness of juvenile body plumage is mainly related to selection pressures on adults, we require first an explanation of why ancestral adult plumages as expressed by present juvenile plumages differ according to certain ecological factors, and then an explanation of why the same ecological factors have subsequently promoted either changes in adults leading to distinct juveniles, or to conservatism in adults leading to adult-like juveniles. Thus, it is more parsimonious to consider that ecology has driven a single change in juvenile than two changes in adult body plumage. Based on this assumption, we aim to test whether ecology and life history independent of phylogeny explain the interspecific variation in degree of distinctness of juvenile plumages to some degree.

Several hypotheses based on the literature can be presented to explain variation in distinctness of juvenile body plumage, which may be grouped according to social, ecological, and physiological selection pressures. With respect to selection pressures as a result of social interactions, adult-like plumage often includes signals used in visual communication among adults and may be favoured by social requirements during juvenile life. First, adult-like plumage of juveniles may be related to the need for accurate parent–offspring communication relating to nestling demand and/or nestling quality (Siefferman et al., 2008).

Thus, it has been recently shown that parents respond to differences in nestling plumage through allocation of care (Penteriani et al., 2007; Galván, Amo & Sanz, 2008; Tanner & Richner, 2008; Ligon & Hill, 2010). Second, juveniles may be involved from the start in interactions with adults other than parents. Thus, a distinct juvenile plumage during the first months of life may be a way of avoiding adult territorial or social aggression (Ligon & Hill, 2009; López et al., 2005). Third, social interactions among juveniles may be crucial for acquiring status and obtaining resources needed for future life stages (Piper, 1995; Ellsworth & Belthoff, 1999; Poisbleau et al., 2009). Because it is likely that adult-like plumages that function in sexual or social selection more efficiently signal individual phenotypic quality, adult-like plumages could be used to signal status and quality among juveniles (Leary, Sullivan & Hillgarth, 1999; Hogstad, 2003). In this scenario, we predict that development of adult-like plumage in the nest instead of a cryptic mottled body plumage will occur mainly in species where social interactions among juveniles during their first months of life may have repercussions for future resource acquisition (Hogstad, 1999).

One of the main ecological selection pressures that has been hypothesized to affect juvenile fitness is predation risk (Rush & Stutchbury, 2008). The post-fledging juvenile life stage is characterized by strong predation pressure given the inexperience and poor flight capabilities of juveniles during their first weeks out of the nest (Naef-Daenzer, Widmer & Nuber, 2001; Berkeley, McCarty & Wolfenbarger, 2007; Miranda, Alberti & Iborra, 2007). Thus, a cryptic juvenile body plumage may be favoured by predation pressure on fledglings and juveniles (Graber, 1955). Accordingly, environmental conditions favouring the probability of predation on juveniles would select for cryptic distinct juvenile plumages.

One of the main physiological costs associated with the development of adult-like plumages in the nest is related to pigment allocation (Deviche, McGraw & Underwood, 2008) and to costs of building the appropriate structure of signalling contour feathers (Butler et al., 2008; Tanner & Richner, 2008). The development of body plumage may also be involved in a trade-off with production of flight feathers. Any factor favouring strong and therefore costly flight feathers may thereby affect the type of body plumage to be developed in the nest. Therefore, depending on the function of juvenile plumage with respect to sociality, predation or costs of development, we can derive certain predictions concerning associations of juvenile body plumage with specific social, ecological, and life-history traits. As presented above, social functions in turn could be related to parent–offspring communication, competition with adults or competition among

juveniles. If parent–offspring communication is important, we would expect the type of juvenile body plumage to be related to the duration of the nestling and post-fledging periods (Galván *et al.*, 2008; Tanner & Richner, 2008). In addition, if avoiding adult-juvenile conflicts are important for juvenile fitness (Ligon & Hill, 2009), the type of juvenile plumage should be related to breeding dispersion, with territorial species exhibiting more distinct plumages than colonial species. Moreover, gregariousness after breeding or during the nonbreeding season may affect the need to signal status or condition either in colony surroundings or winter flocks, so that we could expect more cases of adult-like juvenile body plumage in colonial or gregarious species. On the other hand, if adult-like plumages mainly concern interactions among juveniles, we would expect an association of plumage type with migratory strategy. Migrants may experience different selection pressures than residents because social interactions among juveniles may be postponed at least until arrival at winter quarters, whereas status as juveniles may impact overwinter survival in residents and may be established soon after fledging. Moreover, habitat-dependent signalling efficiency could also affect plumage development, with adult-like plumages being more common in conditions of more efficient signalling if parent–offspring communication or juvenile social competition were selectively important. On the other hand, open-cup nesters, females in particular, should be more cryptic than cavity nesters to avoid nest detection by predators, which would lead to more adult-like plumages in open nesters. Both scenarios predict that open nesters should show a higher incidence of adult-like plumage (i.e. females and nestlings with more cryptic plumage).

Predation of juveniles is probably important in most habitats (Rush & Stutchbury, 2008; Davis & Fisher, 2009; Wightman, 2009), although its effects may depend on visibility and possibilities of hiding for juveniles. If predation pressure after leaving the nest is driving juvenile plumage development, gregariousness and habitat should show significant effects. For example, juveniles in flocks could be safer from predation, whereas forested habitats could offer more possibilities of evasion for inexperienced and poorly flying juveniles. Adult-like plumages would be less costly in such conditions. Thus, gregariousness and habitat structure should predict interspecific variation in adult-like plumage.

Finally, as juvenile plumage is developed by nestlings, the capacity to collect nutritious food by parents during the nestling period may also affect the possibility of developing pigmented or structurally complex adult-like plumages (Butler *et al.*, 2008). Pigmented or structurally more complex adult-like plumages are likely costlier than the distinct juvenile plumages, so that developing nestlings may use saved resources to improve flight feathers or allocate resources to other important functions such as migration. If metabolic costs of body plumage development were crucial, we could expect that offspring diets offering more nutrients necessary for pigmentation, such as carotenoids, or for structural strengthening of feathers, would select for more adult-like plumages. Moreover, migrating juveniles may save costs associated with developing adult-like body plumage and use these resources to improve flight feather quality or other migration related functions, rendering more cryptic and less adult-like plumages in migrants. Sexual interactions are not involved at this early stage, so that mating system and sexual dimorphism may be less important. However, drabness of adult plumage may reduce the metabolic cost of developing an adult-like juvenile plumage.

A way of resolving the ecological and life-history aspects determining the development of distinct or adult-like plumage in the nest is through comparative analyses of species with a well-resolved phylogeny like passerines. In the present study, we address the question of why nestlings in some species develop a specific distinct body plumage, whereas, in others, they grow a body plumage closely similar to adults. Accordingly, we analyze the juvenile plumage of passerine species included in the *Handbook of Birds of The Western Palearctic* (*HBWP*; Cramp & Perrins, 1988–1994) for which there is information about life history and general ecology. We analyze cases of distinct and adult-like juvenile body plumages in relation to migratory strategy, habitat, nestling diet, sexual dimorphism, conspicuousness of adult body plumage, nest type (cavity, domed or open nests), duration of the nestling period, breeding dispersion, and degree of gregariousness during the nonbreeding season.

MATERIAL AND METHODS
DATA COLLECTION

We characterized juvenile body plumage of passerines as adult-like, distinct or intermediate from the coloured plates of volumes V–IX of *HBWP*. These plates represent birds in larger size than in field guides and constitute probably the most scientifically accurate representation of Western Palearctic birds. Only species for which juveniles were separately depicted have been included (250 passerine species). Juveniles were compared with females (juveniles were never similar to males in sexually dimorphic species) in breeding plumage or during spring. If the sex of juveniles was specified in the plate legend (only

in a few cases), they were compared with same-sex adults. Morphology such as tail length or bill length or coloration of structures other than body feathers was not considered. Distinctness refers to clearly different colour patterns and markings and not to intensity of coloration of feathers (adult-like juvenile plumages are mostly paler than adult ones). To reduce the possibility of involuntary bias, a non-informed layperson and two students without knowledge about the hypotheses being tested characterized cases of distinctness and likeness between juveniles and adult females during brief observations of the images in the plates, with any hesitation leading to a consideration of cases as intermediate.

From the first printed edition of *HBWP*, we extracted the information concerning migration strategy, habitat, nestling diet, gregariousness, and breeding dispersion and scored these traits as specified in Table 1. For species with polymorphism with respect to migratory strategy, we used the range of strategies as mentioned in the corresponding section for the species in *HBWP* to obtain a score (Table 1). We also scored female breeding plumage as drab or conspicuous by the same three observers as above. We obtained information in *HBWP* on sexual dimorphism, nest type as cavity, domed or open nests, body mass of females, and duration of nestling period in days (there were too few data on post-fledging dependence to allow inclusion). The unavailability of precise information on some aspects for some species in *HBWP* induced slight differences in sample size for different variables (Appendix 1).

To estimate the duration of juvenile plumage, we used the moult diagrams of the 'Key to Sexing and Ageing of European Passerines' (Busse, 1984). We measured the length of the totally black part of the lowest section of the moult diagram which is the section that refers to body feathers (for details about moult diagrams, see Busse 1984). The totally black part refers to the time period when only non-moulted juveniles are captured and ringed and approximately corresponds to the duration of juvenile plumage for individual birds. We assume that these moult diagrams are the most accurate presentation of the staging of body moult for European passerines available at present.

Species values for all variables can be found in Appendix 1.

COMPARATIVE AND STATISTICAL ANALYSES

Taxonomic groups such as species cannot be considered statistically independent observations as a result of the confounding effects of common ancestry (Harvey & Pagel, 1991). To control for the phylogenetic relationship among the sampled species we used phyloge-

Table 1. Scores obtained from Volumes V–IX of *Handbook of the Birds of the Western Palearctic* and their categorization

Juvenile plumage distinctness
   1 = Adult-like
   2 = Intermediate
   3 = Distinct
Adult plumage conspicuousness (females in spring)
   1 = Conspicuous
   2 = Drab
Migration
   1 = Resident,
   2 = Resident to short distance, resident to partially migratory, resident to eruptive
   3 = Altitudinal, short-distance, partial migrant, resident to migratory
   4 = Migratory to short-distance, migratory to resident
   5 = Migratory
Habitat
   1 = Desert
   2 = Savannah, steppe, cliffs, high mountain
   3 = Scrub, tundra, grassland
   4 = Riparian, groves, wetlands
   5 = Open woodlands
   6 = Forest
Nestling diet
   1 = Mostly invertebrates
   2 = Invertebrates and fruits, invertebrates and seeds
   3 = Mostly seeds, mostly fruits
Breeding dispersion
   1 = Territorial
   2 = Group living
   3 = Grouped territories
   4 = Small colonies
   5 = Colonial
Gregariousness during nonbreeding season
   1 = Territorial
   2 = Not gregarious
   3 = Moderately gregarious
   4 = Gregarious

netic generalized least squares regression (PGLS) models (Pagel, 1997, 1999) as implemented in the R statistical environment (R Development Core Team 2009; v2.9.2, available at http://www.R-project.org) with the appropriate libraries ('ape', 'MASS', and 'mvtnorm') and the additional unpublished function by R. Freckleton (University of Sheffield) (pglm3.3.r; available on request). The PGLS approach characterizes evolutionary changes along each branch of a phylogeny through the variance components of traits and controls for non-independence among species by incorporating a matrix of the covariances among species based on their phylogenetic relationships (Martins & Hansen, 1997; Pagel, 1997, 1999). Thus,

phylogenetic information is incorporated to the error term, thereby controlling for the shared evolutionary history among species (Harvey & Pagel, 1991; Martins & Hansen, 1997). The method applies likelihood ratio statistics to test hypotheses of correlated trait evolution and also to estimate the phylogenetic signal (λ). The phylogenetic signal represents the importance of phylogenetic corrections in the models (Freckleton, Harvey & Pagel, 2002), which varies between 0 (phylogenetic independence) and 1 (species' traits covary in direct proportion to their shared evolutionary history) (Pagel, 1997, 1999). λ was incorporated to the error term to control for the effect of phylogenetic relationship on the degree of phylogenetic dependence of the PGLS models.

Our phylogenetic hypothesis was based on Sibley & Ahlquist (1990) and Livezey & Zusi (2007) for the basal nodes, whereas upper nodes were based on Jønsson & Fjeldså (2006) plus additional information in Aliabadian *et al*. (2007) and Voelker *et al*. (2007) for genera *Oenanthe* and *Turdus*, respectively (Appendix 2). We arbitrarily assigned all internode branches equal to one but constrained tips to be contemporaneous (Pagel 1992).

We considered the index of plumage resemblance between juveniles and adult females as a continuous dummy variable (adult-like = 1; intermediate = 2; distinct = 3). Scores for adult female plumage drabness/conspicuousness (1 = conspicuous; 2 = drab) of the three observers were also used as a dummy variable. The use of dummy variables in regression analyses is well established in the statistical literature (Zar, 1999) because it allows the performance of multivariate regression analyses including discrete variables that can be controlled for phylogenetic influences. Because scores of the three estimations for juvenile plumage distinctness ($r = 0.78$, $P < 0.001$) and adult plumage conspicuousness ($r = 0.66$, $P < 0.001$) were moderately repeatable, average scores for the three observers were used in the analyses.

Before the analyses, body mass of females was $\log_{10}$ transformed and the durations of juvenile plumage and nestling period were $\log_e$ transformed to attain normal distributions. In an attempt to explain interspecific differences in plumage distinctiveness between females and juveniles, we performed PGLS models with plumage resemblance as an dependent variable and variables predicted to affect interspecific differences as independent variables both in univariate and multivariate statistical approaches. The multivariate approach consisted of a backward procedure; starting with the complete model excluding interactions (to reduce the number of factors), we removed one-by-one the variables with the largest associated *P*-values. The model that included all variables with $P < 0.1$, was considered as the final model.

Table 2. Univariate results from the performed phylogenetic generalized least square regression models explaining the distinctness of juvenile plumage

Explanatory variable	N	Beta (SE)	t-value	P
Nest type	245	0.015 (0.076)	0.193	0.847
Sexual dimorphism	250	0.047 (0.117)	0.400	0.690
Plumage conspicuousness	250	−0.444 (0.136)	3.253	0.001
Breeding dispersion	235	0.117 (0.042)	2.779	0.006
Gregariousness (nonbreeding)	217	−0.012 (0.065)	0.181	0.857
Duration of juvenile plumage	163	−0.001 (0.003)	0.166	0.868
$\log_e$ nestling period	217	0.135 (0.273)	0.494	0.622
Migration	249	0.072 (0.030)	2.423	0.016
Nestling diet	214	−0.160 (0.128)	1.247	0.214
Habitat	246	0.103 (0.035)	2.981	0.003
$\log_{10}$ body mass	247	−0.624 (0.250)	2.490	0.013

The effects of juvenile plumage duration and nestling period were estimated after controlling for the effects of body mass.

RESULTS

The average distinctness score was 1.73 ± 0.85 and the mean duration of juvenile body plumage was 59 days (range 27–164 days). Of the 192 unanimously characterized species, 58 (30.2%) showed distinct juvenile body plumages (Appendix 1).

Univariate analyses revealed that body mass, adult plumage conspicuousness, breeding dispersion, migration, and habitat were the variables predicting distinctness of juvenile plumage (Table 2). Multivariate analyses again identified migration [PGLS, partial beta (SE) = 0.07 (0.03), $t = 2.15$, d.f. = 196, $P = 0.033$] and habitat (PGLS, partial beta (SE) = 0.07 (0.03), $t = 2.07$, d.f. = 196, $P = 0.039$] as significant, with these variables entering the final model together with body mass [PGLS, partial beta (SE) = −0.91 (0.25), $t = 3.60$, d.f. = 196, $P < 0.001$] and adult plumage conspicuousness [PGLS, partial beta (SE) = −0.44 (0.14), $t = 3.15$, d.f. = 196, $P = 0.002$]. Only marginal significance were attained by duration of nestling period [PGLS, partial beta (SE) = 0.49 (0.27), $t = 1.81$, d.f. = 196, $P = 0.072$] and breeding dispersion [PGLS, partial beta (SE) = 0.07 (0.04), $t = 1.66$, d.f. = 196, $P = 0.098$]. The final model including these variables explained 15.6% of the variation in juvenile plumage distinctness and was highly significant ($F = 7.22$, d.f. = 6,196, $P < 0.001$). Distinct juvenile plumage appeared more frequently among migrants than among resident species, and more frequently among species inhabiting mesic than species
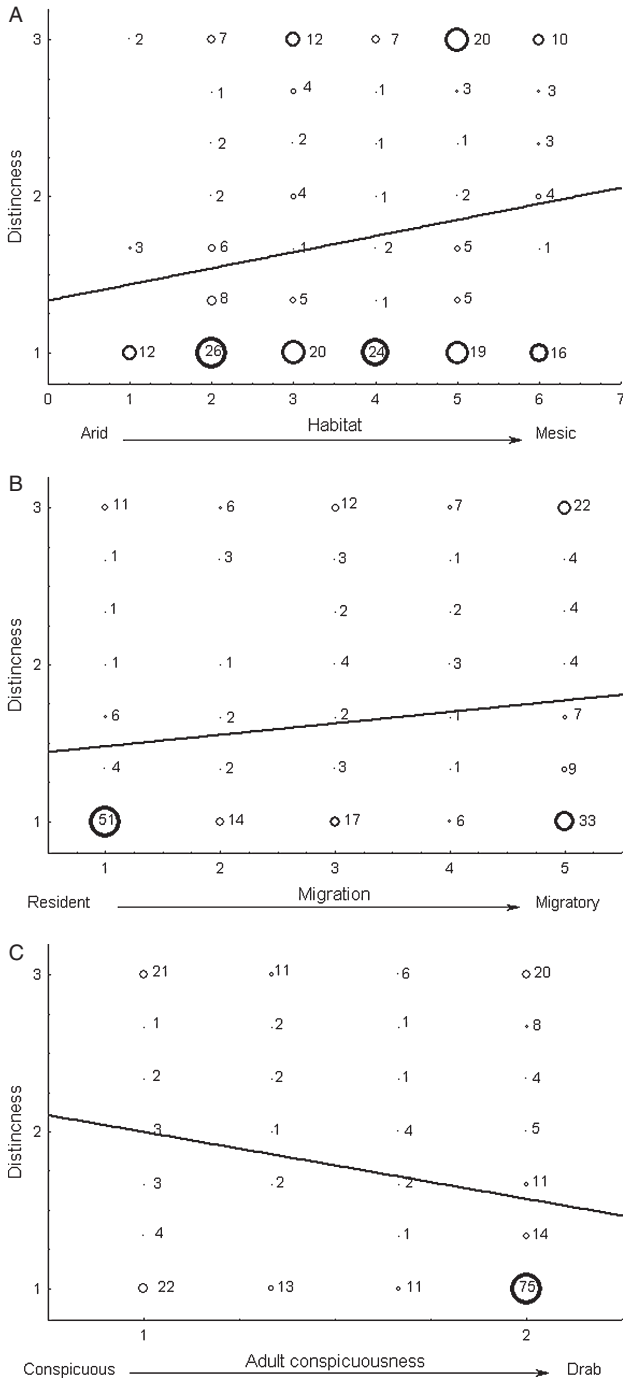
Figure 1. Relationships between average values of scores of juvenile body plumage distinctness (1 = similar to adults, 2 = intermediate, 3 = distinct) obtained by three different independent observers and (A) migratory behaviour (1 = resident; 2 = resident to short distance, resident to partially migratory, resident to eruptive; 3 = altitudinal, short-distance, partial migrant, resident to migratory; 4 = migratory to short-distance, migratory to resident; 5 = migratory) (B) breeding habitat (A) (1 = desert; 2 = savanna, steppe, cliffs, high mountain; 3 = scrub, tundra, grassland; 4 = riparian, groves, wetlands; 5 = open woodlands; 6 = forest), and (C) conspicuousness of adult female breeding body plumage (1 = conspicuous, 2 = drab). Circled areas are proportional to number of species with the same values, which is also indicated by numbers. Beta of regression lines corresponds to phylogenetically corrected partial values of the final model explaining juvenile plumage distinctness that included body mass, conspicuousness of adult plumage, duration of nestling period, migration, and habitat.

level of phylogenetic influence on the detected relationships.

DISCUSSION

No phase of the avian life cycle is less well-known than the weeks after young birds leave the nest during which juvenile body plumage is present. Distinct juvenile body plumages are only present in less than one-third of Western Palearctic passerines, so adult-like (meaning female-like) body plumages are the norm in these species. Juvenile body plumage lasts for periods ranging from 25 days to several months after hatching (Busse, 1984; Cramp & Perrins, 1988–1994; Jenni & Winkler, 1994), meaning that young birds of most species do not migrate or spend the winter in their juvenile body plumage. Because juveniles moult before these critical phases, juvenile body plumage only affects their life directly as a nestling, a recently fledged young fed by parents, and a recently emancipated juvenile, although the effects during these phases may have implications for life during the subsequent nonbreeding season (Leary *et al.*, 1999; Hogstad, 2003). Juvenile plumage may affect parent–offspring communication, territorial interactions between juveniles and adults, and queuing for territories or social status among juveniles. Dominance rank as juvenile may crucially affect social status later (Piper, 1995; Poisbleau *et al.*, 2009). Rank may also relate to predation risk after fledging. Moreover, its development in the nest may involve physiological costs dependent on pigmentation and feather structure related to signalling, and these costs may be traded off against costs of flight feather development. Thus, there may be conflicting selection

inhabiting arid habitats (Fig. 1). It was also more common in smaller species and in species where adults exhibited conspicuous adult female body plumages (Fig. 1).

The phylogenetic signal (λ) was high (0.89) and significantly different from 1 (maximum log-likelihood test, $P < 0.001$) and from 0 (maximum log-likelihood test, $P < 0.001$), which implies a moderately high

pressures for juveniles such as there are for adults. These conflicts may have had different resolutions for juvenile plumage depending on the ecology and life history of the species involved. All these possibilities cannot be directly tested with basic comparative information, although they may be related to crucial specific life-history and ecological traits obtained from the literature. Any ecological factor affecting juvenile sociality, predation risk or body feather growth in the nest could be involved in explaining the observed interspecific variation in the distinctness of juvenile body plumages.

In the present study, we have identified two crucial aspects of avian ecology that affect type of juvenile plumage, namely migratory strategy and habitat. Cases of distinct juvenile plumages are more frequent among migratory species than among residents, and more frequent among species inhabiting forested than arid habitats. Additionally, adult plumage conspicuousness and body mass show strong effects on juvenile body plumage distinctness. Distinct juvenile plumages were more frequent among small birds than among large ones and more frequent among species with more conspicuous adult female body plumages. Phylogeny shows a signal of moderate strength, indicating a clear phylogenetic conservatism in the evolutionary history of juvenile body plumage of passerines. However, ecology also plays a significant role in the evolution of this trait, as indicated by the results obtained in the present study. On the other hand, neither diet, type of nest, sexual dimorphism, nor gregariousness during the nonbreeding season showed any significant effects in multivariate analyses. Breeding dispersion resulted in an association with plumage type in univariate analyses, with a higher frequency of distinct plumages in more colonial species. However, the result for breeding dispersion should be interpreted cautiously because of the multiple univariate tests performed and because the tendency was only marginally significant in multivariate analyses, suggesting that shared variance with other variables included in the final model (i.e. migration and habitat) may be responsible for the univariate result.

Conspicuous adult plumages may involve costly investment in pigments or feather structures related to sexual selection processes that juveniles do not experience. Furthermore, if conspicuousness of body plumage is related to the probability of detection by depredators, the evolution of cryptic plumage would be more likely in species with conspicuous females because juveniles are more vulnerable to predation than adults. Finally, because juveniles always display less or equally conspicuous plumage than females in our analyzed set of passerine species, the evolution of distinct juvenile body plumages could only occur in species where females display conspicuous plumage. If this was the case, any association between plumage distinctness of juveniles and ecological and life-history variables should be controlled by the influence of plumage conspicuousness of adult females, as was the case in our multiple PGLM models.

The negative effect of body mass on distinctness scores could relate to allometric effects on plumage cover and concomitant metabolic costs of pigmented feather growth because smaller species have more body surface per gram. The marginally significant association of nestling period duration with juvenile plumage distinctness suggests that, for species with similar size, those suffering less predation risk in the nest and therefore developing more slowly (Martin, 1995) were those developing distinct juvenile plumage with higher frequency. This relationship does not support a role for parent–offspring communication, which is more protracted for slowly developing nestlings.

Residency probably involves the need to participate in social interactions with coexisting juveniles subsequent to fledging, and these interactions may affect subsequent social status and the capacity to acquire resources necessary for overwinter survival. Migrants, on the other hand, are presumably involved in social interactions in the winter quarters with a different set of individuals than those with which they shared natal areas (except in cases of extreme population connectivity between breeding and wintering areas), so that their plumage after fledging, which is moulted before migration (Busse, 1984; Jenni & Winkler, 1994), should not affect their status during winter. They can therefore save on the costs involved in developing pigmented and/or structurally complex body plumages in the nest (Butler et al., 2008; Deviche et al., 2008), which might affect the probability of successful migration. Although distinct plumages may signal a demand to parents and serve to prolong parental care, this possibility is not supported by the more distinct plumages in migrants with their smaller scope for prolongation of parental duties as a result of the time constraints imposed by migration. Avoidance of adult aggression (Ligon & Hill, 2009) may explain the existence of distinct juvenile plumages. However, adults other than parents can probably easily detect juveniles, even if adult-like, through their morphology (short tails and bills throughout part of the juvenile period), behaviour, and the paleness of contour feathers in juveniles. Moreover, studies of dominance hierarchies demonstrate that adults usually dominate juveniles (Lahti et al., 1996; Carrascal et al., 1998), so that competition with adults is probably unprofitable for juveniles in most species, and not only in migrants. Furthermore, juvenile plumage is present mainly after the

breeding season, when territorial activity of adults is at its lowest as a result of their own post-nuptial moult (Owen-Ashley & Wingfield, 2006; Wacker, Schlinger & Wingfield, 2008). Furthermore, the marginally significant association of distinct plumages with colonial species does not support the possibility that avoiding territorial disputes with adults through distinct body plumages is driving the evolution of juvenile body plumage.

Habitat may be involved through predation risk and through signalling efficiency. Mesic or forested habitats may offer more ways of escaping predators in the vegetation (Fernández-Juricic, Jiménez & Lucas, 2002) or of hiding and remaining inconspicuous (Rush & Stutchbury, 2008). We would predict that, if predation risk is crucial in explaining plumage type, juveniles could be more conspicuous in mesic, more vegetated, and structurally complex habitats. The opposite is observed. Regarding signalling efficiency, more vegetated habitats would probably require stronger signals to allow detection and interpretation by con-specifics (Endler & Théry, 1996; Heindl & Winkler, 2003). Again, the opposite trend is found. An alternative interpretation is that adults may be more conspicuous in mesic habitats to promote signalling efficiency, so that juveniles aiming to avoid predation must develop a different body plumage from adults. Moreover, predation risk in mesic habitats may not militate so much against conspicuousness as in open habitats. Female birds from arid habitats are frequently inconspicuous and drab to avoid detection by predators, possibly explaining why juveniles in these habitats are often similar to females. This interpretation is supported by the independent association of juvenile distinctness with conspicuousness of female plumage. Although speculative, there is the further possibility that juveniles in open habitats are involved in more extended interactions with other juveniles than in structurally complex habitats where lower visibility may reduce the capacity to detect other conspecifics.

To conclude, migratory habits and habitat explain part of the variation in the adoption of distinct or female-like juvenile body plumages in Western Palearctic passerines. This conclusion might also apply to passerines in other geographic areas and to other avian groups such as raptors or waders. As also emphasized in studies performed in other animal groups (Guiasu & Winterbottom, 1998; Creer, 2005; Kraus & Allison, 2009), distinct juvenile colorations may be related to selection pressures operating during the juvenile stage and not be the mere consequence of selection on adult coloration. Other factors remain to be detected. The social functions of juvenile body plumage outside the nest should be carefully studied as has been carried out for adults. The impli-cations of juvenile body plumage for fitness require more attention. The simple assumption of the evolutionary conservativeness of juvenile body plumage does not agree with the ecological signals found when controlling for phylogeny.

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APPENDIX 1

INFORMATION EXTRACTED FROM VOLUMES V–IX OF THE *HANDBOOK OF THE BIRDS OF THE WESTERN PALEARCTIC* AND USED IN THE ANALYSES

	Juvenile plumage distinctness	Nest type	Body mass (Female)	Sexual dimorphism	Plumage conspicuousness	Beeding dispersion	Gregariousness in nonbreeding season	Duration of juvenile plumage (days)	Nestling period (days)	Migration	Nestling diet	Habitat
Turdoides altirostris	1.00	Open	33	No	2.00	1	4		10	1	1	4
Turdoides caudatus	1.00	Open	46	No	2.00	2	4		12	1	3	4
Turdoides squamiceps	1.00	Open	74	No	2.00	2	4		14	1	3	3
Turdoides fulvus	1.00	Open	62	No	2.00	2	4			1	2	1
Sylvia sarda	2.67	Open	10	No	2.00	1	1	61.5	12	2	1	3
Sylvia undata	3.00	Open	10	Yes	1.67	1	1	71.7	12	3	2	3
Sylvia deserticola	3.00	Open	8	Yes	1.67	1				3	1	3
Sylvia conspicillata	1.00	Open	10	Yes	2.00	1	2	40.4	11	3	2	3
Sylvia cantillans	2.33	Open	9	Yes	2.00	1		37.8	11	5	2	3
Sylvia mystacea	1.00	Open	10	Yes	2.00	1			10	5	2	3
Sylvia melanocephala	1.00	Open	12	Yes	2.00	1	2	73.1	12	2	2	3
Sylvia melanthorax	1.33	Open	11	Yes	2.00	1			3	1	3
Sylvia rueppelli	2.00	Open	13	Yes	2.00	1		49.9		5	2	3
Sylvia communis	1.67	Open	14	Yes	2.00	1	1	42.7	11	5	2	5
Sylvia nana	1.00	Open	8	No	2.00	1		47.1		3	2	1
Sylvia nisoria	3.00	Open	26	No	2.00	1		42.8	11	5	2	4
Sylvia leucomelaena	1.33	Open	15	No	2.00	1	1		14	1	2	5
Sylvia hortensis	1.33	Open	22	No	2.00	1		42.4	12	5	2	4
Sylvia curruca	1.00	Open	12	No	1.67	1	3	55.8	11	5	2	4
Sylvia borin	1.33	Open	19	No	2.00	1	3	45.8	11	5	2	5
Sylvia atricapilla	1.00	Open	19	Yes	1.67	1	3	47.8	12	3	2	5
Locustella naevia	1.00	Open	14	No	2.00	1	2	42.9	11	5	1	3
Locustella fluviatilis	1.00	Open	15	No	2.00	1	2	48.2	15	5	1	4
Locustella luscinioides	1.00	Open	16	No	2.00	1	2	43.9	13	5	1	4
Scotocerca inquieta	1.00	Open	8	No	2.00	1	2		14	1	2	1
Acrocephalus melanopogon	1.00	Open	12	No	1.67	1	2	72.4	12	3	1	4
Acrocephalus paludicola	1.00	Open	11	No	1.67	4	2	30.1	13	5	1	4
Acrocephalus schoenobaenus	1.00	Open	12	No	2.00	1	1	36.3	13	5	1	4
Acrocephalus scirpaceus	1.00	Open	12	No	2.00	4	2	43.2	11	5	1	4
Acrocephalus brevipennis	1.00	Open	15	No	2.00	1			1	1	4
Acrocephalus arundinaceus	1.00	Open	28	No	2.00	1	2	50.5	13	5	1	4
Hippolais pallida	1.00	Open	10	No	2.00	3	1	40.9	13	5	2	3
Hippolais caligata	1.00	Open	10	No	2.00	3	1	40.4	13	5	1	4
Hippolais languida	1.00	Open	14	No	2.00	3	2			5	1	3
Hippolais olivetorum	1.00	Open	14	No	2.00	3	1	48.1		5	1	4
Hippolais icterina	1.33	Open	13	No	1.00	3	1	51.4	13	5	2	5
Hippolais polyglotta	1.00	Open	13	No	1.33	3	1	45.7	12	5	2	5
Phylloscopus collybita	1.00	Domed	8	No	2.00	1		37.5	15	4	1	6
Phylloscopus trochilus	1.33	Domed	8	No	2.00	1		60.4	13	5	1	5
Cisticola juncidis	1.00	Domed	11	No	2.00	1	2		14	2	1	3
Prinia gracilis	1.00	Open	7	No	2.00	1	1		12	1	1	4
Pycnonotus leucogenys	1.00	Open	30	No	1.00	1	3		10	1	2	4
Pycnonotus xanthopygos	1.00	Open	44	No	1.00	1	4		14	1	3	4

APPENDIX 1 *Continued*

	Juvenile plumage distinctness	Nest type	Body mass (Female)	Sexual dimorphism	Plumage conspicuousness	Beeding dispersion	Gregariousness in nonbreeding season	Duration of juvenile plumage (days)	Nestling period (days)	Migration	Nestling diet	Habitat
Pycnonotus barbatus	1.00	Open	28	No	1.67	1	4		13	1	3	4
Regulus regulus	3.00	Domed	6	Yes	1.33	1	3	50.3	19	3	1	6
Regulus ignicapillus	3.00	Domed	5	Yes	1.33	1		50.3	23	2	1	5
Riparia paludicola	1.00	Cavity	12	No	2.00	4	4		20	1	1	3
Riparia riparia	1.00	Cavity	14	No	2.00	5	4	50.9	23	5	1	3
Ptyoprogne fuligula	1.00	Cavity	16	No	2.00	0	4		27	1	1	2
Ptynoprogne rupestris	1.00	Domed	20	No	2.00	4	4	53.9	25	3	1	2
Hirundo rustica	1.67	Open	19	No	1.00	4	4	69	20	5	1	3
Hirundo daurica	1.00	Cavity	22	No	1.00	4	4		24	5	1	2
Delichon urbica	1.33	Cavity	20	No	1.00	5	4	57.3	27	5	1	3
Cettia cetti	1.00	Open	12	No	2.00	1	1	60.4	15	4	1	3
Aegithalos caudatus	3.00	Domed	8	No	1.00	2	4	39.8	16	1	1	5
Poecile palustris	1.00	Cavity	12	No	1.33	1	1	31.4	18	1	2	5
Poecile montanus	1.00	Cavity	11	No	1.33	1	4	51.2	18	1	2	6
Poecile cinctus	1.00	Cavity	11	No	1.33	1	4	34.4	19	1	2	6
Poecile lugubris	1.00	Cavity	16	No	1.33	1		60.5	22	1	2	6
Lophophanes cristatus	1.00	Cavity	12	No	1.33	1	4	38.8	20	1	2	6
Periparus ater	1.00	Cavity	9	No	1.00	1	4	50.7	19	2	2	6
Parus major	1.00	Cavity	18	No	1.00	1	4	46.5	19	1	2	6
Cyanistes caeruleus	2.67	Cavity	11	No	1.00	1	4	48.8	19	1	2	5
Cyanistes cyanus	3.00	Cavity	12	No	1.00	1	3	44.4	16	1	2	4
Remiz pendulinus	3.00	Open	9	Yes	1.33	1	4	46.6	22	4	2	4
Panurus biarmicus	3.00	Open	14	Yes	2.00	5	4	71.3	12	2	2	4
Sitta europaea	1.00	Cavity	23	No	1.00	1	1	47.1	23	1	2	6
Sitta krueperi	3.00	Cavity	12	No	1.00	1			17	1	2	6
Sitta ledanti	1.67	Cavity	16	No	1.00	1			23	1	2	6
Sitta whiteheadi	1.00	Cavity	12	Yes	1.33	1	1		23	1	3	6
Sitta tephronota	1.00	Cavity	43	No	1.00	1			25	1	2	2
Sitta neumayer	1.00	Open	30	No	1.00	1			30	1	2	2
Tichodroma muraria	1.33	Cavity	18	No	1.00	1	1	53.5	29	2	1	2
Troglodytes troglodytes	1.00	Domed	8	No	2.00	1	1	82.7	16	4	1	5
Certhia familiaris	1.00	Domed	9	No	2.00	1	2	43.3	15	2	1	6
Certhia brachydactyla	1.00	Domed	9	No	2.00	1	2	45.8	17	1	1	5
Eremopterix nigriceps	1.00	Open	12	Yes	2.00	1	4		13	2	3	1
Eremalauda dunni	1.00	Open		No	2.00	1	4			1	3	1
Ammomanes cincturus	1.00	Open	18	No	2.00	1	4			1	3	1
Ammomanes deserti	1.00	Open	25	No	2.00	1	3			1	3	1
Alaemon alaudipes	1.67	Open	47	No	2.00	1	2		12	1	1	1
Chersophilus duponti	1.00	Open	39	No	2.00	1	2		10	1	1	2
Rhamphocoris clothey	3.00	Open	45	No	1.67	1	3			1	3	2
Melanocorypha calandra	1.00	Open	57	No	2.00	1	4	49.5	10	1	2	2
Melanocorypha bimaculata	1.00	Open	54	No	2.00	1	4	49.5	9	5	2	2
Melanocorypha leucoptera	1.00	Open	45	No	2.00	1	4			3	2	2
Melanocorypha yeltoniensis	1.00	Open	55	Yes	2.00	1	4	49.9	9	3	2	2
Calandrella brachydactyla	1.33	Open	22	No	2.00	1	4	69.3	12	5	2	2
Calandrella rufescens	1.33	Open	20	No	2.00	1	4	69.3	9	2	2	2
Galerida cristata	1.00	Open	44	No	2.00	1	3	51.1	9	1	3	2
Galerida theklae	1.33	Open	37	No	2.00	1	3	51.1	9	1	2	2
Lullula arborea	1.67	Open	32	No	2.00	1	3	51.5	11	3	2	5
Alauda arvensis	1.00	Open	34	No	2.00	1	4	49.7	9	4	3	3
Eremophila alpestris	3.00	Open	37	No	1.00	1	4	67.7	10	4	2	3
Eremophila bilopha	3.00	Open	38	No	1.00	1	3			1	2	2
Emberiza leucocephalos	1.67	Open	27	Yes	2.00	1	4	40.3	9	5	3	5
Miliaria calandra	1.00	Open	40	No	2.00	1	4	90.9	11	2	3	5
Emberiza citrinella	1.00	Open	27	Yes	1.67	1	4	101.4	12	3	3	5
Emberiza cirlus	1.67	Open	24	Yes	2.00	1	3	85.8	12	5	3	5
Emberiza schoeniclus	1.00	Open	18	Yes	1.67	1	4	76.7	11	3	3	4
Emberiza rustica	1.00	Open	18	Yes	2.00	1	4	67.9	9	5	3	5
Emberiza pusilla	1.00	Open	15	No	1.33	1	4	38.7	7	5	3	3
Emberiza cia	3.00	Open	23	Yes	2.00	1	3	72.2	11	2		3
Emberiza striolata	1.00	Cavity	14	Yes	2.00		4		18	1	3	
Emberiza cineracea	1.67	Open	24	Yes	2.00		2			5	3	2
Emberiza buchanani	2.00	Open	21	No	2.00				12	5	3	2
Emberiza hortulana	3.00	Open	19	Yes	1.33	4		49.4	12	5	2	5

APPENDIX 1 *Continued*

	Juvenile plumage distinctness	Nest type	Body mass (Female)	Sexual dimorphism	Plumage conspicuousness	Beeding dispersion	Gregariousness in nonbreeding season	Duration of juvenile plumage (days)	Nestling period (days)	Migration	Nestling diet	Habitat
Emberiza caesia	3.00	Open	20	Yes	2.00	3		43.6	12	5	3	5
Emberiza aureola	2.00	Open	22	Yes	1.67	3	4	69.6	12	5	3	4
Emberiza bruniceps	2.33	Open	23	Yes	2.00	1	4	35	12	5	3	2
Emberiza melanocephala	2.67	Open	27	Yes	2.00	1	4	41.2	14	5	3	3
Emberiza pallasi	2.00	Open	15	Yes	2.00		4	56.9	10	4	3	3
Plectrophenax nivalis	3.00	Cavity	36	Yes	2.00	1	4	69.4	13	4	3	3
Calcarius lapponicus	3.00	Open	23	Yes	2.00	3	4	68.9	9	5	2	3
Fringilla coelebs	1.00	Open	23	Yes	2.00	1	4	56.8	14	3	3	6
Fringilla teydea	1.00	Open	29	Yes	2.00	1	3		17	1	3	6
Fringilla montifringilla	1.00	Open	24	Yes	1.67	3	4	52.4	13	5	3	5
Serinus serinus	2.67	Open	12	Yes	1.33	3	4	89.5	15	3	3	4
Serinus canaria	3.00	Open	15	No	1.00		4		16	1	3	5
Serinus citrinella	3.00	Open	12	No	1.00	3	4	49.7	16	3	4	2
Serinus syriacus	3.00	Open	12	No	1.00	3	4		15	1	4	5
Carduelis carduelis	3.00	Open	15	No	1.00	3	4	82.2	15	3	3	4
Carduelis spinus	2.00	Open	13	Yes	1.67	1	4	59.3	14	4	3	6
Carduelis cannabina	1.33	Open	18	Yes	2.00	3	4	71.3	13	3	4	3
Carduelis flavirostris	1.00	Open	16	No	2.00	1	4	72.8	11	3	4	3
Carduelis flammea	3.00	Open	13	Yes	1.33	3	4	72.8	11	4	4	3
Carduelis hornemanni	3.00	Open	13	Yes	1.33	3	4	67.5	11	3	4	3
Loxia leucoptera	3.00	Open	31	Yes	2.00	3	4	151	23	2	4	6
Loxia curvirostra	2.67	Open	42	Yes	2.00	3	4	151	22	2	4	6
Carduelis chloris	2.67	Open	28	No	1.33	3	4	79.9	14	3	3	5
Carpodacus erythrinus	1.00	Open	24	Yes	2.00	3	4	163.8	11	5	3	5
Carpodacus synoicus	1.00	Cavity	21	Yes	2.00	1	4		15	2	4	1
Carpodacus rubicilla	1.00	Cavity	46	Yes	2.00	3	4		17	2	4	2
Pinicola enucleator	2.00	Open	55	Yes	1.67	1	4	86.6	14	3	4	6
Pyrrhula pyrrhula	3.00	Open	30	Yes	1.33	3	3	75.1	15	3	4	6
Coccothraustes coccothraustes	3.00	Open	53	No	1.33	1	4	68.3	12	3	4	6
Rhodopechys sanguinea	1.00	Open	39	Yes	2.00	3	4		14	3	3	2
Rhodospiza obsoleta	1.00	Open	26	Yes	2.00	3	4		13	1	3	4
Bucanetes mongolicus	2.33	Domed	22	Yes	2.00	3	4		18	3	4	2
Bucanetes githagineus	1.67	Domed	18	Yes	2.00	3	4	59.6	13	2	3	1
Anthreptes platurus	1.00	Open	6	Yes	1.33		4		13	5	2	2
Anthreptes metallicus	1.00	Open	7	Yes	1.67	1	4			2	2	3
Nectarinia osea	2.67	Open	7	Yes	2.00	1	3		16	2	2	4
Anthus novaeseelandiae	1.00		28	No	2.00			73.8	14	5	1	3
Anthus campestris	1.33	Open	21	No	2.00	1	2	57.2	13	5	1	2
Anthus berthelotii	1.00	Open	16	No	2.00	0	2			1	2	2
Anthus similis	1.00	Open	29	No	2.00		2		14	2	2	2
Anthus hodgsoni	1.00	Open	23	No	1.67	1	3		11	5	2	5
Anthus trivialis	1.00	Open	21	No	2.00	1	2	42.9	12	5	1	5
Anthus gustavi	1.00	Open	20	No	2.00	1	2		12	5	1	3
Anthus cervinus	1.33	Open	20	No	2.00	1	4	49.3	13	5	1	3
Anthus pratensis	1.00	Open	20	No	2.00	1	3	51.3	10	2	2	3
Anthus spinoletta	1.67	Cavity	21	No	2.00	1	1	81.1	15	4	1	2
Anthus petrosus	1.00	Cavity	21	No	2.00	1	3	81.1	15		1	
Motacilla flava	2.33	Open	16	No	1.00	1	4	70.2	16	5	1	3
Motacilla cinerea	1.67	Domed	17	Yes	1.33	1	3	59.6	13	3	1	4
Motacilla alba	3.00	Domed	20	No	1.00	1	4	54.5	13	4	1	3
Lagonosticta senegala	1.67	Cavity	9	Yes	1.67	1	3		18	1	3	2
Estrilda astrild	1.67	Open	7	Yes	1.67	1	4		19	1	4	4
Amandava amandava	2.33	Open	10	Yes	1.67		4		19	1	4	4
Euodice cantans	1.33		12	No	2.00					1		2
Ploceus manyar	3.00	Open	17	Yes	1.33		4		17	1	4	4
Prunella modularis	2.33	Open	21	No	2.00	1	2	56.5	11	4	2	5
Prunella montanella	1.00	Open	17	No	1.33	0	2			5	2	5
Prunella ocularis	2.00	Open	20	No	1.67	0	3			1	2	3
Prunella atrogularis	2.33	Open	19	No	1.33	1	3		12	5	2	6
Prunella collaris	1.33	Domed	43	No	1.67	1	3	42	16	1	2	2
Passer domesticus	1.00	Cavity	30	Yes	2.00	5	4	53.6	15	1	3	
Passer hispaniolensis	1.00	Domed	26	Yes	2.00	5	4	53.6	15	2	3	4
Passer montanus	1.67	Cavity	20	No	1.33	5	4	38.3	17	1	3	5
Passer moabiticus	1.00	Open	20	Yes	2.00	5	4		12	5	3	4

APPENDIX 1 *Continued*

	Juvenile plumage distinctness	Nest type	Body mass (Female)	Sexual dimorphism	Plumage conspicuousness	Beeding dispersion	Gregariousness in nonbreeding season	Duration of juvenile plumage (days)	Nestling period (days)	Migration	Nestling diet	Habitat
Passer iagoensis	1.00	Cavity		Yes	2.00	4	4			1	3	1
Passer simplex	1.00	Cavity	20	Yes	2.00	4	4		13	3	3	1
Passer luteus	1.00	Open	14	Yes	2.00	5	4		13	3	3	2
Carpospiza brachydactyla	1.00	Open	21	No	2.00	1			13	3	2	3
Petronia xanthocollis	1.00	Cavity	18	Yes	2.00	5	4			4	2	5
Petronia petronia	1.00	Cavity	32	No	2.00	4	4	75.2	18	1	3	2
Montifringilla nivalis	1.00	Cavity	37	Yes	2.00	3	4	57.4	20	2	2	2
Bombycilla garrulus	2.33	Open	60	No	1.00	0	4	84.5	14	3	2	6
Hypocolius ampelinus	1.00	Open	50	Yes	2.00	5	4			3	3	4
Cinclus cinclus	3.00	Domed	68	No	1.00	1	1	58.4	22	2	1	4
Onychognathus tristramii	1.00	Cavity	120	Yes	1.00		4		29	1	3	2
Sturnus sturninus	1.00		49	Yes	1.33					5		5
Sturnus vulgaris	3.00	Cavity	78	No	1.00	5	4	73.7	21	5	3	5
Sturnus unicolor	3.00	Cavity	90	No	1.00	5	4		21	1	3	5
Sturnus roseus	3.00	Cavity	67	No	1.00	5	4	98.4	24	5	2	2
Acridotheres tristis	1.00	Cavity	120	No	1.00	1	3		28	1	3	
Cercotrichas galactotes	1.00	Open	23	No	2.00	1		37.1	12	5	2	4
Muscicapa striata	3.00	Domed	15	No	1.67	1	2	69.8	14	5	2	5
Ficedula parva	3.00	Cavity	12	Yes	2.00	1	2	66	12	5	1	6
Ficedula hypoleuca	3.00	Cavity	12	Yes	2.00	1	2	50	15	5	1	6
Erithacus rubecula	3.00	Domed	16	No	1.00	1	2	45.8	13	4	2	5
Luscinia svecica	3.00	Open	18	Yes	1.67	1	2	74.2	14	5	2	3
Luscinia luscinia	3.00	Open	25	No	2.00	1	2	27.3	10	5	2	5
Luscinia megarhynchos	3.00	Open	19	No	2.00	1	2	27.3	11	5	2	5
Luscinia calliope	2.67	Open	22	Yes	2.00	1	2	59.4		5	1	5
Tarsiger cyanurus	3.00	Cavity	15	Yes	1.33	1	2	58.7	15	5	2	6
Irania gutturalis	3.00	Cavity	20	Yes	2.00	1	2		12	5	2	2
Phoenicurus ochruros	1.00	Cavity	15	Yes	2.00	1	2	66.8	15	3	2	2
Phoenicurus phoenicurus	2.67	Cavity	15	Yes	2.00	1	2	46.6	14	5	1	6
Phoenicurus mousieri	3.00	Cavity	15	Yes	2.00	1	2			2	1	3
Phoenicurus erythrogaster	1.67	Cavity	25	Yes	2.00	1	3		14	2	2	2
Cercomela melanura	1.67	Cavity	15	No	2.00	1	2			1	1	1
Saxicola rubetra	1.33	Open	17	Yes	2.00	1	2	50.1	12	5	2	3
Saxicola torquata	3.00	Open	15	Yes	2.00	1	2	43.6	13	3	1	3
Oenanthe oenanthe	3.00	Cavity	24	Yes	2.00	1	2	56	14	5	1	2
Oenanthe pleschanka	1.67	Cavity	19	Yes	2.00	1	2	47.2	13	5	1	2
Oenanthe hispanica	2.67	Domed	26	Yes	2.00	1	1	47.2	11	5	1	3
Oenanthe deserti	2.00	Cavity	21	Yes	2.00	1	1	56.1	13	5	1	3
Oenanthe finschii	2.67	Cavity	26	Yes	1.67	1	2		15	3	2	2
Oenanthe lugens	3.00	Cavity	21	Yes	1.67	1	2		14	3	1	1
Oenanthe moesta	3.00	Cavity		Yes	2.00	1	1			1	1	2
Oenanthe xanthoprymna	1.67	Cavity	22	No	1.00	1	1			5	1	2
Oenanthe monacha	1.00	Cavity	18	Yes	2.00	1	2			1	1	1
Oenanthe alboniger	1.00	Cavity	26	No	1.00	1	1			1	2	2
Oenanthe leucopyga	3.00	Cavity	25	No	1.00	1	1		14	1	1	1
Oenanthe leucura	1.00	Cavity	38	Yes	1.00	1	3	49.8	14	1	1	2
Monticola saxatilis	1.00	Cavity	51	Yes	2.00	1	2	47.3	15	5	1	2
Monticola solitarius	1.33	Cavity	58	Yes	2.00	1	2	58.1	18	3	1	2
Zoothera dauma	1.00	Open	155	No	1.33	0	2	38.9		4	2	6
Turdus merula	3.00	Open	100	Yes	2.00	1		75.8	14	3	2	5
Turdus torquatus	2.33	Open	106	Yes	1.33	1	4	73.8	15	4	2	6
Turdus ruficollis	3.00	Open	87	Yes	2.00	1	4	77.4	11	5	2	6
Turdus pilaris	3.00	Open	103	No	1.00	5	4	73	13	5	2	6
Turdus philomelos	2.00	Open	78	No	2.00	1	2	56.2	13	3	2	6
Turdus iliacus	2.00	Open	62	No	1.33	4	4	56.2	11	4	2	6
Turdus viscivorus	2.67	Open	123	No	2.00	1	3	53.1	13	4	2	6
Oriolus oriolus	3.00	Open	69	Yes	1.33	1	3	53.7	16	5	2	5
Tchagra senegala	1.00	Open	55	No	1.00	1	2		16	1	3	3
Lanius collurio	3.00	Open	32	Yes	2.00	1	2	44.6	14	5	1	5
Lanius schach	1.33		33	No	1.00					4		5
Lanius minor	3.00	Open	47	No	1.00	3	1	51.1	17	5	1	5
Lanius meridionalis	2.00	Open	50	No	1.00	1	1		16	3	1	5
Lanius senator	3.00	Open	37	No	1.00	1	1	79.2	16	5	1	5
Lanius excubitor	3.00	Open	67	No	1.00	1	1	62	16	4	1	5

APPENDIX 1 *Continued*

	Juvenile plumage distinctness	Nest type	Body mass (Female)	Sexual dimorphism	Plumage conspicuousness	Beeding dispersion	Gregariousness in nonbreeding season	Duration of juvenile plumage (days)	Nestling period (days)	Migration	Nestling diet	Habitat
Lanius nubicus	3.00	Open	24	Yes	2.00	1	1		19	5	1	5
Corvus ruficollis	1.00	Open	560	No	1.00				36	1	3	1
Corvus riphidurus	1.00	Cavity	565	No	1.00	5			37	1	3	2
Corvus frugilegus	2.00	Open	420	No	1.00	5	4	45.5	33	3	3	5
Corvus corax	1.00	Open	1150	No	1.00	1		57	45	1	3	5
Corvus monedula	3.00	Cavity	230	No	1.00	5	4	42.9	32	3	3	5
Corvus corone	1.00	Open	512	No	1.00	1		43.1	33	1	3	4
Corvus cornix	1.00	Open	488	No	1.00	1		43.1	32	5	3	5
Nucifraga caryocatactes	1.00	Open	188	No	1.33	1	2	50.7	24	1	3	6
Pica pica	1.00	Domed	200	No	1.00	1		48.6	27	1	3	5
Garrulus glandarius	1.00	Open	161	No	1.00	1	2	54.9	21	2	3	6
Cyanopica cyanus	1.00	Open	69	No	1.00	2	4	73.8	15	1	3	5
Perisoreus infaustus	1.00	Open	82	No	1.67	2	4	49.1	22	1	3	6
Pyrrhocorax graculus	2.00	Cavity	210	No	1.00	5	4	39.9	30	2	2	2
Pyrrhocorax pyrrhocorax	1.00	Cavity	300	No	1.00	4	4	47.1	36	1	2	2

APPENDIX 2

PHYLOGENETIC RELATIONSHIP IN 'PHYLIP' STYLE OF THE 250 PASSERINE SPECIES IN APPENDIX 1: BRANCH LENGTHS ASSOCIATED WITH EACH INTERNODE ARE SHOWN AND WERE ARBITRARILY ASSIGNED TO ONE, BUT CONSTRAINING TIPS TO BE CONTEMPORANEOUS (PAGEL, 1997)

(((((Pyrrhocorax_pyrrhocorax: 1.00, Pyrrhocorax_graculus: 1.00): 6.00, ((Perisoreus_infaustus: 1.00, Cyanopica_cyanus: 1.00): 5.00, (Garrulus_glandarius: 5.00, (Pica_pica: 4.00, (Nucifraga_caryocatactes: 3.00, ((Corvus_cornix: 1.00, Corvus_corone: 1.00): 1.00, Corvus_monedula: 2.00, (Corvus_corax: 1.00, Corvus_frugilegus: 1.00): 1.00, Corvus_riphidurus: 2.00, Corvus_ruficollis: 2.00): 1.00): 1.00): 1.00): 1.00): 1.00, (((Lanius_nubicus: 1.00, Lanius_excubitor: 1.00): 1.00, Lanius_senator: 2.00, Lanius_meridionalis: 2.00, Lanius_minor: 2.00, Lanius_schach: 2.00, Lanius_collurio: 2.00): 1.00, Tchagra_senegala: 3.00): 5.00): 1.00, Oriolus_oriolus: 9.00): 11.00, ((((((Turdus_viscivorus: 5.00, Turdus_iliacus: 5.00, (Turdus_philomelos: 4.00, ((Turdus_pilaris: 2.00, (Turdus_ruficollis: 1.00, Turdus_torquatus: 1.00): 1.00): 1.00, Turdus_merula: 3.00): 1.00): 1.00): 1.00, Zoothera_dauma: 6.00): 5.00, (((((((Monticola_solitarius: 1.00, Monticola_saxatilis: 1.00): 4.00, ((Oenanthe_leucura: 3.00, Oenanthe_leucopyga: 3.00, Oenanthe_alboniger: 3.00, Oenanthe_monacha: 3.00, Oenanthe_xanthoprymna: 3.00, Oenanthe_moesta: 3.00, (Oenanthe_lugens: 1.00, Oenanthe_finschii: 1.00): 2.00, (Oenanthe_deserti: 2.00, (Oenanthe_hispanica: 1.00, Oenanthe_pleschanka: 1.00): 1.00): 1.00, Oenanthe_oenanthe: 3.00): 1.00, (Saxicola_torquata: 1.00, Saxicola_rubetra: 1.00): 3.00): 1.00): 1.00, Cercomela_melanura: 6.00, (Phoenicurus_erythrogaster: 1.00, Phoenicurus_mousieri: 1.00, Phoenicurus_phoenicurus: 1.00, Phoenicurus_ochruros: 1.00): 5.00, Irania_gutturalis: 6.00, Tarsiger_cyanurus: 6.00): 1.00, (Luscinia_calliope: 2.00, (Luscinia_megarhynchos: 1.00, Luscinia_luscinia: 1.00): 1.00, Luscinia_svecica: 2.00): 5.00): 1.00, Erithacus_rubecula: 8.00): 1.00, (Ficedula_hypoleuca: 1.00, Ficedula_parva: 1.00): 8.00): 1.00, (Muscicapa_striata: 1.00, Cercotrichas_galactotes: 1.00): 9.00): 1.00): 1.00, ((Acridotheres_tristis: 2.00, Sturnus_roseus: 2.00, (Sturnus_unicolor: 1.00, Sturnus_vulgaris: 1.00): 1.00, Sturnus_sturninus: 2.00): 1.00, Onychognathus_tristramii: 3.00): 9.00, Cinclus_cinclus: 12.00): 1.00, (Hypocolius_ampelinus: 1.00, Bombycilla_garrulus: 1.00): 12.00): 6.00, ((((((Montifringilla_nivalis: 2.00, (Petronia_petronia: 1.00, Petronia_xanthocollis: 1.00): 1.00): 2.00, Carpospiza_brachydactyla: 4.00, (Passer_luteus: 3.00, Passer_simplex: 3.00, Passer_iagoensis: 3.00, Passer_moabiticus: 3.00, (Passer_montanus: 2.00, (Passer_hispaniolensis: 1.00, Passer_domesticus: 1.00): 1.00): 1.00): 1.00): 4.00, (((Prunella_collaris: 1.00, Prunella_atrogularis: 1.00, Prunella_ocularis: 1.00, Prunella_montanella: 1.00, Prunella_modularis: 1.00): 3.00, (Ploceus_manyar: 3.00, (Euodice_cantans: 2.00, (Amandava_amandava: 1.00, Estrilda_astrild: 1.00, Lagonosticta_senegala: 1.00): 1.00): 1.00): 3.00, ((Motacilla_alba: 2.00, (Motacilla_cinerea: 1.00, Motacilla_flava: 1.00): 1.00): 4.00, (((((Anthus_petrosus: 1.00, Anthus_spinoletta: 1.00): 1.00, Anthus_pratensis: 2.00): 1.00, Anthus_cervinus: 3.00): 1.00, (Anthus_gustavi: 2.00, (Anthus_trivialis: 1.00, Anthus_hodgsoni: 1.00): 1.00): 2.00): 1.00, Anthus_similis: 5.00, ((Anthus_berthelotii: 1.00, Anthus_campestris: 1.00): 1.00, Anthus_novaeseelandiae: 2.00): 3.00): 1.00): 1.00): 1.00): 4.00, ((Nectarinia_osea: 2.00, (Anthreptes_

metallicus: 1.00, Anthreptes_platurus: 1.00): 1.00): 9.00, (((Bucanetes_githagineus: 1.00, Bucanetes_mongolicus: 1.00): 8.00, (Rhodospiza_obsoleta: 1.00, Rhodopechys_sanguinea: 1.00): 8.00, (Coccothraustes_coccothraustes: 8.00, ((Pyrrhula_pyrrhula: 1.00, Pinicola_enucleator: 1.00): 6.00, ((Carpodacus_rubicilla: 1.00, Carpodacus_synoicus: 1.00, Carpodacus_erythrinus: 1.00): 5.00, (Carduelis_chloris: 5.00, ((Loxia_curvirostra: 1.00, Loxia_leucoptera: 1.00): 3.00, (Carduelis_hornemanni: 1.00, Carduelis_flammea: 1.00): 3.00, ((Carduelis_flavirostris: 1.00, Carduelis_cannabina: 1.00): 1.00, Carduelis_spinus: 2.00): 2.00, (Carduelis_carduelis: 3.00, (Serinus_syriacus: 2.00, Serinus_citrinella: 2.00, (Serinus_canaria: 1.00, Serinus_serinus: 1.00): 1.00): 1.00): 1.00): 1.00): 1.00): 1.00): 1.00, (Fringilla_montifringilla: 1.00, Fringilla_teydea: 1.00, Fringilla_coelebs: 1.00): 8.00): 1.00, ((Calcarius_lapponicus: 1.00, Plectrophenax_nivalis: 1.00): 3.00, (Emberiza_pallasi: 3.00, Emberiza_melanocephala: 3.00, Emberiza_bruniceps: 3.00, Emberiza_aureola: 3.00, Emberiza_caesia: 3.00, Emberiza_hortulana: 3.00, Emberiza_buchanani: 3.00, Emberiza_cineracea: 3.00, Emberiza_striolata: 3.00, Emberiza_cia: 3.00, ((Emberiza_pusilla: 1.00, Emberiza_rustica: 1.00): 1.00, Emberiza_schoeniclus: 2.00): 1.00, ((Emberiza_cirlus: 1.00, Emberiza_citrinella: 1.00): 1.00, Miliaria_calandra: 2.00): 1.00, Emberiza_leucocephalos: 3.00): 1.00): 6.00): 1.00): 1.00): 1.00, ((((Eremophila_bilopha: 1.00, Eremophila_alpestris: 1.00): 1.00, (Alauda_arvensis: 1.00, Lullula_arborea: 1.00): 1.00, (Galerida_theklae: 1.00, Galerida_cristata: 1.00): 1.00): 1.00, (Calandrella_rufescens: 1.00, Calandrella_brachydactyla: 1.00): 2.00): 1.00, (Melanocorypha_yeltoniensis: 1.00, Melanocorypha_leucoptera: 1.00, Melanocorypha_bimaculata: 1.00, Melanocorypha_calandra: 1.00): 3.00, Rhamphocoris_clothey: 4.00, Chersophilus_duponti: 4.00, Alaemon_alaudipes: 4.00, ((Ammomanes_deserti: 1.00, Ammomanes_cincturus: 1.00): 1.00, (Eremalauda_dunni: 1.00, Eremopterix_nigriceps: 1.00): 1.00): 2.00): 9.00): 5.00, (((((Certhia_brachydactyla: 1.00, Certhia_familiaris: 1.00): 1.00, Troglodytes_troglodytes: 2.00): 2.00, (Tichodroma_muraria: 3.00, (Sitta_neumayer: 2.00, Sitta_tephronota: 2.00, Sitta_whiteheadi: 2.00, (Sitta_ledanti: 1.00, Sitta_krueperi: 1.00): 1.00, Sitta_europaea: 2.00): 1.00): 1.00): 13.00, (Panurus_biarmicus: 16.00, (Remiz_pendulinus: 6.00, (((Cyanistes_cyanus: 1.00, Cyanistes_caeruleus: 1.00): 1.00, Parus_major: 2.00): 3.00, (Periparus_ater: 4.00, Lophophanes_cristatus: 4.00, (Poecile_lugubris: 3.00, (Poecile_cinctus: 2.00, (Poecile_montanus: 1.00, Poecile_palustris: 1.00): 1.00): 1.00): 1.00): 1.00): 1.00): 10.00, (Aegithalos_caudatus: 1.00, Cettia_cetti: 1.00): 14.00, (((Delichon_urbica: 3.00, ((Hirundo_daurica: 1.00, Hirundo_rustica: 1.00): 1.00, (Ptynoprogne_rupestris: 1.00, Ptyoprogne_fuligula: 1.00): 1.00): 1.00): 1.00, (Riparia_riparia: 1.00, Riparia_paludicola: 1.00): 3.00): 10.00, ((Regulus_ignicapillus: 1.00, Regulus_regulus: 1.00): 12.00, (((Pycnonotus_barbatus: 1.00, Pycnonotus_xanthopygos: 1.00): 1.00, Pycnonotus_leucogenys: 2.00): 10.00, ((Prinia_gracilis: 1.00, Cisticola_juncidis: 1.00): 10.00, (((Phylloscopus_trochilus: 1.00, Phylloscopus_collybita: 1.00): 5.00, (((((Hippolais_polyglotta: 1.00, Hippolais_icterina: 1.00): 1.00, (Hippolais_olivetorum: 1.00, Hippolais_languida: 1.00): 1.00): 1.00, ((Hippolais_caligata: 1.00, Hippolais_pallida: 1.00): 1.00, Acrocephalus_arundinaceus: 2.00, Acrocephalus_brevipennis: 2.00, Acrocephalus_scirpaceus: 2.00, (Acrocephalus_schoenobaenus: 1.00, Acrocephalus_paludicola: 1.00, Acrocephalus_melanopogon: 1.00): 1.00): 1.00): 1.00, Scotocerca_inquieta: 4.00): 1.00, ((Locustella_luscinioides: 1.00, Locustella_fluviatilis: 1.00): 1.00, Locustella_naevia: 2.00): 3.00): 1.00): 4.00, (((Sylvia_atricapilla: 1.00, Sylvia_borin: 1.00): 7.00, ((Sylvia_curruca: 2.00, (Sylvia_hortensis: 1.00, Sylvia_leucomelaena: 1.00): 1.00): 5.00, Sylvia_nisoria: 7.00, (Sylvia_nana: 6.00, (Sylvia_communis: 5.00, (((Sylvia_rueppelli: 1.00, Sylvia_melanthorax: 1.00): 2.00, ((Sylvia_melanocephala: 1.00, Sylvia_mystacea: 1.00): 1.00, Sylvia_cantillans: 2.00): 1.00): 1.00, Sylvia_conspicillata: 4.00, ((Sylvia_deserticola: 1.00, Sylvia_undata: 1.00): 1.00, Sylvia_sarda: 2.00): 2.00): 1.00): 1.00): 1.00): 1.00): 1.00, (Turdoides_fulvus: 1.00, Turdoides_squamiceps: 1.00, Turdoides_caudatus: 1.00, Turdoides_altirostris: 1.00): 8.00): 1.00): 1.00): 1.00): 1.00): 1.00): 1.00): 1.00): 1.00): 1.00): 0.00.