Urban establishment success of corvids

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1. Synopsis

Introduction

The proportion of the human population that currently live in cities increases rapidly throughout the world. As urban areas expand, natural habitats become altered, fragmented and native biodiversity often declines (Marzluff 2001).

Urban environments have a number of characteristics that might enhance the establishment of certain species. First, urban areas have a longer growing season, which might facilitate species with multiple broods per year. Second, urban environments are characterized by specific habitats that might be suitable for certain species. Third, urbanized areas are characterized by high resource abundance that might support species that are able to exploit anthropogenic food. Fourth, urbanization is associated with the proximity of humans and therefore, species with high thresholds for fear and short flight initiation distances might have selective advantages (Møller 2008, 2009, Shochat et al. 2006).

Consequently, urban ecologists revealed several patterns of species abundance and diversity. For example, Blair (1996) divided the bird community in California (USA) across an urban gradient that ranged from relatively undisturbed areas outside the city to the highly developed city center into discrete categories. ‘Urban avoiders’ were native species that dominated the community in areas with a low level of urbanization. ‘Suburban adapters’ were native and non-native species that occurred in environments with intermediate levels of urbanization. Finally, ‘urban exploiters’ were represented by a small number of species, mainly non-native that dominated in the most urbanized areas (Blair 1996).

A more general view on patterns of species richness and abundance has been termed biotic homogenization, a pattern, which is largely consistent across cities in different geographical regions. This pattern describes declining species richness and increasing abundance along a gradient of increasing urbanization (Chace and Walsh 2006, Clergeau et al. 2006).

However, in recent years research has progressed into mechanistic urban ecology (Shochat et al. 2006), with studies on the responses of animals to altered conditions in urban areas, such as the adaption of song frequency (Slabbekoorn and Peet 2003), timing of reproduction (Partecke et al. 2004) and the adoption of new food resources (Fisher and Hinde 1949, Grobecker and Pietsch 1978). Hence, it is assumed that urban environments expose birds to new selective pressures that might lead to rapid evolution (Yeh 2004) and genetic differentiation (Wandeler et al. 2003).

However, it is not very well understood, which traits might drive species differences in the establishment success in urban environments. It is generally assumed that species with a broad environmental tolerance are more likely to exploit anthropogenic food resources, are less sensitive to habitat fragmentation and are therefore more likely to establish in urban areas, than species with a narrow environmental tolerance. Supporting evidence comes from comparative approaches, which showed that urban birds are more environmental tolerant than their rural congeners (Bonier et al. 2007, Møller 2009). However, both studies estimated environmental tolerance of a species from its geographical distribution and therefore, the association between geographical distribution and urbanization, pose the question which traits and mechanism drive differences in geographical distribution.

Probably the most promising hypothesis that might explain differences in urban establishment success of birds has been termed the brain size – environmental change hypothesis (Sol et al. 2005a). It states that enlarged brains might have evolved as an adaptation to cope with novel or altered conditions and that birds might respond to these conditions by producing innovative behavior (Sol et al. 2005a). Supporting evidence comes from studies on the invasion biology of birds that were able to show that birds with enlarged brains and a higher innovation rate in their region of origin, have an enhanced invasion potential into new environments (Sol et al. 2005a, Sol and Lefebvre 2000, Sol et al. 2002).

Hence, if large brained and more innovative birds are more successful in invading new environments, one might also predict that they more readily settle in anthropogenically modified, and in particular urban habitats (Kark et al. 2007, Møller 2009, Timmermans 1999). However, so far brain size has not been found to be related to urbanization (Kark et al. 2007, Timmermans 1999) and only Møller (2009) found that urban birds had a higher innovation rate compared to their rural congeners.

However, sympatric European corvid species are particularly suited to address the question, which traits might determine differences in urbanization, because these species differ in their establishment success in urban environments (Kelcey and Rheinwald 2005, Otto and Witt 2002, Witt et al. 2005) and moreover, in their behavior (Lockie 1956, Waite 1984), their ecology (Bossema et al. 1986, Waite 1984) and their cognitive abilities (Emery and Clayton 2004, Lefebvre et al. 1997).

Urban success

In Berlin, Germany, corvid species differ in their abundance and distribution. The abundance of corvid species and the number of occupied habitats is progressively increased from common raven, to jackdaw, to rook, to Eurasian jay, to black-billed magpie and to hooded crow (Otto and Witt 2002, Tab. 1). It suggests that hooded crow and black-billed magpie are more successful in establishing in urban environments compared to the other corvid species. However, patterns of abundance and distribution can differ between cities (compare Kelcey and Rheinwald 2005, Witt et al. 2005). For example, in Warsaw, the jackdaw is the most abundant corvid species and reaches a population of about 12000 breeding pairs (Witt et al. 2005).

Therefore, indices that were derived from an international inquiry on the population changes of birds in 19 eastern European cities (Konstantinov et al. 1996, Tab. 1) might complement a more general view on the urban success of corvid species across Europe. Again, these indices suggest that hooded crow and black-billed magpie might be assumed to be the most successful urban exploiters, because they established with increasing populations in most of the 19 cities, of which population changes were inquired (Tab. 1).

Tab. 1: The abundance of the studied corvid species (column 2) and the number of occupied habitats (column 3) in Berlin (Otto and Witt 2002). The data in column 4–6 is based upon an international inquiry on the population changes of birds in 19 eastern European cities (Konstantinov et al. 1996): The number of towns, in which corvid species occurred, is given in column 4. Column 5 indicates, the number of towns, in which populations increased and column 6, the number of towns, in which populations decreased.

	abundance (Berlin)	No. of habitats (Berlin)	No. of towns (Europe)	increase (Europe)	decrease (Europe)
Hooded crow	4500	4	19	18	0
Black-billed magpie	4300	4	19	16	1
Eurasian jay	1200	3	11	6	1
Rook	165	2	18	9	7
Jackdaw	115	2	19	7	4
Common raven	15	1	10	6	0

Habitat preferences

However, the goal of this thesis was to identify traits that might explain differences in the establishment success of corvids in urban environments. As stated earlier, urban environments are characterized by specific habitats that might be suitable for particular species (Møller 2009). In Berlin, ornithologists defined seven broad habitat categories (OAG Berlin (West) 1984), which include forests, bodies of water, open habitats (fields, meadows and airfields), urban green, build-up and industrial areas. Because avian morphological studies suggest that morphology covaries with behavior (Newton 1967, Wolf et al. 1976) and with habitat preferences (Bairlein et al. 1986, Korner-Nievergelt and Leisler 2004, Leisler et al. 1987), we studied the skull morphology of corvids in Chapter 2 and the wing-, hind-limb- and foot morphology in Chapter 3.

We defined foraging strategies and habitat preferences of corvids along gradients, because although these species evolved several differences, they are known to overlap in behavior and ecology (Haffer and Bauer 1993, Waite 1984). Foraging were defined along a gradient from pecking to probing, while habitat preferences were defined from forest to open habitats. Our results on skull morphology suggest that probing in contrast to pecking is associated with a long, curved bill and sidewise oriented eyes (e. g. rooks). Morphological associations with open habitats in contrast to forest habitats covaried with wingtip pointedness (e. g. rooks and jackdaws).

It was expected that hind-limb and foot morphology would reflect gradients from hopping to walking and from tree to ground foraging. However, the analysis of hind-limb and foot morphology did not separate the corvid species very well. These results indicated the flexibility of corvids in their foraging behavior and habitat associations. Furthermore, the difference between these species might be the frequency, in which they use these different habitat types and/or behaviors (compare Chapter 2 and Chapter 3).

However, the association of rook and jackdaw to open habitats is also reflected in their distribution in Berlin as both species occur only in proximity to airfields (Otto and Witt 2002). It is thought that pointed (e. g. rook and jackdaw) as opposed to rounded wings (e. g. black-billed magpie and Eurasian jay) are associated with an increased flight speed, which is traded in for maneuverability (Norberg 1990, Swaddle and Lockwood 1998), with a slow take off from ground (Swaddle and Lockwood 1998, van der Veen and Lindström 2000) and with a high flight initiation and landing distance after predator encounter (Fernández-Juricic et al. 2006). Furthermore, behavioral and morphological traits of rooks and jackdaws might indicate that their ability to detect predators is decreased compared to the other corvid species. While our results on jackdaws indicate a wide binocular field and thus a small visual field (compare Chapter 2), rooks preferred foraging technique – probing – might restrict visual coverage about the head (Fernández-Juricic et al. 2004, Guillemain et al. 2001, 2002). Hence, these traits might illustrate the necessity for jackdaws and rooks to forage in open areas, because this habitat probably allows an earlier predator detection and therefore an earlier flight initiation, in contrast to e. g. forests. Hence, traits related to the predator avoidance might explain limitations in the establishment success of jackdaws and rooks, but do not question the potential to respond adaptively to conditions in urban environments.

Møller (2008, 2009) reported that urban birds had lower flight initiation distances than rural birds, which suggests that urban birds adapted to the proximity to humans. Hence, it is imaginable that jackdaws and rooks might be able to forage on small-sized lawns in close proximity to humans, which in turn might provide protection against predation (Møller 2008, 2009). For example, Eurasian jays were formerly known as shy and wary birds, which in its ancestral forest habitats were foremost recognized by their alarm calls (Goodwin 1976, Haffer and Bauer 1993). In recent years however, Eurasian jays were able to expand their habitat range in Berlin and now occurs even in the city center (Otto and Witt 2002). Hence, differences in predator avoidance related traits might suggest that the predisposition for urbanization differs between corvids and that some species have to adapt more than others.

In that context, one striking result of Chapter 2 and Chapter 3 is that hooded crow is closest to the mean shape in every morphological analysis. This result might suggest that hooded crow is more flexible in its feeding and habitat choice compared to the other corvid species. If, for example, the gradient from forest to open habitats corresponds to a gradient from rounded to pointed wings, then a species with a moderate wingtip shape, might be more flexible in its habitat associations, because it might be able to dwell in both habitats. However, most of the variation in the analysis of skull morphology is explained by differences in size, in contrast to the analysis of wing morphology. Hence, a better estimate for species differences in skull morphology is the shape deviation from the allometric relationship. Therefore, we performed a multivariate linear regression of the Procrustes shape variables on log centroid size (compare Chapter 2) and calculated scores from the vector of regression slopes (Fig. 1a). Figure 1b illustrates that hooded crow and black-billed magpie are very similar in relative shape of the skull, because these species show the least deviation from the allometric relationship of the studied corvid species. Hence, black-billed magpie and hooded crow might be assumed to be more flexible in feeding compared to the other corvid species.

Anthropogenic food

It is assumed that species that are more flexible in their feeding are more likely to exploit anthropogenic food resources (Clergeau et al. 1998, McKinney 2002) and therefore, might have selective advantages in urban environments over species that stick to their ancestral diet (Marzluff 2001, Shochat et al. 2006). In fact, several experimental studies on corvids suggest that food supplementation produced higher breeding densities and lowered nest-predation risks due to social nest defense. Furthermore, food-supplemented breeding pairs had a higher nesting success and produced

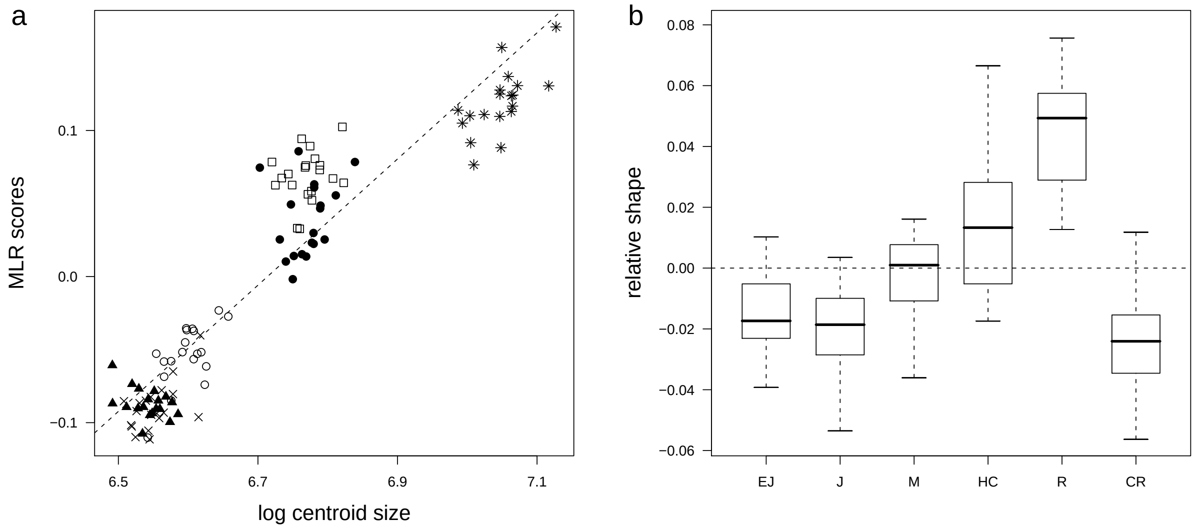

Fig. 1: Scores calculated from the regression vectors of a multivariate linear regression (MLR) of Procrustes shape variables on log centroid size (**a**) and the corresponding residuals, which were interpreted as relative shape differences (**b**).

× jackdaw (J) ▲ Eurasian jay (EJ) ○ black−billed magpie (M) ● hooded crow (HC) □ rook (R) ✳ common raven (CR) more, heavier and bigger fledglings (Högstedt 1981, Richner 1992, Soler and Soler 1996, Stone and Trost 1991).

In that respect, another important morphological measure is the within-species variability in morphological traits. According to the niche variation hypothesis, niche breadth is reflected in the variability of bill size and shape (Brandl et al. 1994, Grant 1968, Price 1987, van Valen 1965, van Valen and Grant 1970). It is thought that an increase in the variability in bill size covaries with an access to a wider range of resources, while an increase in bill shape variability reflects an increased range of foraging techniques (Brandl et al. 1994, compare also Bolnick et al. 2007, 2003, Price 1987).

Within-species morphological variability in turn is thought to be promoted by feeding innovations. According to the behavioral drive hypothesis feeding innovations might spread among members of a population through individual and social learning and as a consequence, the species might be exposed to new selective pressures that in turn increase anatomical variability (Sol and Price 2008, Sol et al. 2005b, Wyles et al. 1983). Furthermore, feeding innovations have been associated with the adoption of new food resources, too (Lefebvre et al. 2002, 1997).

In Chapter 4, we therefore tested the relationship between morphological variability in skull shape and feeding innovations. Within-species morphological variability were estimated from the first three dimensions of a principal component analysis (PCA) on skull shape variables (compare Chapter 2) and feeding innovations were collated by Lefebvre and students as the frequency of new and unusual feeding behaviors per species reported in the short note section of ornithological journals (compare Chapter 4 and 5, Lefebvre et al. 1997, Sol et al. 2005a). Although, our results were not significant, within-species variabilities in two out of three dimensions of the PCA, PC 1 and PC 3, revealed an almost significant trend. It was striking that major variation across species in PC 1 and PC 3 occurred at the bill, as opposed to PC 2. Furthermore, in contrast to PC 2, corvid species showed pronounced shape differences in PC 1 and PC 3. These patterns cannot be explained at the moment. However, it is likely that the inability to detect a significant correlation is due to the low number of species studied, rather than to a non-existent relationship.

Cognitive constraints

There is a growing body of evidence that feeding innovation frequency is associated with relative brain size or a part thereof (Lefebvre et al. 1997, Nicolakakis and Lefebvre 2000, Timmermans et al. 2000). Hence, feeding innovations received considerable attention in recent literature (Lefebvre et al. 1997, Reader and Laland 2002) and have been related to tool-use (Lefebvre et al. 2002), social learning (Bouchard et al. 2007, Reader and Laland 2002) and the ability to invade and colonize new habitats (Sol et al. 2005a, Sol and Lefebvre 2000). Therefore, as stated earlier, probably the most promising hypothesis to explain differences in the establishment success in urban environments has been termed the brain size – environmental change hypothesis. It predicts that birds with enlarged brains and a higher propensity for innovative behavior more readily colonize new or altered environments (Sol et al. 2005a).

In Chapter 5, we therefore tested whether relative brain size and/or feeding innovation frequency predicts the establishment success of birds in urban environments. Urban establishment success were estimated by four indices, i. e. absolute and relative population density of Berlin, as well as the population increase and decrease in 19 eastern European cities (compare Tab. 1). Our results indicate that both relative brain size and innovation frequency predict the population density of birds in Berlin and therefore support the brain size – environmental change hypothesis. Birds with enlarged brains and a high propensity for innovative behavior seem to successfully colonize urban environments. However, our results also suggest that innovation frequency is a better predictor for urban success than relative brain size, which is consistent with the finding that the relationship between relative brain size and feeding innovation was only significant when phylogeny was controlled for.

Two, not mutually exclusive explanations were posed that might explain these results. First, it is thought that differences in relative brain size might have evolved in the early diversification of avian lineages (Nealen and Ricklefs 2001, Sol 2003), while innovation frequency might reflect the current degree of behavioral flexibility (Sol 2003). This hypothesis is supported by patterns of variation in relative brain size and innovation frequency at different evolutionary scales. While major variation in feeding innovation frequency is located on the species level, major variation in relative brain size is concentrated at higher taxonomic levels (Nealen and Ricklefs 2001, Nicolakakis et al. 2003, Sol 2003). Second, it is thought that different cognitive systems might be traded off against one another and therefore reflect the limited modularity of bird minds and brains (Lefebvre and Bolhuis 2003). Supporting evidence comes from a negative relationship between the degree of food caching and innovation frequency in European Paridae and North American Corvidae (Lefebvre and Bolhuis 2003).

Therefore, one might conclude that cognitive traits reflect the specialization of a species, particularly because feeding innovations are considered as a measure of behavioral flexibility (Klopfer and MacArthur 1960, Lefebvre and Bolhuis 2003). Furthermore, the information-processing hypothesis states that specialists are more effectively in exploiting a given resource than generalists, because generalists must evaluate a greater diversity of resources than specialists and thus face cognitive challenges, that are predicted to constrain the efficiency and accuracy of their choices (Bernays 2001, Egan and Funk 2006).

Future directions

The results of this chapter, as well as the results of this thesis suggest that behavioral flexibility – or in other words, the degree of specialization – is reflected in cognition and morphology (compare Fig. 1 and Chapter 4). In addition, feeding innovations are generally considered as a measure of flexibility that predict both, urbanization and invasion potential. Hence, one might assume that measures of morphology might directly predict these potentials in a given taxon.

This thesis also suggests that urban environments expose organisms to new selective forces, and therefore – according to the behavioral drive hypothesis – urban populations should be more variable in morphology, compared to rural populations. Following this argumentation, urban environments might be considered as a unique setting, which allows to test the behavioral drive hypothesis across numerous taxa and in addition, directly test the effect of urban feeding innovations on urban morphological variability as well as rural feeding innovations on rural morphological variability. Although, there is supporting evidence for the behavioral drive hypothesis (e. g. Nicolakakis et al. 2003, Sol and Price 2008, Sol et al. 2005b), these studies were performed at higher evolutionary time scales, e. g. testing the relationship between innovation frequency and the number of species per taxon (Nicolakakis et al. 2003).

However, another very promising correlate of urbanization was found in geographical distribution (Bonier et al. 2007, Møller 2009). These studies found that urban birds had a broader geographical distribution compared to their rural congeners. Bonier et al. (2007) assumed that geographical distribution might be a measure of environmental tolerance, because variation in environmental conditions increases with latitudinal and elevational distributions. The brain size – environmental change hypothesis suggests that birds with enlarged brains and a high propensity for innovative behavior might cope with a broader range of environmental conditions (Sol et al. 2005a). Therefore, one might suggest, relative brain size and feeding innovations determine the geographical distribution of a species.

Thesis

The following chapter explores the functional morphology and integration of corvid skulls with emphasis on the feeding ecology and the third chapter investigates the morphological separation with emphasis on habitat associations of these species. The fourth chapter explores the relationship between morphological variability and feeding innovations and in Chapter 5 we finally test the relationship between brain size, feeding innovations and the establishment success in urban environments. Chapter 2 is already published and Chapter 3–5 will be submitted to scientific journals with the following authorships, author's contributions and titles:

Chapter 2: Kulemeyer C, Asbahr K, Gunz P, Frahnert S, Bairlein F (2009): Functional morphology and integration of corvid skulls – a 3D geometric morphometric approach. Frontiers in Zoology, 6: 2.

CK designed the study, analyzed the data and drafted the manuscript. KA placed landmarks and semilandmarks. PG participated and supervised the data analysis. SF and FB supervised the study and were also involved in drafting the manuscript.

Chapter 3: Kulemeyer C, Vogel I, Asbahr K, Frahnert S, Bairlein F: Morphological separation of sympatric corvids.

CK designed the study, analyzed the data and drafted the manuscript. IV and KA took morphological measurements. SF and FB supervised the study and were also involved in drafting the manuscript.

Chapter 4: Kulemeyer C, Frahnert S, Bairlein F: Morphological variability and feeding innovations of corvids.

CK designed the study, analyzed the data and drafted the manuscript. SF and FB supervised the study and were also involved in drafting the manuscript.

Chapter 5: Kulemeyer C, Frahnert S, Bairlein F: Brain size, feeding innovations and urban establishment success.

CK designed the study, reconstructed the endocrania, analyzed the data and drafted the manuscript. SF and FB supervised the study and were also involved in drafting the manuscript.

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2. Functional morphology and integration of corvid skulls – a 3D geometric morphometric approach[1]

Abstract

Background: Sympatric corvid species have evolved differences in nesting, habitat choice, diet and foraging. Differences in the frequency with which corvid species use their repertoire of feeding techniques is expected to covary with bill-shape and with the frontal binocular field. Species that frequently probe are expected to have a relatively longer bill and more sidewise oriented orbits in contrast to species that frequently peck. We tested this prediction by analyzing computed tomography scans of skulls of six corvid species by means of three-dimensional geometric morphometrics. We (1) explored patterns of major variation using principal component analysis, (2) compared within and between species relationships of size and shape and (3) quantitatively compared patterns of morphological integration between bill and cranium by means of partial least squares (singular warp) analysis.

Results: Major shape variation occurs at the bill, in the orientation of orbits, in the position of the foramen magnum and in the angle between bill and cranium. The first principal component correlated positively with centroid-size, but within-species allometric relationships differed markedly. Major covariation between the bill and cranium lies in the difference in orbit orientation relative to bill-length and in the angle between bill and cranium.

Conclusion: Corvid species show pronounced differences in skull shape, which covary with foraging mode. Increasing bill-length, bill-curvature and sidewise orientation of the eyes is associated with an increase in the observed frequency in probing (vice versa in pecking). Hence, the frequency of probing, bill-length, bill-curvature and sidewise orientation of the eyes is progressively increased from jackdaw, to Eurasian jay, to black-billed magpie, to hooded crow, to rook and to common raven (when feeding on carcasses is considered as probing). Our results on the morphological integration suggest that most of the covariation between bill and cranium is due to differences in the topography of the binocular fields and the projection of the bill-tip therein, indicating the importance of visual fields to the foraging ecology of corvids.

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Background

Sympatric corvids in Central Europe have evolved differences in nesting (Bossema et al. 1986, Holyoak 1968, Röell and Bossema 1982), habitat choice (Bossema et al. 1986, Rolando et al. 1998, Waite 1984), diet (Holyoak 1968, Lockie 1956, Waite 1984) and foraging (Berrow et al. 1991, Lockie 1956, Rolando et al. 1998, Waite 1984). Although these species overlap in their feeding techniques, the quantity with which they use their repertoire

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is markedly different between species. In behavioral studies, three main feeding techniques have been defined: (1) probing, which is characterized by feeding below the surface, (2) pecking, which is characterized by feeding at the surface and (3) turning objects, which represents searching and feeding beneath animal dung and other surface litter (Berrow et al. 1991, Högstedt 1980, Lockie 1956, Rolando et al. 1998, Waite 1984). Probing is frequently observed in rook, hooded crow and common raven, while pecking and turning objects is often found in Eurasian jay, jackdaw, black-billed magpie and hooded crow (Berrow et al. 1991, Goodwin 1976, Haffer and Bauer 1993, Lockie 1956, Rolando et al. 1998, Waite 1984). It is assumed that foraging behavior covaries with bill morphology (Benkman 1993, Newton 1967, Swennen et al. 1983, Wolf et al. 1976) and that probing is observed more frequently in birds with long and curved bills, while pecking and turning objects are observed more frequently in birds with straight and short bills (Barbosa and Moreno 1999, Beecher 1978, Nebel et al. 2005, Zweers and Gerritsen 1997).

While bill morphology has been studied intensively, its covariation with other components of the avian skull has hardly been considered and never been quantified (e. g. Beecher 1951, 1978, Bock 1964, Lorenz 1949). For instance, the adaptive significance of the frontal binocular field in foraging ecology is well known in birds (Martin 1985, 2007). Thus, most of the variation in the topography of binocular fields, its width, vertical extent and the horizontal and vertical projection of the bill-tip within the binocular field, have been explained by differences in foraging behavior (Martin 1985, 2007). Hence, probing in contrast to pecking and turning objects is thought to require a smaller frontal binocular field, because its principal function lies in the degree to which vision is used in the guidance of the bill towards food objects (Martin 1985, 2007). In morphological studies, several authors assumed that orbit convergence, i. e. the orbit orientation in skulls, is associated with the degree of the binocular field overlap (Cartmill 1974, Heesy 2004, Martin 1985).

In this paper, we analyzed computed tomography (CT) scans of skulls of six corvid species by means of three-dimensional geometric morphometrics to (1) explore patterns of major variation using principal component analysis, (2) compare within and between species relationships of size and shape and (3) quantitatively compare patterns of morphological integration between bill and cranium. We expect corvid species that frequently probe to have a longer and more curved bill and more sidewise oriented orbits, when compared with corvids, which frequently peck and turn objects.

Methods

Data

Our sample consists of 115 adult skulls of six corvid species: common raven (*Corvus corax*), hooded crow (*Corvus corone cornix*), rook (*Corvus frugilegus*), jackdaw (*Corvus monedula*), black-billed magpie (*Pica pica*) and Eurasian jay (*Garrulus glandarius*). The specimens are almost equally distributed across species and came from Museum für Naturkunde Berlin, Staatliches Museum für Naturkunde Görlitz and Staatssammlung für Anthropologie und Paläoanatomie München, which are all located in Germany. All corvid skulls were scanned by computed tomography at Charite-Universitätsmedizin Berlin.

We digitized three-dimensional coordinates of 32 homologous landmarks on evolutionary stable structures and 116 equally spaced semilandmarks on 16 curves (Tab. 1, Fig. 1). Semilandmarks refer to a series of points that are sampled along outlines and that are allowed to slide along curves to minimize bending energy. In subsequent statistical analysis, these relaxed semilandmarks can be treated as homologous within the sample (Bookstein et al. 1999, Bookstein 1997, Gunz et al. 2005).

Digitization of landmarks and semilandmarks, as well as the processing of semilandmarks were done with Edgewarp 3.30 (Bookstein and Green 2002).

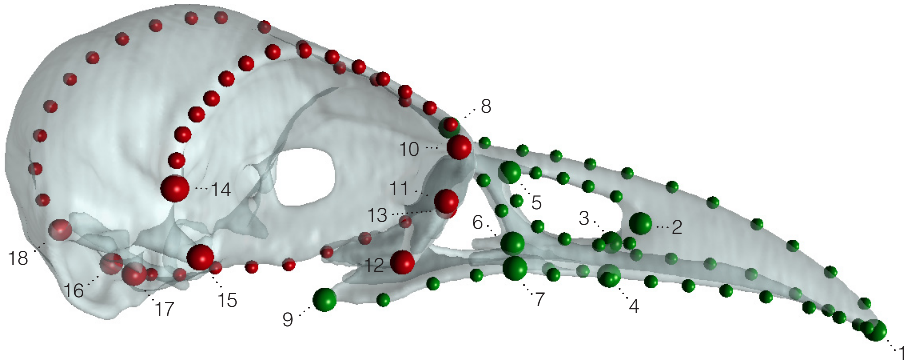

Fig. 1: **Landmarks and semilandmarks.** Lateral view of a corvid skull with landmarks (big dots) and semilandmarks (small dots) partitioned into two blocks: bill (green) and cranium (red).

Tab. 1: **Landmark description.** Descriptions of landmarks (Baumel and Witmer 1993) that were digitized on two blocks: bill and cranium; either placed on the midsagittale or on the left and right (L, R).

Number	Description
bill	86 Landmarks and semilandmarks
1	bill-tip
2 L, R	maximum of curvature at the rostral end of the external nares
3	most caudal point of the ossified palatine
4 L, R	bifurcation of the Os palatinum and the Os maxillare close to the rim of the Os maxillare
5 L, R	maximum of curvature at the caudal end of the external nares
6 L, R	maximum of curvature at the rostral end of the Fossa et Fenestra antorbitalis
7 L, R	maximum of curvature at the lateral intersection of the Processus maxillaris and the Os jugale
8	mid-point of the cranio-facial hinge
9 L, R	most posterior point of the Angulus caudolatum (Os palatinum)
cranium	66 Landmarks and semilandmarks
10 L, R	most dorso-lateral point of the Os lacrimale
11 L, R	most medial point (maximum of curvature) of the Os lacrimale
12 L, R	most ventro-lateral point of the Os lacrimale
13	most ventro-rostral point of the Os mesethmoidale
14 L, R	most distal point of the Processus postorbitalis
15 L, R	most distal point of the Processus zygomaticus
16	most caudal point of the Condylus occipitalis
17 L, R	Ostium canalis ophthalmici externi
18	most dorsal point of the Foramen magnum

Geometric morphometrics

The resulting dataset was subjected to a generalized least squares Procrustes analysis (GPA, Rohlf and Slice 1990), in which distances between homologous landmarks are minimized by translating, rotating and scaling all forms to a common reference (consensus). In other words, shape refers to the geometric information that is left after removing the effects of size, position and orientation. The information about overall body-size of the specimens is preserved in centroid size, which serves as a scaling factor in GPA and which is calculated as the square root of the sum of squared distances of landmarks and semilandmarks from their centroid.

In birds, especially in those with long bills, landmarks and semilandmarks that are placed closely to the bill-tip will have a great influence on centroid size, because they change the position of the centroid and thus change the distance of the whole landmark set to its centroid. Bills are known to vary greatly according to foraging mode. Hence, centroid sizes calculated from the whole landmark set, i. e. including the bill, will not be a good predictor of overall body-size if bill-length in the studied species is highly variable. Therefore, we adjusted GPA by using centroid size calculated only from landmarks and semilandmarks placed on the cranium and the antorbital fenestra: landmarks 6–18 and associated semilandmarks (Fig. 1, Tab. 1).

Procrustes shape coordinates, returned by GPA, were subjected to a principal component analysis (PCA) to explore patterns of major variation across the entire skull (Fig. 2). To test the influence of size on shape, a multivariate linear regression of the Procrustes shape coordinates on log centroid size was performed.

Partial least squares

Partial least squares analysis (PLS) is often referred to as singular warp analysis when applied to Procrustes shape coordinates (Bookstein 1991, Bookstein et al. 2003, Rohlf and Marcus 1993). PLS is used to find correlated pairs of linear combinations between two blocks of variables. These linear combinations are constructed to display patterns of covariation between the two blocks, just as PCA extracts patterns of variation across the entire block.

To study the morphological integration between bill and cranium, the Procrustes shape coordinates were partitioned prior to the PLS into these functional units (Fig. 1), which we refer to as the *"whole fit"* dataset. In addition, landmark coordinates of these functional units were scaled and superimposed separately, which we refer to as the *"separate fit"* dataset. In the *whole fit* dataset, the functional units retain their relative position and their size proportions to each other, whereas this geometric information is lost in the *separate fit* dataset. Hence, the analysis of the *separate fit* dataset concentrates purely on differences in shape.

As we are interested whether there are within-group patterns of integration that are shared across species, we standardized the *whole fit* and the *separate fit* dataset by subtracting the species mean from the shape coordinates of the corresponding specimens. These Procrustes residuals were subjected to two PLS, one on the residual shape coordinates of the *whole fit* (PLS_{whole}) and one on the residual shape coordinates of the *separate fit* dataset (PLS_{sep}). We used the algorithm introduced by Mitteroecker and Bookstein (2007, 2008) (scaled PLS), which allows a separate scaling of the PLS vectors. This ensures that the amount of shape deformation is correctly scaled when we visualize the shape changes of the two blocks together in the PLS_{whole} analysis.

All computations were done in Mathematica 6.0 and R 2.6.1. The surface representations of the shape deformations were rendered in Amira 4.0.

Results

Species differences

The PCA of the full landmark set clearly (except from hooded crow and rook) separates

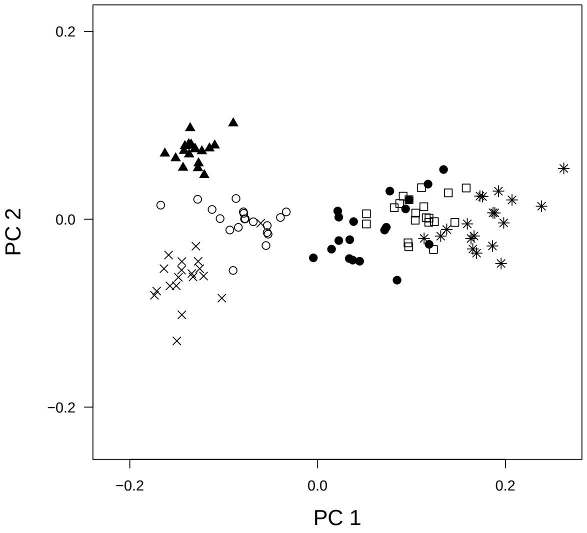

Fig. 2: **First two dimensions of the PC scores.** Two-dimensional plot of the principal component scores calculated from the Procrustes shape coordinates of the full landmark set.

▲ Eurasian jay × jackdaw ○ black−billed magpie ● hooded crow □ rook ✳ common raven

the corvid species, which only marginally overlap in the first two principal components (PC, Fig. 2). PC 1 explained 73.7 % of the total variation and was interpreted as an increase in relative bill-length, -width and -curvature, an increase in relative cranium length and -width, a decrease in relative cranium height, as an upward positioned foramen magnum and as sidewise oriented orbits (Fig. 3a). PC 2 explained 9.5 % of the total variation and was interpreted as an increase in the angle between bill and cranium, which results from a rotation of the cranium. In addition, PC 2 was interpreted as an increase in the curvature of

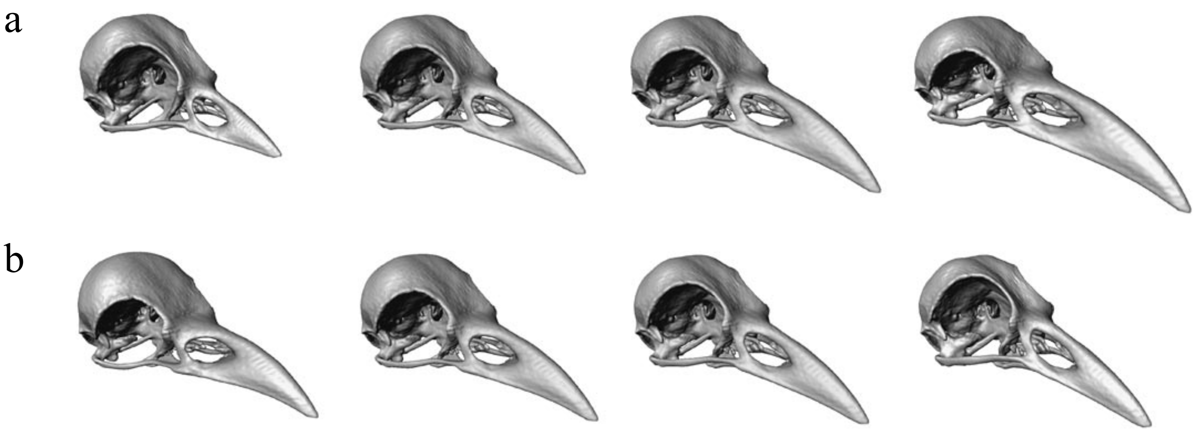

Fig. 3: **Shape deformations according to the first two dimensions of the PCA.** The sequence of surface representations (from left to right) as deformations of the average shape correspond to increasing scores in PC 1 **(a)** and PC 2 **(b)** in Figure 2. The surface morphs differ from its neighbors by equal multiples of the standard deviation of the actual variability. The first and last column is extrapolated by 2 **(a)** and 4 **(b)** standard deviations, respectively. **(a):** Major variation in PC 1 lies in the relative length and curvature of the bill, in cranium height, in the position of the foramen magnum and in the position and orientation of the orbits. **(b):** Major variation in PC 2 lies in the angle between bill and cranium, in the position of the foramen magnum, in the position and orientation of the orbits and in bill-curvature.

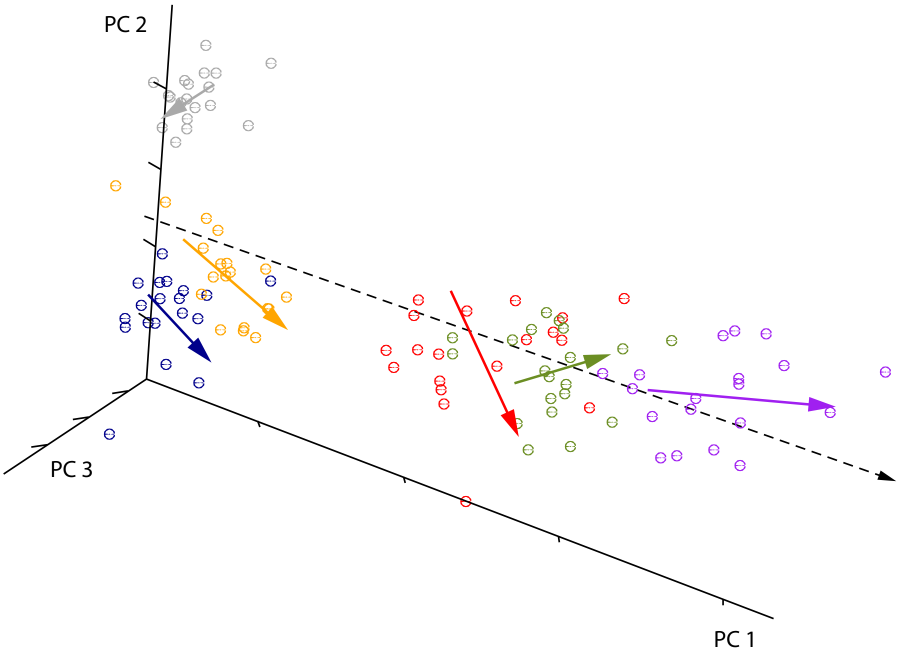

Fig. 4: **Multivariate regression of shape variables on log centroid size.** Three-dimensional plot of the principal component scores. The colored lines are intraspecific regressions of the shape coordinates on log centroid size and thus estimate allometry within species. The dashed line is the regression of shape coordinates on log centroid size over all species.

● jackdaw ● Eurasian jay ● black−billed magpie ● hooded crow ● rook ● common raven

the bill, a decrease in the relative width of bill and cranium, a downward positioned foramen magnum and upward and sidewise oriented orbits (Fig. 3b). While the scores of PC 1 correlate positively with the log of centroid size ($r = 0.927$, Fig. 4) and thus reflect shape changes that are associated with differences in size, the scores of PC2 do not correlate with log centroid size ($r = -0.08$). Note that although rooks have higher scores in PC 1 than hooded crows, centroid size between these two species does not differ (ANOVA, $p = 0.959$). Thus, shape differences between rooks and hooded crows are not allometric. To explore the influence of size on skull shape, a multivariate linear regression was performed. The correlation between the vector of regression slopes and the first eigen-vector of the PCA is very high ($r = 0.998$, Fig. 4), so that shape changes predicted by the multivariate regression with increasing centroid size resembles shape changes along PC 1. We also regressed the Procrustes shape coordinates on log centroid size for each species separately (Fig. 4). Figure 4 clearly shows that the relationship of size and shape differ markedly between species and thus from the regression vector over all species. As the number of studied individuals per species is small, shape changes that occur with increasing centroid size within species are not visualized.

Morphological integration

Whole fit

To assess the covariation between the bill and cranium, we performed a PLS analysis on the residual shape coordinates of the *whole fit* dataset, in which the entire landmark set was subjected to one Procrustes fit. The relationship between the functional units is plotted as scores returned by PLS_{whole} in Figure 5 and 6. These graphs illustrate how well shape and relative position of one block is predicted by shape and relative position of the other (and vice versa). The PLS_{whole} vectors were visualized as surface deformations in

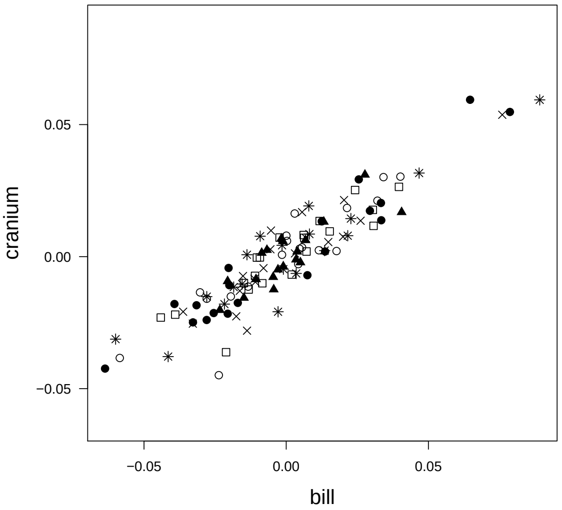

Fig. 5: **First dimension of the PLS$_{whole}$ scores.** First dimension of the partial least squares scores calculated from two landmark blocks, bill and cranium, of the *whole fit* dataset.

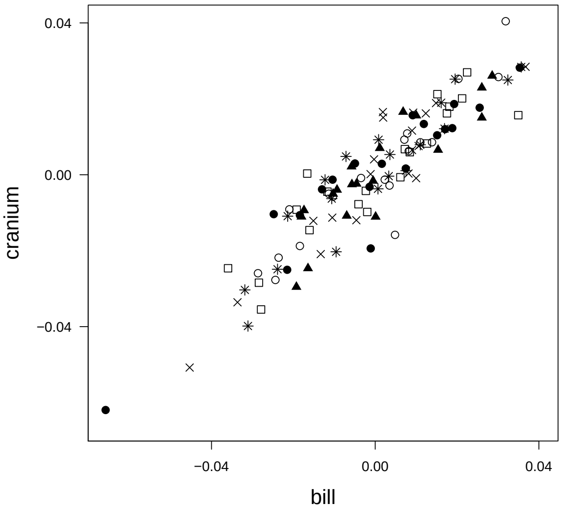

Fig. 6: **Second dimension of the PLS$_{whole}$ scores.** Second dimension of the partial least squares scores calculated from two landmark blocks, bill and cranium, of the *whole fit* dataset.

▲ Eurasian jay × jackdaw ○ black−billed magpie ● hooded crow ☐ rook ✳ common raven

Figure 7 and 8. The correlation between the scores of the first dimension is strikingly high ($r = 0.923$, Fig. 5) and represents the direction of integration shared by all species. Shape changes of PLS$_{whole}$ 1, visualized in Figure 7, represent the difference between individuals with a long bill and cranium, an upward positioned foramen magnum as well as sidewise oriented orbits and individuals with a short bill and cranium, a downward positioned foramen magnum and forward oriented orbits. The correlation between scores of the second dimension is very strong ($r = 0.922$, Fig. 6). Again, the pattern of integration is shared across all species. Major shape changes of PLS$_{whole}$ 2 were interpreted as an increase in the angle between bill and cranium, which results from a rotation of the cranium. These deformations are associated with an increase in bill-curvature, an upward positioned foramen magnum as well as a bending and thus positional adjustment of the palatinum relative to the sphenoidale. Hence, the second dimension represents differences between individuals with a decreased angle between bill and cranium, a curved bill and a more dorsal foramen magnum and individuals with an increased angle between bill and cranium,

Fig. 7: **Shape deformations according to the first PLS$_{whole}$ dimension.** The sequence of surface representations (from left to right) as deformations of the average shape correspond to increasing scores of the first PLS$_{whole}$ dimension in Figure 5a. The surface morphs differ from its neighbors by equal multiples of the standard deviation of the actual variability. The first and last column is extrapolated by 4 standard deviations. Major covariation between blocks lies in bill- and cranium-length and in the orientation of the eyes.

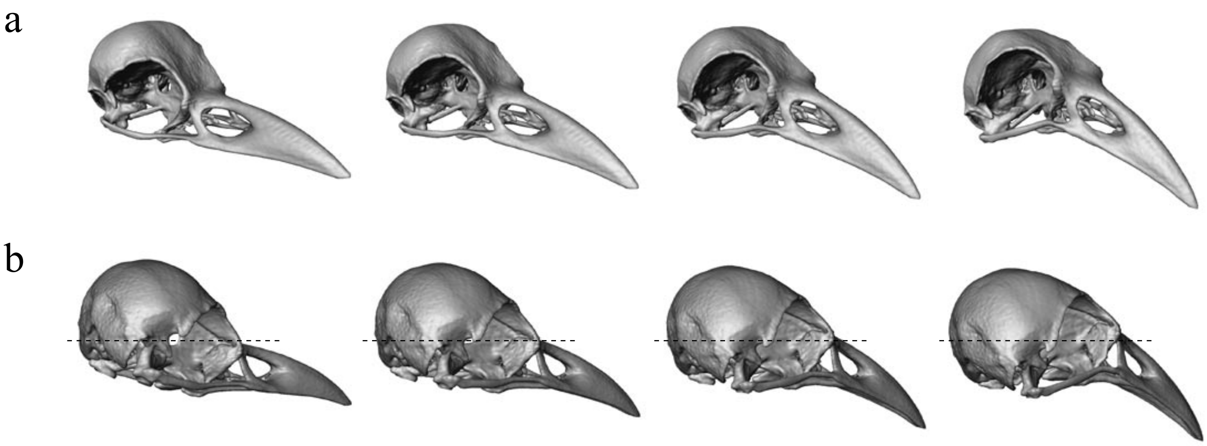

Fig. 8: **Shape deformations according to the second PLS$_{whole}$ dimension.** The sequence of surface representations (from left to right) as deformations of the average shape correspond to increasing scores of the second PLS$_{whole}$ dimension in Figure 5b. The surface morphs differ from its neighbors by equal multiples of the standard deviation of the actual variability. The first and last column is extrapolated by 4 standard deviations. Major covariation between blocks lies in the angle between bill and cranium and in the position of the foramen magnum. **(b):** Exemplary representation of the positional change of the foramen magnum. The dashed line represents the dorsal margin of the foramen magnum of the consensus.

a straight bill and a more ventral foramen magnum (Fig. 8).

Separate fit

The covariation independent of the relative position between the bill and cranium was explored by a PLS analysis on the residual shape coordinates of the *separate fit* dataset, in which the two blocks were subjected to separate Procrustes fits. The correlation between the scores of the first PLS$_{sep}$ vector is strong ($r = 0.867$, Fig. 9) and the corresponding shape changes (Fig. 10) resemble shape

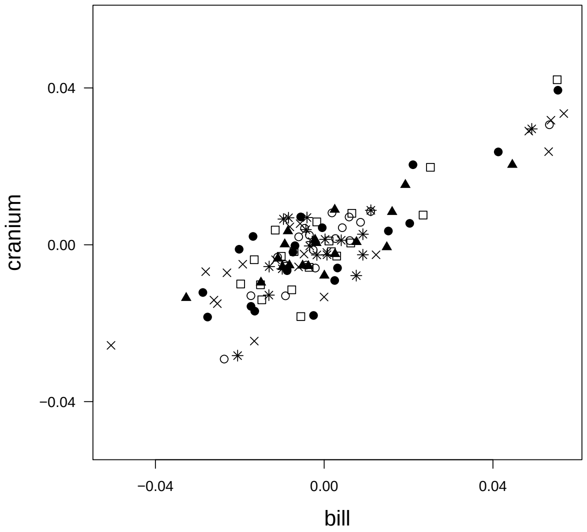

Fig. 9: **First dimension of the PLS$_{sep}$ scores.** First dimension of the partial least squares scores calculated from two landmark blocks, bill and cranium, of the *separate fit* dataset.

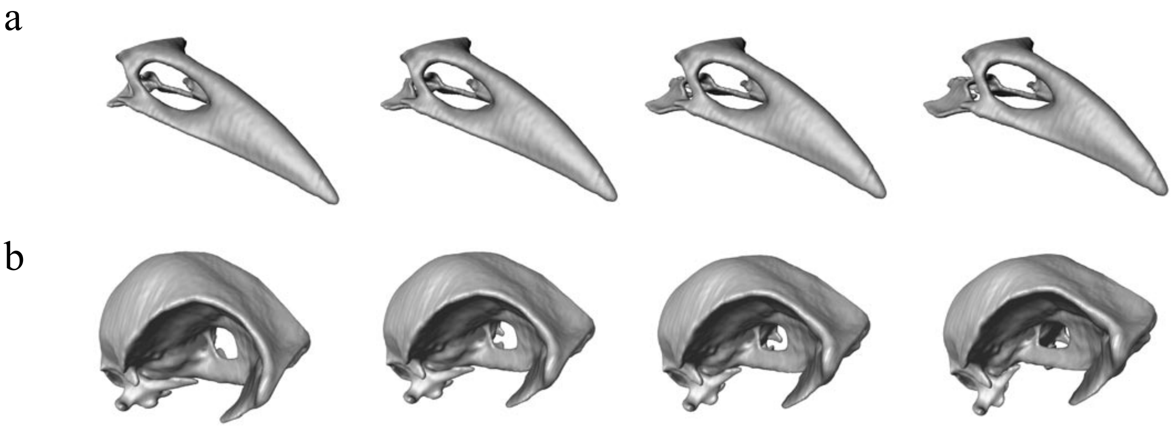

Fig. 10: **Shape deformations according to the first PLS$_{sep}$ dimension.** The sequence of surface representations (from left to right) as deformations of the average shape of the two blocks, bill **(a)** and cranium **(b)**, correspond to increasing scores of the first PLS$_{sep}$ dimension in Figure 9. The surface morphs differ from its neighbors by equal multiples of the standard deviation of the actual variability. The first and last column is extrapolated by 4 standard deviations. Major covariation between blocks lies in relative bill- and palatinum length **(a)** and in the relative position of the cranio-facial hinge **(b)**.

changes displayed by the third dimension of PLS$_{whole}$ ($r = 0.915$, not visualized). These differences in shape represent individuals with a long, straight bill, a decreased relative palatinum length and a downward positioned cranio-facial hinge as well as downward positioned orbits, in contrast to individuals with a short, curved bill, an elongated palatinum, an upward positioned cranio-facial hinge and upward positioned orbits (Fig. 10). The correlation between the scores of the second PLS$_{sep}$ vector was low ($r = 0.518$) and therefore, the corresponding shape changes are not visualized.

Discussion

In avian morphological studies, geometric morphometric methods are not commonly applied and when they are, they encounter particular difficulties (compare Brewer and Hertel 2007, Marugán-Lobón and Buscalioni 2006, van der Meij 2005). As bony junctions on avian skulls are not externally visible, there are only few anatomical landmarks of type I (Bookstein 1991). Instead of relying on the scarce anatomical landmarks, here we quantified the skull using the method of semilandmarks. These semilandmarks can be placed on "forms without landmarks" (Bookstein 1997, Gunz et al. 2005) and make it possible to incorporate curvature information in coordinate-based morphometrics.

Because the shape of the bill, particularly its length, is highly variable (Marugán-Lobón and Buscalioni 2006, van der Meij 2005), landmarks placed on the tip of the bill create a "pinocchio effect". If two crania were completely identical in shape, but had bills of different lengths, then the least squares properties of the Procrustes registration would "create" shape differences on every landmark. This methodological artifact, however, only affects the Procrustes superimposition, not the thin-plate spline. Because semilandmarks (in their bending energy version) are built upon the thin-plate spline algebra and the visualizations are computed as thin-plate spline deformations, they are not affected by registration problems.

In this study we adjusted GPA by using centroid size calculated only from landmarks and semilandmarks placed on the cranium and the antorbital fenestra (see Methods). For similar reasons van der Meij (2005) did not include landmarks placed on the bill-tip in GPA and added these landmarks to the fitted data after applying the same scaling, rotation and translation as for the other landmarks. Marugán-Lobón and Buscalioni (2006) ran separate GPAs, one including the landmark on the bill-tip and one without.

Species differences

Major shape variation occurs at the bill (PC1), in the position of the orbits and foramen magnum (PC1 and PC2) and in the angle between bill and cranium (PC2). These results are consistent with quantitative studies on avian skull morphology, which also report of major variation at the bill, in the position of the foramen magnum and in the angle between bill and cranium (Marugán-Lobón and Buscalioni 2006, van der Meij 2005).

According to scores in PC 1, the common raven has the longest, widest, most curved bill; the longest, widest and most flattened cranium; the most upward positioned foramen magnum; and the most sidewise oriented orbits, followed by the rook, hooded crow, black-billed magpie and Eurasian jay (Fig. 2, Fig. 3a). PC 1 correlates positively with log centroid size and in addition, the first eigenvector is highly correlated to the vector of regression slopes returned by a multivariate linear regression of the Procrustes shape coordinates on log centroid size. Although, these results suggest that shape changes with increasing centroid size are similar across species, the within-species multivariate regression of the Procrustes shape coordinates on log centroid size indicates that the allometric relationships differ markedly between species (compare Schuh 1968, Fig. 4). Despite the fact that our intraspecific sample is small and consists only of adult, unsexed corvids, it seems likely that shape changes observed between species are not only due to differences in size, but can also be assumed to vary according to differences in ecology. In birds, it is known that the shape allometry of the bill is very variable between species (e. g. Grant 1986). Furthermore it can even vary within species, e. g. due to sexual dimorphism (Schuh 1968). These allometric differences are often associated with ecological factors such as foraging behavior (Holyoak 1970, Radford and Du Plessis 2003).

PC 2 separates the small corvid species (jackdaw, black-billed magpie and Eurasian jay, Fig. 2) and does not correlate with log centroid size. Hence, the corresponding shape changes are not allometric. The Eurasian jay with the highest scores in PC 2 has the highest angle between bill and cranium, most curved and thinnest bill and cranium, most downward positioned foramen magnum and most upward and sidewise oriented orbits, followed by black-billed magpie and jackdaw (Fig. 3b). Bigger corvid species (hooded crow, rook and common raven) overlap in PC 2 and have scores approximately equal to black-billed magpie (Fig. 2).

Morphological integration

Partial least squares is a relatively novel technique to study integration and we have employed the most recent algorithm that takes the scaling of the PLS loading vectors into account (compare Bookstein et al. 2003, Mitteroecker and Bookstein 2007, Rohlf and Corti 2000). The results of the PLS analysis showed that none of the dimensions displayed a clear distinction between species. Instead, the pattern of covariation between blocks is shared across all species and thus might be due to similar constraints (ecological, developmental and/or biomechanical) between species.

Most of the covariation in the first dimension of the PLS_{whole} describes differences in bill- and cranium-length and in the orientation of the orbits (Fig. 7). Thus, it is seems likely that PLS_{whole} 1 describes shape differences that are due to individual differences in size. The second dimension of PLS_{whole} and the first dimension of PLS_{sep} indicate that most of the covariation occurs at the cranio-facial hinge and results in a change in the angulation between bill and cranium (Fig. 8, Fig. 10). While this difference in angulation exhibited by PLS_{whole} 2 is due to a rotation of the bill and cranium in opposite directions (Fig. 8), in PLS_{sep} 1 (and PLS_{whole} 3) it is due to a local effect, i. e. to a change in the position of the cranio-facial hinge (Fig. 10). In corvids, the cranio-facial hinge is known to be a bending zone, a clearly recognizable area of thin bone, between the movable upper bill and the cranium (Bock 1964, Bout and Zweers 2001). Thus, it is not surprising that variation in the morphological integration between individuals occur in this specialized zone (compare Barnikol 1952, Lang 1952).

Both, the cranio-facial hinge and the palatinum are part of the mechanism that enables corvids to move the upper bill (rhynchokinetics, Bock 1964, Bout and Zweers 2001). Hence, variation in the relative length (PLS_{sep} 1) and in the relative position (PLS_{whole} 2) of the palatinum are likely to influence the properties of the rhynchokinetics (e. g. opening angle, bite force).

Functional implications
Bill

Previous studies on the foraging behavior of corvids suggest that the studied species vary in the frequency with which they use their repertoire of foraging techniques (Berrow et al. 1991, Högstedt 1980, Lockie 1956, Rolando et al. 1998, Waite 1984). Rooks are most frequently observed probing followed by hooded crow, black-billed magpie and jackdaw (and vice versa in pecking Berrow et al. 1991, Högstedt 1980, Lockie 1956, Rolando et al. 1998, Waite 1984). These differences are expected to covary with bill-length (Barbosa and Moreno 1999, Beecher 1978, Nebel et al. 2005, Zweers and Gerritsen 1997) and -curvature, because a curved bill is thought to allow inspection of a greater volume of sediment than a straight bill of equal length (Zweers and Gerritsen 1997). Hence, our results suggest that bill-length and -curvature is progressively increased from jackdaw, to Eurasian jay, to black-billed magpie, to hooded crow and to rook and thus meet our predictions stated above.

These differences become even more apparent, when feeding on carcasses is considered as probing as well. The common raven, which has the longest and most curved bill of the studied corvid species, feed primarily on carcasses, which are, when unopened, accessed through orifices. Thus, a long bill might be beneficial to intrude deeply into the orifices and in addition a heavily curved bill enhances the ability to rip meet apart (Goodwin 1976, Haffer and Bauer 1993, Holyoak 1968). Although there are no comparative studies on the foraging behavior of Eurasian jays that we know of, our results on bill-length suggest that they probe more frequently than jackdaws and less frequently than black-billed magpie (and vice versa in pecking).

The frequency with which corvid species turn objects is not as clear as for probing and pecking (Berrow et al. 1991, Lockie 1956, Rolando et al. 1998, Waite 1984). All studies in which jackdaws were observed, reported that jackdaws show the highest frequency in turning objects compared with rook (Lockie 1956, Waite 1984), carrion crow and black-billed magpie (Waite 1984). Our results indicate that jackdaws have the steepest angle between bill and cranium. It seems likely that this feature is beneficial to turn objects, because an upward positioned bill-tip relative to the cranium might facilitate shoveling movements with the bill, compared with a more downward positioned bill-tip as in e. g. Eurasian jay.

Orbits

Birds that frequently probe are also assumed to require a smaller binocular field as opposed to birds that frequently peck and turn objects, because the frontal binocular field is thought to guide the bill towards food objects (Martin 1985, 2007). It is likely that changes in orbit position indicate changes in eye position and in addition, several authors assumed that orbit convergence is associated with the degree of the binocular field overlap (Cartmill 1974, Heesy 2004, Martin 1985). When assuming similar photoreceptor densities (compare Martin 1985, 2007, Martin and Katzir 1999), our results indicate that common ravens have the narrowest binocular field, followed by rook, hooded crow, Eurasian jay, black-billed magpie and jackdaw and thus would meet the prediction that probing is associated with a smaller binocular field compared to pecking.

Another important aspect of the frontal

binocular field in birds is the horizontal projection of the bill-tip. Species that handle food objects between their mandibles have been reported to be able to observe their own bill-tip (Martin 1986, Martin and Coetzee 2004, Martin et al. 2007, Oehme 1962). It has been hypothesized that this ability is concordant with an increased angle between bill and cranium and/or upward positioned eyes, which result in the bill aperture pointing toward the midpoint of the eyes (Beecher 1978, Lorenz 1949, Zusi 1993). Although, it is not known whether corvids are able to observe their own bill-tip, it seems reasonable that at least the Eurasian jay should have the capability for two reasons. First, the Eurasian jay is known to handle food items, i. e. acorns, between its mandibles (Bossema 1979, Haffer and Bauer 1993) and second, the jay displays morphological adjustments which results in the bill aperture pointing toward the mid point of the eyes (Fig. 3b). Consequently the first PLS_{whole} vectors, which also indicate major covariation between bill-length and orbit orientation, might be considered as an adjustment of the frontal binocular field relative to the bill-tip, so that the horizontal projection of the bill-tip within the binocular field does not change between individuals with different bill-length.

Another likely explanation for the increased angle between bill and cranium and upward positioned eyes found in Eurasian Jays, when compared with the other corvid-species, might be a more downward projection of the bill-tip within the binocular field and an increased vertical extent of the binocular field. These features might be beneficial when gleaning for caterpillar larvae at the lower surface of leaves as reported in Owen (1956), because it would allow Eurasian jays to gather visual information above head, while the head is held horizontal.

On the other hand, the decreased angle between bill and cranium and downward positioned eyes found in jackdaws would result in a more upward projection of the bill-tip within the binocular field and might allow jackdaws to gather visual information below the head when the head is held horizontal. This ability might be beneficial when turning objects and searching for food under surface litter, which is a frequent foraging strategy of jackdaws (Lockie 1956, Waite 1984). Accordingly, the second PLS_{whole} and first PLS_{sep} vectors indicate major covariation between blocks in the angle between bill and cranium, so that differences in the angulation might result in differences in the vertical projection of the bill-tip within the binocular field.

Foramen magnum

Species with high scores on PC 1 (e. g. common raven) and low scores on PC 2 (e. g. jackdaw) are characterized by an upward positioned foramen magnum, compared to Eurasian jay and black-billed magpie. The within-species multivariate regression of size on shape showed a strong relationship of size on the position of the foramen magnum in hooded crow, black-billed magpie and jackdaw, but either no or a weak relationship in common raven, Eurasian jay and rook (compare Fig. 4). The position of the foramen magnum might be associated with head posture (compare Duijm 1951, Marugán-Lobón and Buscalioni 2006, exemplified in Fig. 8). Hence, species with an upward positioned foramen magnum, e. g. common raven and jackdaw, might be characterized by a more horizontal head posture and according to PCA have also a more flattened cranium, compared to Eurasian jay and black-billed magpie. Differences in head posture and height of the cranium might be attributed to constraints in sustained flight. Species with a horizontal head posture and a flattened cranium might experience a reduced drag in flight, compared to species with a vertical head posture and increased cranial height (Winkler et al. 2004). Furthermore, differences in head posture between the studied corvid-species seem to covary with wingtip-shape (Kulemeyer et al. 2007), which have been reported to influence flight ability (Norberg 1990). Thus, the *Corvus*-species are characterized by pointed wingtips and possibly by a horizontal head posture and hence, might show an increased flight ability, compared to Eurasian jay and black-billed magpie (Goodwin 1976, Haffer and Bauer 1993).

As the number of studied species is small, further research is necessary to evaluate the relationship between the position of the foramen magnum and head posture and their covariation to other morphological traits.

Conclusion

In this study we compared skull morphology and the integration between the bill and cranium of six corvid species by means of three-dimensional geometric morphometrics of computed tomography scans. Our results indicate that pronounced shape differences occur between the studied corvid species. Although most of the shape variation correlates with size, these shape differences cannot be attributed only to allometry, because the allometric components differ markedly between species. Thus, shape differences between species can also be considered to result from differences in ecology, especially because skull morphology covaries with foraging mode. Increasing bill-length, bill-curvature and sidewise orientation of the eyes is associated with an increase in the observed frequency in probing (vice versa in pecking). Hence, the frequency of probing, bill-length, bill-curvature and sidewise orientation of the eyes is progressively increased from jackdaw, to Eurasian jay, to black-billed magpie, to hooded crow, to rook and to common raven (when feeding on carcasses is considered as probing). With regards to morphological integration, our results suggest that most of the covariation between bill and cranium is due to differences in the topography of the binocular fields and the projection of the bill-tip therein, indicating the importance of visual fields in the foraging ecology of corvids. Further research, especially the morphological integration between bill, cranium and components that are involved in the rhynchokinetics of birds, is of great interest to study functional and species wide trends.

Competing interests

The author(s) declare that they have no competing interests.

Authors contribution

CK designed the study, analyzed the data and drafted the manuscript. KA placed landmarks and semilandmarks. PG participated and supervised the data analysis. SF and FB supervised the study and were also involved in drafting the manuscript. All authors read and approved the final manuscript.

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3. Morphological separation of sympatric corvids

Abstract

Background: Sympatric corvid species have been reported to overlap in their habitat associations. As avian morphological studies suggest that morphology covaries with behavior and with habitat preferences, we studied the wing-, leg- and foot morphology of six corvid species. We expected wingtip shape to covary with habitat associations along a gradient from forest to open habitats, hind limb morphology with a gradient from hopping to walking and foot morphology with a gradient from tree to ground foraging.

Results: Corvid species show pronounced differences in wingtip shape. Wingtip pointedness is progressively increased from black-billed magpie, to Eurasian jay, to hooded crow, to rook and common raven and to jackdaw. Major variation in hind limb morphology corresponds to a tarsometatarsus/femur ratio, which is progressively increased from common raven, to Eurasian jay, to rook, to hooded crow, to jackdaw and to black-billed magpie. Major variation in foot morphology was interpreted as an elongated fourth digit. Black-billed magpie and jackdaw appeared to have a short fourth digit, rook, Eurasian jay and hooded crow a moderate and common raven a long fourth digit.

Conclusion: The analysis of wingtip shape separates the corvid species very clearly. Wingtip pointedness was associated with open habitats and wingtip roundedness with habitats, that are characterized by dense shrub or tree layers. The analysis of hind limb and foot morphology does not differentiate these species very well. It is likely that this is due to the fact that the studied corvid species in general are very divers in their habitat associations. All studied corvid species breed in trees and forage on the ground. Furthermore, all species hop and walk and hence, the difference between these species is the frequency, in which they use these different habitat types and/or behaviors.

Introduction

In Central Europe coexisting corvid species differ in behavioral and ecological traits such as nesting (Bossema et al. 1986, Holyoak 1968, Röell and Bossema 1982), foraging (Berrow et al. 1991, Lockie 1956, Rolando et al. 1998, Waite 1984), diet (Holyoak 1968, Lockie 1956, Waite 1984) and habitat choice (Bossema et al. 1986, Rolando et al. 1998, Waite 1984). Despite these differences, corvids are known to overlap in their habitat associations (Haffer and Bauer 1993, Waite 1984) and therefore, these can be best described along a gradient from forest, to savanna like- to open habitats (Haffer and Bauer 1993). In accordance, corvid species differ in their foraging habitat with respect to preferred distance to protective cover and therefore differ in their flying distance from resting/breeding to their foraging grounds. Species that forage in open habitats generally fly greater distances, in contrast to species that forage closer to shrubs and trees (Bossema et al. 1986). Furthermore, corvid species differ in behavior in their foraging habitat. For example, species that more frequently forage in shrubs and trees tend to hop more often, than species that forage more frequently on the ground, which tend to walk (Leisler 1977, Rüggeberg 1960).

Avian morphological studies suggest that morphology covaries with behavior (Kaboli et al. 2007, Kulemeyer et al. 2009, Newton 1967, Wolf et al. 1976) and with habitat preferences (Bairlein et al. 1986, Kaboli et al. 2007, Korner-Nievergelt and Leisler 2004, Leisler et al. 1987). For example, short and rounded wings have been associated with forest habitats, because they allow birds to maneuver easily among trees. In contrast, long and pointed wings have been associated with open habitats where maneuverability is traded in for flight speed (Norberg 1990, Swaddle and Lockwood 1998). Furthermore, differences in habitat associations, such as foraging on the ground or in trees, as well as behavioral differences in these habitats, e. g. hopping or walking, are thought to be reflected in hind limb and foot morphology (Leisler 1977, Rüggeberg 1960).

In this paper, we studied the wing-, leg- and foot morphology of six corvid species and expect that these morphological traits covary with their habitat association.

Methods

We studied six corvid species: Common Raven (*Corvus corax*), Hooded Crow (*Corvus corone cornix*), Rook (*Corvus frugilegus*), Jackdaw (*Corvus monedula*), Black-billed Magpie (*Pica pica*) and Eurasian Jay (*Garrulus glandarius*). Morphological data were obtained by measuring museum skins from the Natural History Museum Berlin, and skeletal material from the Natural History Museum Berlin, the Natural History Museum Goerlitz, the State Collection of Anthropology and Palaeoanatomy Munich.

From the museum skins, we measured wingtip shape following Lockwood et al. (1998). For better comparison, we numbered feathers according to the terminology of Lockwood et al. (1998), which differs from conventional feather notation. Feather length was measured with a metal rule to the nearest 0.5 mm.

From the skeletal material, we measured the length of femur, tibiotarsus, and tarsometatarsus of 146 adult specimens and the length of the phalanges of 86 adult specimens. Measurements on the skeletal material were taken with a digital Vernier callipers to the nearest 0.1 mm.

Statistical analysis

The aim of morphometric studies is usually focused on shape, but most of the variation in multivariate morphometric data is due to differences in size (Leisler et al. 1989). Furthermore, it has been observed that the principal component analysis (PCA), generally used in morphometric studies to reduce dimensionality, does not distinguish between size and shape, as the first principal component incorporates both effects (Mosimann 1970, Somers 1986). Consequently, various methods have been proposed to remove size effects before or during multivariate analyses (e. g. Mosimann 1970, Somers 1986, see Lockwood et al. 1998 for a review). In this study we use size-constrained component analysis (SCCA), introduced by Lockwood et al. (1998), which has been widely used in ornithological literature (e. g. Burns and Ydenberg 2002, Fernández and Lank 2007, Fernández-Juricic et al. 2006). SCCA is derived from a PCA, with the first component being a measure for isometric size and the second (C2) and third component (C3) being measures of shape. Therefore SCCA scores of C2 and C3 are size-independent and explain differences in shape.

Measurements on wings, hind-limbs and foots were log-transformed, standardized to equal unit variance and the obtained datasets were then subjected to three SCCAs.

Results

The Loadings of SCCA on measurements of wingtip shape are given in table 1. C1 was interpreted as a measure of isometric size and explained 97,7 % of the total variation.

Tab. 1: SCCA loadings of wingtip measurements. Q1–Q8: distal most primaries, numbered ascendingly (with feather Q1 the most distal). C1 was interpreted as isometric size, C2 as wingtip roundedness and C3 as wingtip concavity.

	C1	**C2**	**C3**
Q1	−0.347	−0.572	0.741
Q2	−0.353	−0.386	−0.466
Q3	−0.356	−0.180	−0.321
Q4	−0.357	−0.077	−0.219
Q5	−0.357	0.042	−0.077
Q6	−0.355	0.254	−0.022
Q7	−0.352	0.431	0.163
Q8	−0.351	0.483	0.222

C2 accounted for 2.0 % of the total variation and represented wingtip roundedness. C3 explained only 0.2 % of the total variation and was interpreted as wingtip concavity following Lockwood et al. (1998). In the analysis of wingtip shape, the SCCA almost clearly separates the six corvid species. Wingtip pointedness is progressively increased from black-billed magpie, to Eurasian jay, to hooded crow, to rook, to common raven and to jackdaw. C3 indicates that common raven and Eurasian jay have an increased wingtip concavity compared to the other corvid species (Fig. 1a).

Loadings of the SCCA on the hind-limb morphology are given in table 2. C1 explained 99.4 %, C2 0.4 % and C3 0.2 % of the total variation. C2 was interpreted as increased relative femur length and decreased tarsometatarsus length and the third component as decreased relative tibiotarsus length (Swaddle and Lockwood 1998). Hence, femur length is progressively increased and tarsometatarsus length progressively decreased from black-billed

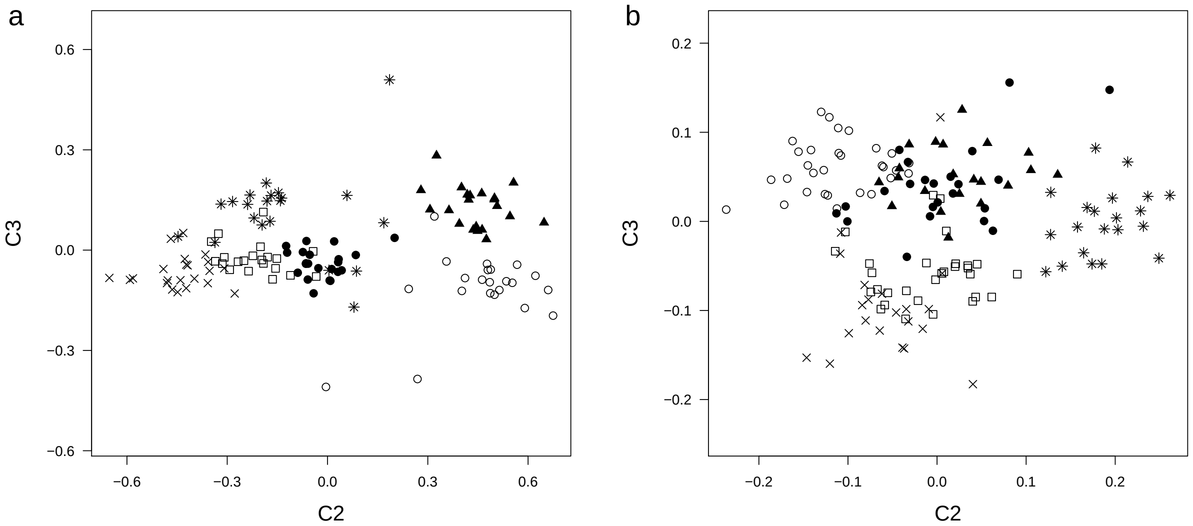

Fig. 1: Second and third dimension of the SCCA on wingtip **(a)** and hind-limb **(b)** measurements. **(a):** C2 was interpreted as wingtip roundedness and C3 as wingtip concavity. **(b):** C2 was interpreted as increased femur length and reduced tarsus length. C3 was interpreted as decreased tibia length.

▲ Eurasian jay × jackdaw ○ black−billed magpie ● hooded crow □ rook ✳ common raven

Tab. 2: SCCA loadings of hind-limb measurements. C1 was interpreted as isometric size and C2 as increased femur length and reduced tarsus length. C3 was interpreted as decreased tibia length.

	C1	C2	C3
femur	0.577	0.691	0.435
tibiotarsus	0.578	0.030	−0.815
tarsometatarsus	0.577	−0.722	0.382

magpie, to jackdaw, to hooded crow, to rook, to Eurasian jay and to common raven. C3 was interpreted as a decreased relative tibiotarsus length. It separates jackdaw and rook from the other corvid species (Fig. 1b).

Loadings of the SCCA on measurements of foot morphology are given in table 3. C1 explained 96.6 %, C2 1.3 % and C3 0.7 % of the total variation. The second dimension of the SCCA on measurements of foot morphology was interpreted as an elongated fourth digit. Hence, the common raven is characterized by a long fourth digit compared to black-billed magpie. C3 was interpreted as elongated proximal and shortened distal phalanges (Tab. 3). Therefore, Eurasian jay and black-billed magpie have elongated proximal and shortened distal phalanges, in contrast to jackdaw and rook (Fig. 2).

Discussion

Wingtip

Our results indicate that wingtip roundedness is progressively increased from jackdaw, to rook, to common raven, to hooded crow, to Eurasian jay and to black-billed magpie (C2, Fig. 1a) and hence, wingtip shape reflects habitat preferences with respect to tree and shrub density during foraging. While corvid species with rounded wings prefer to forage in close proximity to shrubs and trees, corvid species with pointed wings prefer open habitats (Bossema et al. 1986, Goodwin 1976, Haffer and Bauer 1993).

Rounded wings as opposed to pointed wings have been associated with an increased maneuverability, which is traded in for flight speed (Norberg 1990, Swaddle and Lockwood 1998), with rapid take off from ground

Tab. 3: SCCA loadings of foot measurements. C1 was interpreted as isometric size and C2 as an elongated fourth digit. C3 was interpreted as elongated proximal and shortened distal phalanges.

	C 1	C 2	C 3
I.1	−0.315	−0.454	0.027
II.1	−0.316	−0.323	0.411
II.2	−0.320	−0.100	−0.141
III.1	−0.319	−0.210	0.150
III.2	−0.319	−0.196	−0.039
III.3	−0.317	−0.193	−0.463
IV.1	−0.314	0.372	0.389
IV.2	−0.315	0.418	0.219
IV.3	−0.315	0.384	0.056
IV.4	−0.313	0.315	−0.608

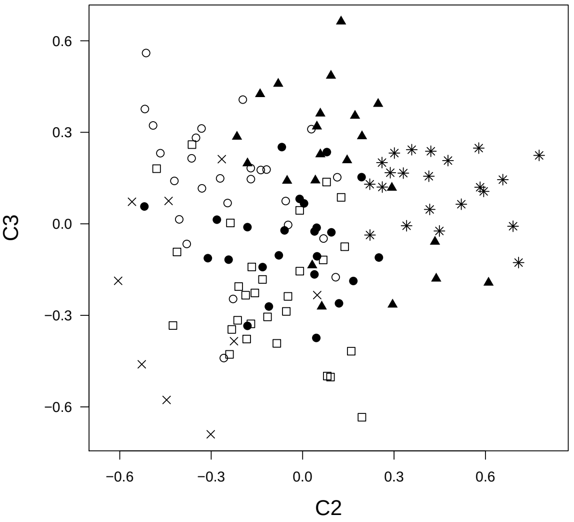

Fig. 2: SCCA loadings of foot measurements. C2 was interpreted as an elongated fourth digit and C3 as elongated proximal and shortened distal phalanges.

▲ Eurasian jay × jackdaw ○ black−billed magpie ● hooded crow □ rook ✳ common raven

(Swaddle and Lockwood 1998, van der Veen and Lindström 2000) and with a lower flight initiation and landing distance after predator encounter (Fernández-Juricic et al. 2006). These traits might illustrate, why black-billed magpie and Eurasian jay forage in close proximity to protective cover, in contrast to the corvid species with pointed wings. While pointed wings are more advantageous in sustained flight in open habitats, rounded wings are more advantageous in habitats with dense shrub and tree layers. In addition, corvid species with pointed wings have been observed to fly greater distances from their resting/breeding to their foraging grounds (Bossema et al. 1986, Strebel 1991), especially in winter (Schramm 1974).

However, wingtip concavity (C3) of Eurasian jay and common raven (Fig. 1a), in contrast to convexity, cannot be well interpreted, but it is striking that both Eurasian jay and common raven are known to breed deep in the forest in contrast to the other corvid species (Haffer and Bauer 1993).

Hind limb

The second dimension of the SCCA on hind limb morphology was interpreted as an elongated femur and shortened tarsometatarsus. The second component separates common raven (high scores) from black-billed magpie (low scores), while the other corvid species are intermediate (Fig. 1b). The third dimension of the SCCA was interpreted as a shortened tibiotarsus length. This component separates jackdaw and rook (low scores) from all other corvid species (high scores, Fig. 1b).

In birds, it is generally assumed that an increase in relative length of the distal elements of the hind limb is associated with stride length (Barbosa and Moreno 1999). The index of C2 corresponds to a decreased tarsometatarsus/femur ratio, which in ungulates (mammals) have been associated with a reduced running speed (Garland and Janis 1993). Following this argumentation, running speed is progressively increased from common raven, to Eurasian jay, to rook, to hooded crow, to jackdaw and to black-billed magpie. This interpretation is consistent with studies on foraging behavior, as black-billed magpie and jackdaws more frequently jump-catch insects compared to the other corvid species (Haffer and Bauer 1993, Lockie 1956).

In contrast, C3 separated rook and jackdaw from black-billed magpie and the other corvid species. As rook and jackdaw predominantly forage socially and therefore, cursorially and continuously exploit prey on the ground, we interpreted the third dimension as cursiorial in contrast to hopping locomotion. This interpretation is consistent with previous studies that reported that black-billed magpie and Eurasian jay tend to hop in contrast to the *Corvus*-species (Kunkel 1962) and that black-billed magpie are characterized by an enhanced movability compared to the jackdaw (Lorenz 1931).

Foot

The second dimension of the SCCA on foot morphology is an index that reflects an elongated fourth digit. It separates black-billed magpie and jackdaw from the common raven, while rook, Eurasian jay and hooded crow are intermediate in that respect (Fig. 2). It is interpreted as the difference in the pincer-like grip on perches such that the common raven, in contrast to magpie and jackdaw, also uses the exterior fourth digit rather than only the interior (III) digit for the pincer-like grip on perches (Rüggeberg 1960).

The third component was interpreted as elongated proximal and shortened distal phalanges. It separates Eurasian jay and black-billed magpie from jackdaw and rook (Fig. 2). Short distal phalanges and long proximal phalanges have been associated with an enhanced flexibility and movability of the foot for the pincer-like grip on small branches and twigs (Rüggeberg 1960).

Conclusion

The analysis on wingtip shape separates the corvid species very clearly and wingtip shape reflects habitat associations of corvids. Wingtip pointedness was associated with open habitats and wingtip roundedness with habitats, that are characterized by dense shrub or tree layers. The analysis of hind limb and foot morphology in contrast, does not differentiate these species very well. It is likely that this is due to the fact that the studied corvid species in general are very divers in their habitat associations. All studied corvid species breed in trees and forage on the ground. Furthermore, all species hop and walk and hence, the difference between these species is the frequency, in which they use these different habitat types and/or behaviors.

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4. Skull morphology, niche breadth and feeding innovations

Abstract

Background: According to the niche variation hypothesis, niche breadth is thought to be reflected in the variability of bill size and shape. Hence, a species, which is more variable in morphology is likely to use a wider range of resources and feeding techniques and therefore might be more likely to innovate new feeding behaviors than a species, that is restricted to a single feeding technique. Alternatively, the behavioral drive hypothesis states, that feeding innovations might spread among members of a population through individual and social learning and as a consequence, the species might be exposed to new selective pressures, that in turn might increase anatomical variability. Here, we tested the relationship between innovation frequency and within-species variability in skull shape of sympatric European corvid species. Skull shape variability was estimated from a principal component analysis on a three dimensional landmark dataset basing upon computed tomography scans.

Results: Major variation across species in PC 1 and PC 3 describes differences in bill shape, while major variation in PC 2 lies in the angle between bill and cranium and in the position and orientation of the eyes. None of the within-species variabilities in the first three dimensions of the PCA on skull shape correlated with log innovation frequency. However, variabilities in the first and third PC revealed an almost significant trend.

Conclusion: Our results suggest, that the inability to detect a significant correlation is due to the low number of species studied, rather than to a non-existent relationship. It is remarkable that in contrast to within-species variabilities in PC 2, variabilities in PC 1 and PC 3 revealed an almost significant trend for two reasons. First major variation across species in the first and second dimension of the PCA describes differences in bill shape, as opposed to PC 2. Second, PC 1 and PC 3 separate corvid species in contrast to PC 2, which only separates Eurasian jays from jackdaws. However, this pattern cannot be well explained at the moment and therefore, it might be of interest to further study the relationship between within-species variability in skull shape and feeding innovation frequency.

Introduction

There are numerous reports that birds respond with innovative solutions to new feeding possibilities (e. g. Fisher and Hinde 1949, Grobecker and Pietsch 1978). Anecdotal evidence of these innovations were operationalized by Lefebvre and students through frequency counts of new and unusual feeding behaviors that are published in the short note section of ornithological journals (Lefebvre et al. 2002, 1997, Nicolakakis and Lefebvre 2000, Sol and Lefebvre 2000, Timmermans et al. 2000). Feeding innovations have received considerable attention, because they were shown to correlate with relative brain size (Lefebvre et al. 1997, Nicolakakis and Lefebvre 2000, Timmermans et al. 2000), tool-use (Lefebvre et al. 2002), social learning (Bouchard et al. 2007, Reader and Laland 2002) and with an enhanced ability to invade and colonize new habitats (Sol et al. 2005, Sol and Lefebvre 2000).

It is generally assumed that birds that

have a broader diet, respond more often to new feeding possibilities by producing innovative behavior (Klopfer and MacArthur 1960, Lefebvre and Bolhuis 2003, Timmermans et al. 2000). According to the niche variation hypothesis, feeding niche breadth is reflected in the variability of bill size and shape (Brandl et al. 1994, Grant 1968, van Valen 1965, van Valen and Grant 1970). Hence, it can be assumed that a species that is more variable in bill morphology, uses a greater range of feeding techniques and is therefore more likely to innovate new feeding behaviors than a species, that is restricted to a single feeding technique (compare Bolnick et al. 2007, 2003, Price 1987).

Alternatively, the relationship between feeding innovations and morphological variability can be viewed as what is known as the behavioral drive hypothesis (Wyles et al. 1983). According to this hypothesis, feeding innovations might spread among members of a population through individual and social learning. As a consequence, the species might be exposed to a new set of selective forces, that in turn increase anatomical variability (Wyles et al. 1983).

Here, we explore the relationship between morphological variability and feeding innovations in Sympatric European corvids, that have evolved differences in diet (Holyoak 1968, Lockie 1956, Waite 1984), foraging (Berrow et al. 1991, Lockie 1956, Rolando et al. 1998, Waite 1984), differ in their morphology (Kulemeyer et al. 2009, Schuh 1968) and their propensity for innovative behavior (Lefebvre et al. 1997).

In an earlier study, we explored the skull morphology of six corvid species basing upon computed tomography scans by means of three-dimensional geometric morphometrics and showed that these corvid species exhibited pronounced differences in skull shape, which covaried with foraging mode. We showed that there was a consistent covariation between the shape of the bill and the shape of the cranium, such as the orientation of the eyes relative to the bill as well as the angle between bill and cranium. Most of covariation between these functional units were interpreted to result in differences in the topography of the binocular field relative to the bill, which illustrated the importance the visual field in the foraging ecology of corvids (Kulemeyer et al. 2009).

Therefore, we tested whether variability in the shape of the skull is associated with feeding innovations.

Methods

In Kulemeyer et al. (2009) we studied 115 skulls of six corvid species: common raven (*Corvus corax*), hooded crow (*Corvus corone cornix*), rook (*Corvus frugilegus*), jackdaw (*Corvus monedula*), black-billed magpie (*Pica pica*) and Eurasian jay (*Garrulus glandarius*). The specimens came from Museum für Naturkunde Berlin, Staatliches Museum für Naturkunde Görlitz and Staatssammlung für Anthropologie und Paläoanatomie München, which are all located in Germany. All corvid skulls were scanned by computed tomography at Charite-Universitätsmedizin Berlin.

We digitized 32 three-dimensional landmarks and 116 equally spaced semilandmarks on 16 curves (for details, see Kulemeyer et al. 2009). Digitization of landmarks and semilandmarks, as well as the processing of semilandmarks were done with Edgewarp 3.30 (Bookstein and Green 2002). The resulting dataset was subjected to a generalized least squares Procrustes analysis (GPA, Rohlf and Slice 1990), in which distances between homologous landmarks are minimized by translating, rotating and scaling all forms to a common reference (consensus). In other words, shape refers to the geometric information that is left after removing the effects of size, position and orientation. The information about overall body-size of the specimens is preserved in centroid size, which serves as a scaling factor in GPA.

The Procrustes shape coordinates, returned by GPA, were subjected to a principal component analysis (PCA). To test whether within species-variability in skull shape predicts feeding innovation frequencies of corvids, we standardized the species-specific shape variance of each of the first three dimensions of the PCA.

Feeding innovations frequency have been collated in an exhaustive survey of 30 years (1970–2000) in the short note section of 65 ornithological journals as the frequency of new and unusual feeding behaviors per species (Lefebvre et al. 1997, Nicolakakis and Lefebvre 2000). Examples of recorded feeding innovations are given in Lefebvre et al. (1997) and the data for the studied corvid species was taken from Garamszegi et al. (2005). Innovation frequencies were log transformed because of their non-normal distribution (Nicolakakis and Lefebvre 2000).

Results

The first three dimensions of the PCA on the full landmark set are plotted as scores in Figure 1, which illustrate the morphological differences between the studied corvid species. The corresponding shape changes were visualized as surface deformations in Figure 2. The first principal component (PC) explained 73.7 % of the total variation and was interpreted as an increase in relative bill-length, -width and -curvature and downward positioned and sidewise oriented orbits (Fig. 2a). PC 1 correlated significantly with the log of centroid size ($r = 0.93$), in contrast to PC 2 and PC 3, which did not correlate with size ($r = -0.08$, $r = -0.23$, respectively). PC 2 explained 9.5 % of the total variation and was interpreted as an increased angle between bill and cranium, as a decreased bill-curvature and as upward positioned and sidewise oriented orbits (Fig. 2b). The third component explained 3.4 % of the variation and was interpreted as more slender bill, an increased cranium height and as downward positioned and sidewise oriented eyes (Fig. 2c).

None of the within-species variabilities in the first three dimensions of the PCA on skull shape correlated with log innovation frequency. However, the first and third PC revealed an almost significant trend (Tab. 1, Fig. 3).

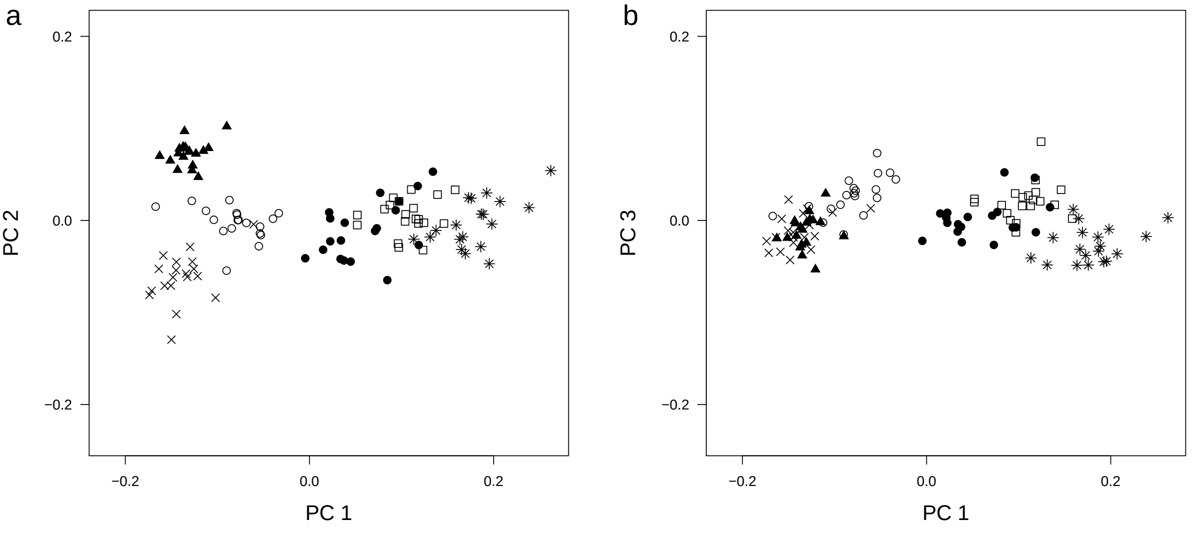

Fig. 1: First two dimensions **(a)** and the first and third dimension **(b)** of the principal component scores calculated from the Procrustes shape coordinates of the full landmark set (Kulemeyer et al. 2009).

▲ Eurasian jay ✕ jackdaw ○ black−billed magpie ● hooded crow □ rook ✳ common raven

Fig. 2: The sequence of surface representations (from left to right), as deformations of the average shape, correspond to increasing scores in PC 1 **(a)**, PC 2 **(b)** and PC 3 **(c)**. The surface morphs differ from its neighbors by equal multiples of the standard deviation of the actual variability. The first and last column is extrapolated by 2 **(a)**, 4 **(b)** and 6 **(c)** standard deviations, respectively. **(a):** Major variation in PC 1 lies in the relative length and curvature of the bill and in the orientation of the orbits. **(b):** Major variation in PC 2 lies in the angle between bill and cranium and in the orientation of the orbits. **(c):** Major variation in PC 3 lies in the relative length, depth and height of the bill and in the orientation of the orbits (Kulemeyer et al. 2009).

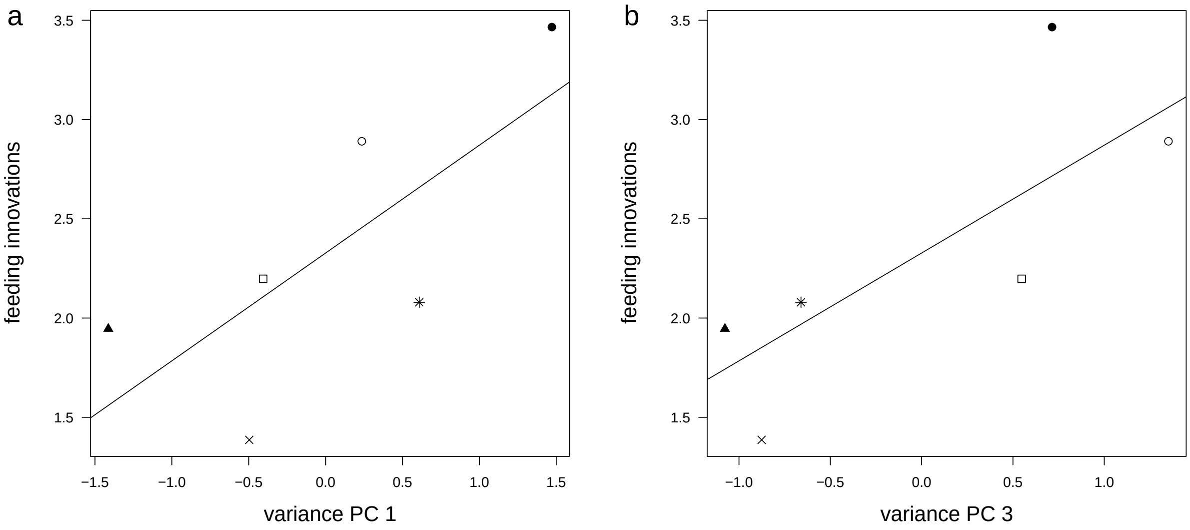

Fig. 3: Linear regression of feeding innovation frequency on species variance in PC 1 **(a)** and PC 3 **(b)**

▲ Eurasian jay × jackdaw ○ black−billed magpie ● hooded crow □ rook ✳ common raven

Tab. 1: Results of univariate regression analyses of within-species variability in three principal components (PC 1, PC 2 and PC 3) on innovation frequency of corvid species.

	slope	r^2	$F_{1,4}$	p
variance PC 1	0.543	0.542	4.730	0.095
variance PC 2	0.223	0.092	0.403	0.560
variance PC 3	0.580	0.618	6.484	0.064

Discussion

Our results indicate that within-species variability in relative skull shape do not predict feeding innovation frequency of corvids. However, two out of three morphological variables – within-species variability in PC 1 and PC 3 – revealed an almost significant trend (Tab. 1). It is striking that major variability across species in PC 1 and PC 3 describes differences in bill shape, while major variability in PC 2 lies in the angle between bill and cranium and in the position and orientation of the orbits (Fig. 2). Furthermore, in contrast to PC 1 and PC 3, PC 2 does not separate corvid species, except from Eurasian jay and jackdaw (Fig. 1). These patterns cannot be explained at the moment. However, our results might suggest, that the inability to detect a significant correlation is due to the low number of species studied rather than to a non-existent relationship. Hence, it might be of interest to further test whether variability in skull shape is correlated with innovation frequency in a greater range of species.

Despite of the low number of species studied, three possible explanations might account for the inability to detect a significant relationship of feeding innovations and morphological variability. First, the morphology was explored from skulls of museum specimens, whose bills had no rhamphoteca. Hence, the variability in shape of the ossified bill does not necessarily reflect the actual – and for feeding probably the relevant – variability of the bill with a rhamphoteca.

Second, as described earlier, within-species variability differ between the three dimensions of the PCA (Tab. 1). Because a PCA extracts major variation across individuals, the results are dependent on the number and species studied and thus it might be possible, that a PCA is not able to extract a "vector of variation", that is meaningful with respect to feeding. For example, in morphometric studies it is well known that a PCA does not distinguish between size and shape, as the first PC incorporates both effects (Mosimann 1970, Somers 1986).

Third, innovation frequency is of anecdotal nature and many confounding variables might influence its accuracy, such as population size, research effort and reporting bias. While none of these confounding variables have been found to significantly influence innovation rate (Nicolakakis and Lefebvre 2000), there are other potential confounds that might influence the link between feeding innovations and morphological variability: Innovation frequency were recorded from ornithological journals that covered northwestern Europe and, for example, compiled the innovation frequency of two subspecies of the carrion crow (*Corvus corone corone* and *Corvus corone cornix*, Timmermans 1999), while our study, explored only the skull morphology of the hooded crow (*Corvus corone cornix*). Furthermore, birds might invent novel feeding techniques more frequently when exposed to novel environments, because they encounter new situations more often, compared to birds that stick to ancestral habitats. Hence, for example jackdaws are quite uncommon northwestern European cities, while in towns of northeastern Europe, jackdaws are very abundant, especially in Warsaw (Witt et al. 2005). Hence, feeding innovations that have been reported in northeastern European countries might draw a different picture about the behavioral flexibility of jackdaws.

However, it is known that sexually dimorphic birds vary in bill shape (Radford and Du Plessis 2003) and niche use and even at the individual level, there is a growing body of evidence that individual specialization occurs (e. g. Price 1987). For example, the bill tip of the oystercatcher shows large individual differences, which has been associated with individual differences in foraging techniques (Goss-Custard and Sutherland 1984, Swennen et al. 1983). Therefore, the individual specialization might contribute to niche breadth and the pool of foraging techniques of the entire population (compare Bolnick et al. 2007, 2003. Hence, it is likely that a species with an enlarged repertoire of foraging techniques invents new feeding behaviors more often, compared to a species, that is restricted to a single foraging technique.

Alternatively, according to the behavioral drive hypothesis, a species might store new feeding innovations in their repertoire through individual and social learning, which might expose the species to new selective pressures and in turn increase its morphological variability (Wyles et al. 1983).

Conclusion

None of the within-species variabilities in the first three dimensions of the PCA correlated significantly with feeding innovation frequency. However, within-species variability in PC 1 and PC 3 showed an almost significant trend. It is striking that in contrast to within-species variabilities in PC 2, variabilities in PC 1 and PC 3 revealed an almost significant trend for two reasons. First major variation across species in the first and second dimension of the PCA describes differences in bill shape, as opposed to PC 2, which describes differences in orbit orientation and the angle between bill and cranium. Second, PC 1 and PC 3 differentiate corvid species in contrast to PC 2, which only separates Eurasian jays from jackdaws. Our results suggest, that the inability to detect a significant correlation is due to the low number of species studied, rather than to a non-existent relationship and therefore, it might be of interest to further study the relationship between within-species variability in skull shape and feeding innovation frequency.

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5. Brain size, feeding innovations and urban establishment success

Abstract

Background: According to the brain size-environmental change hypothesis, birds are expected to respond to novel conditions by producing innovative behavior, which in turn spreads among the population through individual and social learning. Hence, if large brained and more innovative birds are better able to adapt to new conditions, one might also assume that these birds have an enhanced establishment success in urban environments. We tested this prediction within the Corvidae and Passerida. Relative brain size of the Corvidae were estimated from a three-dimensional reconstruction of the endocrania basing upon computed tomography scans of corvid skulls and in addition, the effect of pneumatization on the endocranial volume was explored. We then tested whether relative brain size and innovation frequency is associated with four estimates of urban success within Corvidae and Passerida, i. e. absolute and relative population density, as well as population increase and decrease.

Results: Three-dimensional reconstruction of the endocranium from CT-scans is particularly suited to account for – rather frequent – damages to the inner layer of bone overlaying the brain and the pneumatization of the cranial vault. The difference in the endocranial volume caused by pneumatization averages in the studied corvid species between 12 and 19 %. Within Corvidae, relative brain size correlated neither with feeding innovation frequency, nor with any estimates of urban success. Innovation frequency in contrast, correlated with three out of four estimates of urban success. Within Passerida relative brain size correlated significantly with feeding innovation frequency when controlled for phylogenetic effects. Furthermore, both, relative brain size and feeding innovation frequency correlated significantly with absolute population density. When relative brain size and innovation frequency were entered in a multiple regression with absolute population density only innovation frequency remained significant. The same results were obtained when controlled for phylogeny.

Conclusion: Our results strongly support the brain size – environmental change hypothesis and indicate that birds with enlarged brains and a high propensity for innovative behavior more readily establish in urban environments. However, our results also suggest that feeding innovation frequency is a better predictor for urban establishment success than relative brain size as revealed by a multiple regression.

Introduction

The Passeriformes is the most diverse clade of birds and comprise about half of all extant avian species. Passerine birds have diversified on all continents and occupy nearly all terrestrial ecosystems, encompassing a great behavioral and ecological diversity (Barker et al. 2004, Sibley and Ahlquist 1990, Sibley and Monroe 1990). One family of the Passeriformes, the Corvidae, drew special attention to researchers, because corvid species are characterized by cognitive skills that are similar to those of humans and apes (Emery and Clayton 2004), such as tool-use (Hunt 1996, Hunt and Gray 2004), episodic-like memory (Clayton and Dickinson 1998), predicting behavior of conspecifics (Bugnyar and Kotrschal 2004), mirror self-recognition (Prior et al. 2008), cooperative problem solving (Seed et al. 2008) and a high propensity for innovative behavior (Lefebvre et al. 1997). Furthermore, corvid brains are significantly larger than predicted by its body size and are of relatively the same size as the chimpanzee brain (Emery and Clayton 2004).

It is thought that large brains might have evolved as an adaptation to cope with novel or altered conditions, which was termed the brain size-environmental change hypothesis (Sol et al. 2005). According to this hypothesis, birds are expected to respond to novel or altered conditions by producing innovative behavior, which in turn spreads among the population through individual and social learning (Sol et al. 2005). Furthermore, a large brain is thought to enhance the survival of environmental challenges through innovative behavior (Sol et al. 2007) and therefore compensate the high developmental and maintenance cost of growing enlarged brains (Allman 2000, Iwaniuk and Nelson 2003). Hence, relative brain size has been associated with feeding innovations (Lefebvre et al. 2001, 1997, Nicolakakis and Lefebvre 2000), social learning (Bouchard et al. 2007), an enhanced adult survival (Sol et al. 2007), with long term population trends (Shultz et al. 2005) and with an enhanced establishment success when introduced into novel environments (Sol et al. 2005, Sol and Lefebvre 2000, Sol et al. 2002).

If large brained and more innovative birds are better able to adapt to new conditions, one might also assume that these birds have an enhanced establishment success in urban environments (Kark et al. 2007, Møller 2009, Timmermans 1999). Supporting evidence comes from numerous reports on birds that responded to conditions in urban areas, such as the adaption of song frequency (Slabbekoorn and Peet 2003), timing of reproduction (Partecke et al. 2004) and feeding innovations (Fisher and Hinde 1949, Grobecker and Pietsch 1978).

However, so far brain size has not been found to be related to urbanization (Kark et al. 2007, Timmermans 1999). While Kark et al. (2007) tested the hypothesis that brain size and feeding innovation is correlated with urbanization only on birds of Jerusalem, Timmermans (1999) tested the prediction at the parvorder level on three continents and measured urbanization from field guides as the number of species that are reported to occur in urban environments. Furthermore, only Møller (2009) found that urban birds had a higher innovation rate compared to their rural congeners. Therefore, we tested the prediction that brain size and feeding innovation is related to urbanization within Passerida and Corvidae on different spatial scales.

Passerid and corvid species differ in behavioral traits that have been related to brain size such as caching (de Kort and Clayton 2006, Lefebvre and Bolhuis 2003, Lucas et al. 2004), social learning (Schwab et al. 2008, Wechsler 1988) and feeding innovation frequency (Lefebvre and Bolhuis 2003, Timmermans 1999). Furthermore, these species not only differ in their degree of urbanization but also the species themselves vary in their establishment success in different European cities (Witt et al. 2005).

We (1) reconstructed the endocrania of six European corvid species three-dimensionally by means of computed tomography (CT) scans, (2) measured the endocranial volume, (3) explored the effect of pneumatization on the endocranial volume and (4) tested whether relative brain size and innovation frequency is associated with urbanization in corvids. In a next step we verified the relationship between relative brain size, innovation frequency and urbanization in a broader taxonomic level, the Passerida, and controlled for similarities due to common ancestry. We expect that bird species with larger brains relative to their body mass and a higher propensity for innovative behavior to have an enhanced establishment success in urban environments (urban success).

Methods

3D reconstruction from CT-scans

The sample consisted of 104 skulls of six corvid species: common raven (*Corvus corax*), carrion crow (*Corvus corone cornix*), rook

(*Corvus frugilegus*), jackdaw (*Corvus monedula*), black-billed magpie (*Pica pica*) and Eurasian jay (*Garrulus glandarius*). The specimens are almost equally distributed across species and came from Museum für Naturkunde Berlin, Staatliches Museum für Naturkunde Görlitz and Staatssammlung für Anthropologie und Paläoanatomie München, which are all located in Germany. All corvid skulls were scanned by CT at Charite-Universitätsmedizin Berlin (see also Kulemeyer et al. 2009), using a Toshiba Aquilion16. The transverse high-resolution images were generated with a slice thickness of 0.5 mm, an interslice spacing of 0.2 mm (for a slice overlap of 0.3 mm) and a pixel size of 0.185 mm resulting in a voxel size of $0.185 \times 0.185 \times 0.03$ mm.

Structures of interest were highlighted, i. e. segmented, from the scan data with a semiautomated segmentation tool, the "magic wand" that use different gray values of bone and air. At foramina, manual line drawings delineated the boundary of the skull. A three-dimensional reconstruction of the segmented CT-scans allowed the calculation of the endocranial volume. Segmentation, three-dimensional reconstruction and volume measurement were done with Amira 4.0.

Pneumatization and relative brain size

Pneumatization describes the process, in which air deposits in the bone overlaying the brain. As a consequence, the bone grows wider and becomes separated into two layers of bone. In corvids, the process is directed inwards and is associated with a decrease in brain mass due to juvenile brain hypertrophy (Winkler 1979). Hence, the endocranial volume and in turn, brain size, depends on the degree of pneumatization. Furthermore, the CT-scans of corvid skulls revealed that the specimens differed in their degree of pneumatization and that damages in the cranial vault were rather frequent. Therefore, we scored the skulls according to their degree of pneumatization (Fig. 1) from one (not pneumatized) to five (fully pneumatized) and separated fully pneumatized ($n = 19$) from partially or not pneumatized skulls ($n = 85$) in subsequent analysis: The endocrania of fully pneumatized skulls were modeled twice to access the influence of pneumatization on the endocranial volume. First, the endocranium was modelled with the inner layer (pneumatized skull) and second with the outer layer (proxy for non-pneumatized skulls) as the boundary (Fig. 1, Fig. 2). From the endocranial volume of the remaining skulls relative brain size was estimated as the following: We regressed the endocranial volume of 88 corvid species taken from Iwaniuk and Nelson (2003) on body mass to obtain a robust estimation of the allometric relationship within corvids. The coefficients returned were then used to calculate the residual endocranial volume as an estimate for the relative brain size of the studied corvid species.

Data on brain size of the Passerida and the corresponding body mass was taken from Portmann (1947), which was supplemented by data from Garamszegi et al. (2005). Relative brain size was again calculated as the residuals of a linear regression of log brain size on log body mass.

Fig. 1: Sample inverted CT slices of three different corvid specimens. The inner layer of the pneumatized bone is drawn in red. **(a)**: unpneumatized skull, **(b)**: partially pneumatized skull, **(c)**: fully pneumatized skull with damages at the inner layer.

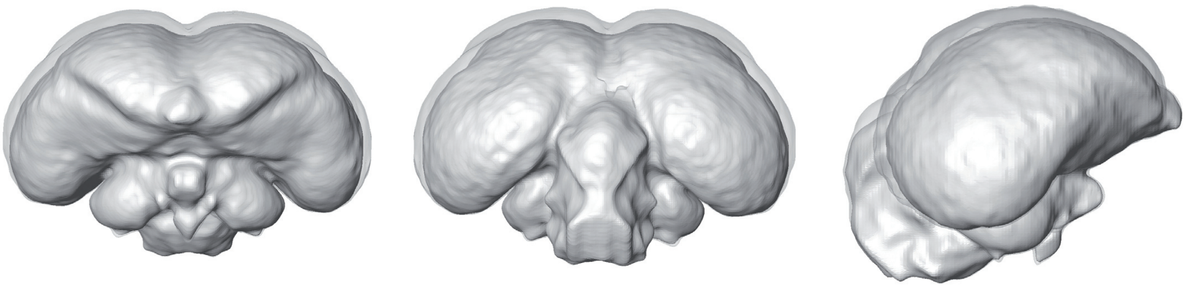

Fig. 2: Three-dimensional reconstruction of a sample corvid endocranium. The pneumatized area is drawn in light gray.

Urban success and innovation frequency

Several confounding variables might influence estimates of urban success, so that one measure might not be sufficient to describe the urbanization of passerid and corvid species. For example, the population density of a bird species in a city might be influenced by its density in the surrounding rural habitats and/or its geographical distribution, while population trends might be influenced by the former state of the population, e. g. a saturated population cannot increase. Therefore, we used four indices to measure the urban success of the studied corvid species:

First, the absolute population density (Otto and Witt 2002) and second, the relative population density of Berlin, Germany. Relative population density was calculated as an index of the absolute relative to the expected density – the density of the whole country, i. e. Germany – in the form $X = observed - expected/\sqrt{observed}$. The population densities of Germany were taken from BirdLife International (2004). The third and fourth measure were employed to account for variabilities in population densities of corvid and passerid species in different European cities (Witt et al. 2005). They were based upon an international inquiry on the population changes of birds in eastern European cities (Konstantinov et al. 1996). We derived two indices, first the number of towns, in which populations increased and second the number of towns, in which populations decreased. These measures were then divided by the number of all towns ($n = 19$), from which population trends have been reported.

Feeding innovations have received considerable attention as a measure of behavioral flexibility in recent literature (Lefebvre et al. 2004, Reader and Laland 2002). It is the frequency of new and unusual feeding behaviors per species reported in the short note section of 65 ornithological journals, which were collated in an exhaustive survey of 30 years (1970–2000) (Lefebvre et al. 1997, Nicolakakis et al. 2003). Examples of recorded feeding innovations are given in Lefebvre et al. (1997) and the data for the studied corvid and passerid species was taken from Garamszegi et al. (2005).

Statistical analyses

Innovation frequency and the absolute population density of Passerida were log transformed, because their non-normal distribution.

The indices of urban success were regressed on relative brain size and innovation frequency. When then repeated the analysis within Passerida, controlling for similarities in relative brain size, innovation frequency and indices of urban success due to common ancestry by using phylogenetic independent contrast (Felsenstein 1985). These phylogenetically corrected values were analyzed using regressions, which were forced through the origin. The estimated phylogeny (Fig. 3) is based on Barker et al. (2004) and was complemented by taxa specific trees of Sylvioidea (Alström et al. 2006), Muscicapoidea (Cibois and Cracraft 2004) and Passeroidea (Nguembock et al. 2009). As the composite phylogeny is based on different studies, consistent estimates for branch lengths were unavailable.

Therefore, we used the algorithm proposed by Grafen (1989) to estimate branch length. The underlying assumption of this approach is that the ages of taxa are proportional to the number of species they contain. The phylogenetic independent contrast was calculated within Passerida but not within Corvidae, because the number of species studied was low.

However, as we performed multiple pairwise tests of statistical significance on the same data, we used the conservative Bonferroni correction to maintain the family wise error rate. All statistical analysis were performed in R-2.6.1 (R Development Core Team 2007), the phylogenetic independent contrast with the package APE (Paradis et al. 2004).

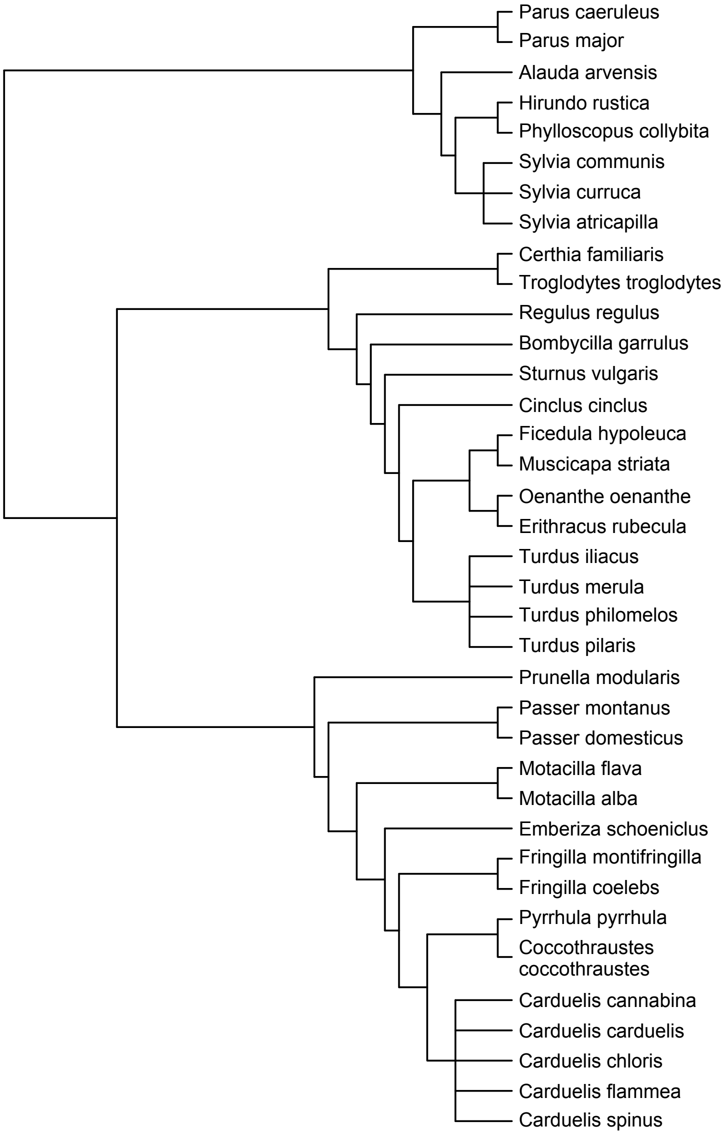

Fig. 3: Composite phylogeny of the passerid species studied. Branch length were estimated by the algorithm proposed by Grafen (1989) and are drawn proportionally.

Results

Pneumatization and relative brain size

Three-dimensional reconstruction of the endocranium from CT-scans is particularly suited to account for – rather frequent – damages to the inner layer of bone overlaying the brain and the pneumatization of the cranial vault (Fig. 1). Fully pneumatized corvid skulls ($n = 19$) were modeled twice to access the effect of pneumatization. The difference in the endocranial volume caused by pneumatization averages in the studied corvid species between 12 and 19 % (Fig. 2). It is not possible to access species differences in the effect of pneumatization due to the low sample size (three skulls per species). Hence, the observed differences between species are probably due to individual differences in the degree of pneumatization. From the remaining corvid skulls, from which relative brain sizes were calculated, the degree of pneumatization did not differ between species (ANOVA, $F = 1.25$, $p < 0.295$, $n = 85$). Relative brain size was computed as the residuals from the estimated allometric relationship of a broader survey of corvid endocrania (Fig. 4, Iwaniuk and Nelson 2003). Relative brain size is significantly different between species (ANOVA, $F = 10.3$, $p < 0.001$) and is progressively increased from rook, to Eurasian jay, to common raven, to hooded crow, to jackdaw and to black-billed magpie (Fig. 5).

Relative brain size of passerid birds were calculated from data of Portmann (1947) and Garamszegi et al. (2005). The estimated allometric relationship between log body mass and log brain size differed between Passerida and Corvidae (Fig. 4). It suggests that corvid species in general, i. e. independent of body mass, have an increased brain size.

Brain size, innovation frequency and urban success

Species mean relative brain size did not correlate with innovation frequency in the Corvidae and Passerida (Corvidae: $r^2 = 0.16$, $F_{1,4} = 0.75$, $p = 0.436$ and Passerida: $r^2 = 0.04$, $F_{1,35} = 1.37$, $p = 0.251$, Fig. 6a).

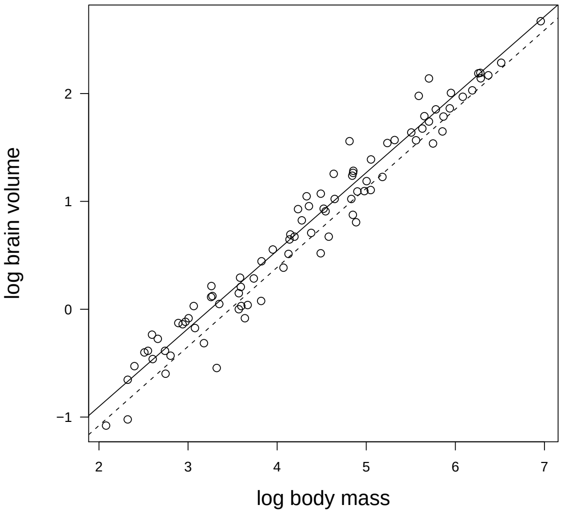

Fig. 4: Regression of log endocranial volume on log body mass within the Corvidae, data taken from Iwaniuk and Nelson (2003), $n = 88$. The dashed line represents the corresponding allometric relationship in the Passerida, data taken from Portmann (1947) and Garamszegi et al. (2005), $n = 58$.

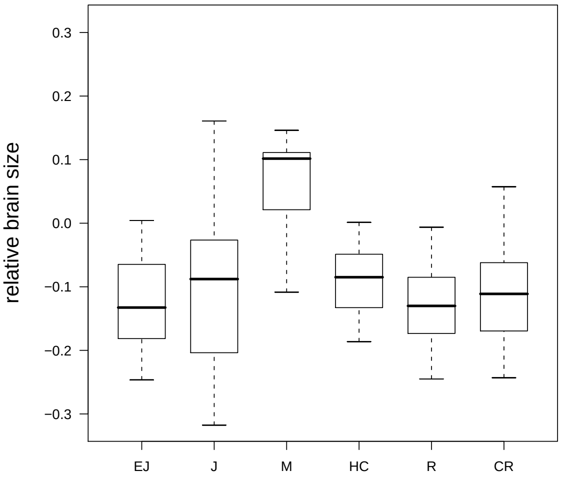

Fig. 5: Boxplot of relative brain size in the studied corvids (median, quartiles and range), $n = 85$. **EJ**: Eurasian jay, **J**: jackdaw, **M**: black-billed magpie, **HC**: hooded crow, **R**: rook, **CR**: Common Raven.

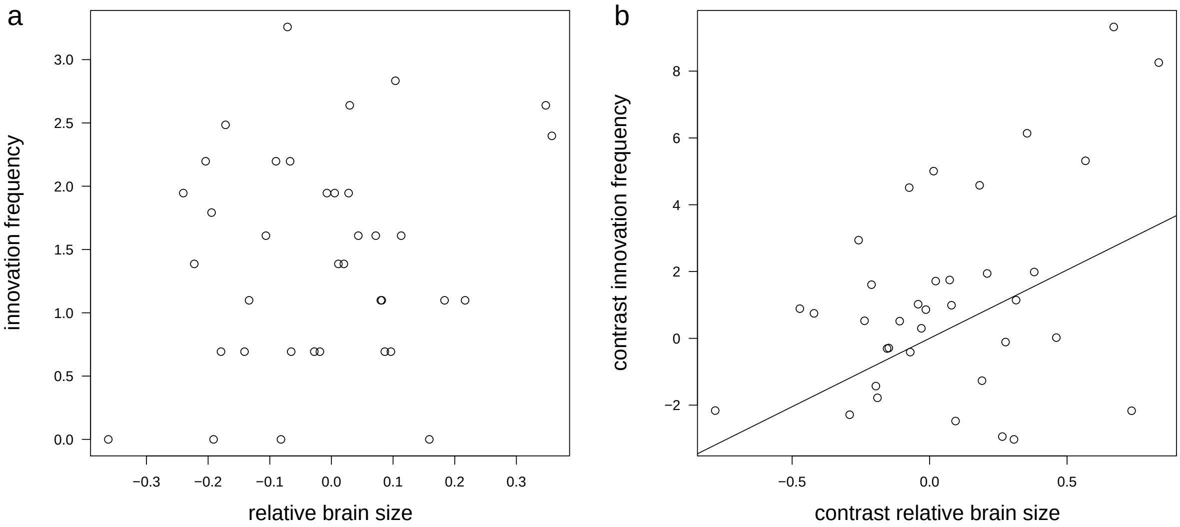

Fig. 6: Regression of innovation frequency on relative brain size in passerid birds, $n = 44$. The relationship is shown without (a) and with (b) control for phylogenetic effects.

When controlled for common ancestry using a phylogenetic independent contrast, the relationship between relative brain size and innovation frequency within Passerida is significantly associated (Passerida: $r^2 = 0.20$, $F_{1,35} = 8.80$, $p = 0.005$, Fig. 6b).

The results of the univariate regressions of measures of urban success on relative brain size and innovation frequencies within Corvidae are presented in Table 1 and within Passerida in Table 2. The analysis within the Passerida were repeated after controlling for phylogenetic effects. These results are presented in Table 3.

Within Corvidae, relative brain size did not correlate with any indices of urban success. Three of four indices were significantly correlated with innovation frequency, i. e. absolute and relative population density of Berlin, as well as the population increase in eastern Eu-

Tab. 1: Results of univariate regression analyses of measures of urban success on relative brain size and innovation frequency within the Corvidae. Urban success was estimated on different spatial scales. Population density was calculated from data of Berlin and population trends (increase and decrease) were derived from data of 19 eastern European cities. Significant correlations are indicated as $^*p < 0.05$. None of the correlations remained significant after a Bonferroni correction.

Corvidae	slope	r^2	$F_{1,4}$	p
relative brain size				
absolute population density	18.88	0.42	2.84	0.167
relative population density	8.12	0.48	3.71	0.126
population increase	1.98	0.33	1.99	0.230
population decrease	−0.54	0.09	0.38	0.569
innovation frequency				
absolute population density	2.86	0.79	14.77	0.018 ∗
relative population density	1.18	0.84	21.44	0.010 ∗
population increase	0.35	0.84	20.76	0.010 ∗
population decrease	−0.09	0.19	0.94	0.387

Tab. 2: Results of univariate regression analyses of measures of urban success on relative brain size and innovation frequency within the Passerida. Significant correlations are indicated as $*p < 0.05$, $**p < 0.01$. Bold p-values indicate correlations that remained significant after a Bonferroni correction was applied.

Passerida	slope	r^2	F	p
relative brain size				
absolute population density	4.775	0.136	$F_{1,27} = 4.262$	0.049 $*$
relative population density	4.819	0.027	$F_{1,27} = 0.741$	0.397
population increase	0.498	0.206	$F_{1,22} = 5.704$	0.026 $*$
population decrease	−0.121	0.017	$F_{1,22} = 0.384$	0.542
innovation frequency				
absolute population density	1.499	0.424	$F_{1,27} = 19.855$	**0.001** $***$
relative population density	1.479	0.079	$F_{1,27} = 2.327$	0.139
population increase	0.135	0.052	$F_{1,22} = 1.516$	0.231
population decrease	0.051	0.050	$F_{1,22} = 2.021$	0.169

ropean cities. However, these significant correlations disappeared after a Bonferroni correction was applied (Tab. 1).

Within Passerida relative brain size correlated significantly with absolute population density of Berlin and population increase in eastern European cities, but neither with relative population density, nor with population decrease. Furthermore, the significant correlations disappeared after Bonferroni correction (Tab. 2, Fig. 7a). When controlled for phylogenetic effects, the correlation between relative brain size and absolute population density remained significant, but again the significance disappeared after Bonferroni correction (Tab. 3, Fig. 7b).

However, innovation frequency was signifi-

Tab. 3: Results of univariate regression analyses of phylogenetically corrected measures of urban success on relative brain size and innovation frequency within the Passerida. The independent contrast was calculated with the phylogeny given in Fig. 3. Significant correlations are indicated as $*p < 0.05$, $**p < 0.01$ and $***p < 0.001$. Bold p-values indicate correlations that remained significant after a Bonferroni correction was applied.

contrast Passerida	slope	r^2	F	p
contrast relative brain size				
contrast absolute population density	7.013	0.141	$F_{1,27} = 4.426$	0.045 $*$
contrast relative population density	2.183	0.003	$F_{1,27} = 0.086$	0.772
contrast population increase	0.679	0.113	$F_{1,22} = 2.791$	0.109
contrast population decrease	0.024	0.025	$F_{1,22} = 0.563$	0.461
contrast innovation frequency				
contrast absolute population density	1.215	0.396	$F_{1,27} = 17.690$	**0.001** $***$
contrast relative population density	0.838	0.044	$F_{1,27} = 1.230$	0.277
contrast population increase	0.061	0.088	$F_{1,22} = 2.134$	0.158
contrast population decrease	−0.141	0.009	$F_{1,22} = 0.194$	0.664

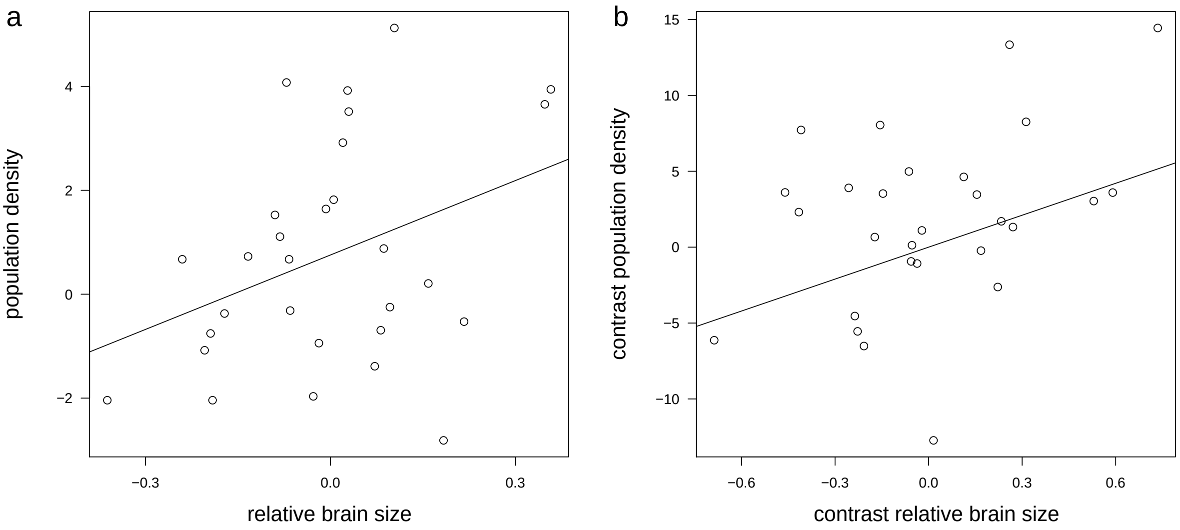

Fig. 7: Regression of absolute population density on relative brain size in passerid birds, $n = 29$. The relationship is shown without (a) and with (b) control for phylogenetic effects.

cantly correlated with absolute population density with and without control for phylogenetic effects (Tab. 2, Tab. 3, Fig. 8) and remained significant after Bonferroni correction.

In multiple linear regression of absolute population density on relative brain size and innovation frequency, only innovation frequency remained significant (relative brain size: $p = 0.067$ and innovation frequency: $p = 0.001$, overall r^2 of the multiple model $= 0.49$, $F_{2,26} = 12.73$, $p = 0.001$), as well as in the multiple regression on the independent contrasts (relative brain size: $p = 0.340$ and innovation frequency: $p = 0.002$, overall r^2 of the multiple model $= 0.42$, $F_{2,26} = 9.298$, $p = 0.001$).

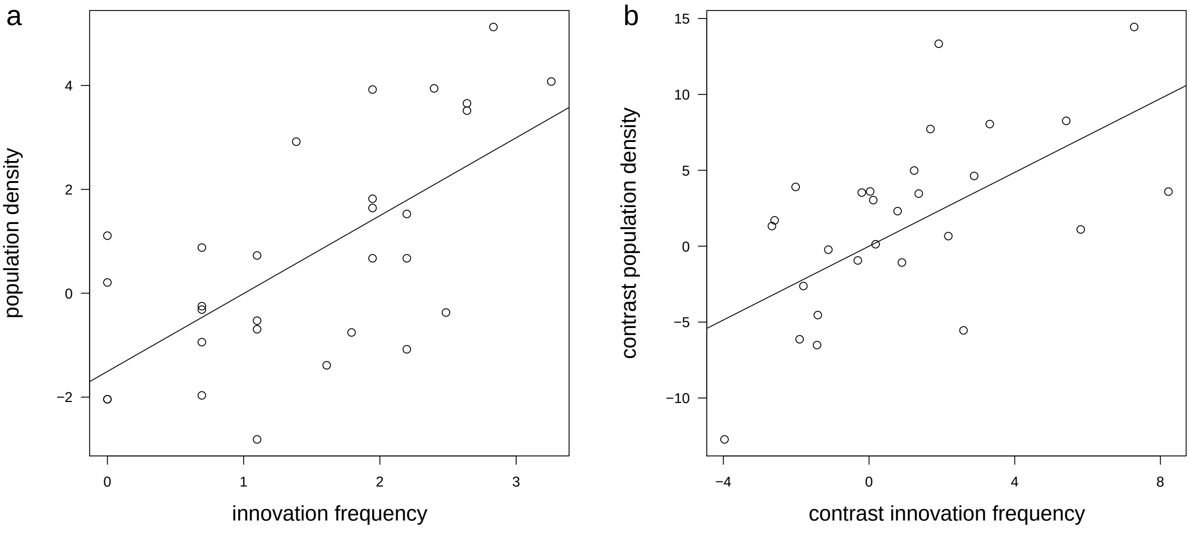

Fig. 8: Regression of absolute population density on innovation frequency in passerid birds, $n = 29$. The relationship is shown without (a) and with (b) control for phylogenetic effects.

Discussion

Pneumatization and relative brain size

In corvids, brain maturation takes about two years and is accompanied by a decrease in brain mass (Winkler 1979). This process is associated with pneumatization, which in these species is directed inwards and not externally visible. Our results suggest that the difference in endocranial volume due to pneumatization is about 15 % and it is likely that the decrease in brain mass during maturation has about the same magnitude. Traditional methods that measure the endocranial volume by filling the endocranial vault with lead shot do not allow to consider the effect of pneumatization, because in corvids, the degree of pneumatization is not externally visible as opposed to smaller passerids. Furthermore, traditional methods cannot account for rather frequent damages to the inner layer of the pneumatized bone. Thus, with traditional methods, results on the endocranial volume is considerably influenced by age and thus by the degree of pneumatization of the studied corvid specimens and above all by the inner condition of the skulls.

Differences in the endocranial volume due to pneumatization become even more substantial in studies across avian orders, because the process of pneumatization differs between taxa. For example, in pigeons the pneumatization is directed outwards (as opposed to corvids) and hence, do not influence their endocranial volume. Accordingly, pigeons do not undergo a decrease in brain mass during maturation. Hence, it is likely that studies on the endocranium overestimate its volume in corvids and therefore their brain size, especially in studies across several avian orders.

Brain size and innovation frequency

Relative brain size and innovation frequency did not correlate, neither in corvid nor in passerid species. When passerid species were controlled for common ancestry by a phylogenetic independent contrast, there was a significant correlation between relative brain size and innovation frequency. Hence, these results suggest that the phylogenetically uncorrected regression fail to predict innovation frequency from relative brain size due to common ancestry. Two, not mutually exclusive explanations were posed that might clarify these results.

First, while most of the variation in innovation frequency is found on the species level, variation in relative brain size is mostly concentrated at higher taxonomic levels (Nealen and Ricklefs 2001, Nicolakakis et al. 2003, Sol 2003). Hence, it has been hypothesized that innovation frequency might reflect the current degree of foraging flexibility, while relative brain size appears to describe differences in cognitive abilities that evolved in the early diversification of avian lineages (Sol 2003). Therefore, previous studies on feeding innovations were performed at higher taxonomic levels and found a significant relationship between innovation frequency and the relative size of the brain (Nicolakakis et al. 2003), forebrain (Lefebvre et al. 2001, 1997) and hyperstriatum ventrale and neostriatum complex (HV+Neo, Timmermans et al. 2000). Of these measures, HV+Neo was the best predictor of feeding innovations (Timmermans et al. 2000), which is thought to play a similar integrative role as the mammalian neocortex.

Second, it has been hypothesized that the modularity of bird minds and brains might be limited and hence, different cognitive systems might be traded off against one another (Lefebvre and Bolhuis 2003). For example, Lefebvre and Bolhuis (2003) showed that the degree of food caching and innovation frequency are negatively correlated in European Paridae and North American Corvidae. Although this relationship was not found in the European Corvidae, it is reasonable that innovation frequency and food storing are traded off against each other, because birds that rely on fewer stores have to spend more time searching for new feeding opportunities (Lefebvre and Bolhuis 2003).

Urban success

We employed four indices of urban success to account for possible confounding variables that might influence these estimates. For example, the population density of a city might be influenced by regional effects, such as the density of the surrounding rural habitats. In contrast, relative population density might not accurately reflect urban success, especially in rare species. Although, it is thought that urban species composition and abundance is due to local rather than regional effects (Clergeau et al. 1998, Witt et al. 2005, but see Clergeau et al. 2001) we employed both, absolute and relative population density of Berlin. The third and fourth measure – population increase and -decrease in 19 eastern European towns – were included to account for variabilities in population densities throughout European cities (Witt et al. 2005).

However, five out of six correlations of relative brain size and innovation frequency with absolute population density were significant, in contrast to the other measures of urban success (Tab. 1–3). The only correlate that failed to predict absolute population density was the relative brain size of Corvidae (Tab. 1). Within Passerida, our results suggest that both, relative brain size and innovation frequency, predict absolute population density with and without control for phylogeny (Tab. 2–3, Fig. 7–8). However, our results also suggest that innovation frequency is a better predictor for absolute population density than relative brain size for two reasons. First, the correlations between innovation frequency and absolute population density remained significant after Bonferroni correction as opposed to correlations with relative brain size (Tab. 2–3). Second, when relative brain size and innovation frequency were entered in a multiple regression with absolute population density – with and without control for common ancestry – only innovation frequency remained significant.

Because of the anecdotic nature of innovation frequency, it is potentially dependent on several confounding variables such as population size and research effort (Nicolakakis and Lefebvre 2000). While none of these confounding variables have been found to significantly influence innovation rate (Nicolakakis and Lefebvre 2000), there are other potential confounds that might influence the link between innovation frequency and urban success: Birds that are exposed to novel environments, such as urban habitats, encounter new situations more often and thus might invent novel feeding techniques more frequently, compared to birds that stick to ancestral habitats. Furthermore, the source for feeding innovations are ornithological journals that cover northwestern Europe (Nicolakakis et al. 2003). In towns of this area, for example, jackdaws are quite uncommon, while in northeastern European cities, jackdaws are very abundant, especially in Warsaw (Witt et al. 2005). Hence, feeding innovations that have been reported in northeastern European countries might draw a different picture about the behavioral flexibility of jackdaws. However, the best support for the link between innovation rate and establishment success in new environments comes from studies on the invasion success of birds. These studies revealed that successful invaders showed a higher frequency of foraging innovations in their region of origin (Sol et al. 2005, Sol and Lefebvre 2000, Sol et al. 2002).

Another measure of flexible behavior that might be associated with urban success is nesting innovation frequency (compare Nicolakakis and Lefebvre 2000), because nest sites in urban environments are scarce (Chace and Walsh 2006, Lim and Sodhi 2004, Wang et al. 2008, Yeh et al. 2007) and nest placement is shaped by different selective pressures such as predation (Yeh et al. 2007) or human disturbance (Wang et al. 2008). Although nest building is thought to be more constrained than feeding (see Hansell 1984, Nicolakakis and Lefebvre 2000), a considerable number of nesting innovations were collated (Nicolakakis and Lefebvre 2000). Furthermore, many raptor species, for example, use artificial and new nest sites in urban environments, which is often associated with an enhanced reproduction compared to ancestral nest sites (Chace and Walsh 2006). Hence, it might be interesting to test whether nesting innovation frequency is associated with urban success.

Conclusion

Our results suggest that, within Corvidae, innovation frequency predicts urban success in contrast to relative brain size. Within Passerida, both, relative brain size and innovation frequency predict population density of Berlin, with and without control for phylogeny. Therefore, our results support the brain size – environmental change hypothesis and indicate that birds with enlarged brains and a high propensity for innovative behavior more readily establish in urban environments. However, our results also suggest that feeding innovation frequency is a better predictor for urban establishment success than relative brain size as revealed by a multiple regression.

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6. Summary

Corvid species colonize European cities with different success. Therefore, the goal of this thesis is to identify traits that might explain differences in the establishment success of corvids in urban areas. Sympatric European corvid species are particularly suited to address this question, because these species differ in behavior, ecology and cognitive abilities.

Urban environments are characterized by specific habitats that might be suitable for particular species. As avian morphological studies suggest that morphology covaries with behavior and habitat preferences, we studied the skull morphology of corvids with respect to foraging in Chapter 2 and wing-, hind limb- and foot morphology with respect to ancestral habitat preferences in Chapter 3. In Chapter 1, we discuss a potential link to urban habitats.

In Chapter 2, we expected in the analysis of skull morphology that species that frequently probe to have a relatively longer bill and more sidewise oriented orbits in contrast to species that frequently peck. We tested this prediction by analyzing computed tomography (CT) scans of skulls of six corvid species by means of three-dimensional geometric morphometrics. We first explored patterns of major variation, second compared within and between species relationships of size and shape and third compared patterns of morphological integration between bill and cranium. Major shape variation occurs at the bill, in the orientation of orbits, in the position of the foramen magnum and in the angle between bill and cranium. Major covariation between the bill and cranium lies in the difference in orbit orientation relative to bill-length and in the angle between bill and cranium. We conclude that corvid species show pronounced differences in skull shape, which covary with foraging mode. Increasing bill-length, bill-curvature and sidewise orientation of the eyes is associated with an increase in the observed frequency in probing (vice versa in pecking). Our results on the morphological integration suggest that most of the covariation between bill and cranium is due to differences in the topography of the binocular fields and the projection of the bill-tip therein, indicating the importance of visual fields to the foraging ecology of corvids.

In Chapter 3, we measured the wing-, leg- and foot morphology. It is assumed that wingtip shape is associated with a gradient from forest- to open habitats, while hind limb- and foot morphology is thought to be reflected in gradients from hopping to walking and from tree to ground foraging. The analysis of wingtip shape almost clearly separate the six corvid species. Rounded wings were associated with forest- and pointed with open habitats. The analyses on hind limb and foot morphology do not differentiate these species very well. It is likely that this is due to the fact that the studied corvid species in general are very divers in their behavior and habitat associations. All studied corvid species rest and/or breed in trees and forage on the ground. Furthermore, all species hop and walk and hence, the difference between these species is the frequency, in which they use these different habitat types and/or behaviors.

It is assumed that species, which are more flexible in their feeding are more likely to exploit anthropogenic food resources and therefore, might have selective advantages in urban environments over species that stick to their ancestral diet. Feeding innovation frequency is thought to measure the adoption of new food resources and to reflect the behavioral flexibility of a species. According to the behavioral drive hypothesis feeding innovations might spread among members of a population through individual and social learning and as a consequence, the species might be exposed to a new selective pressures that in turn increase morphological variability.

In Chapter 4, we therefore studied the relationship between morphological variability and feeding innovations. Within-species variability in skull shape was estimated from a

principal component (PC) analysis on a three dimensional landmark dataset basing upon CT-scans. Major variation in PC 1 and PC 3 describes differences in bill shape, while major variation in PC 2 lies in the angle between bill and cranium and in the position and orientation of the eyes. None of the within-species variabilities in the first three dimensions of the PCA on skull shape correlate with innovation frequency. However, the within-species variability in the first and third PC revealed an almost significant trend. These results are striking, because major variation across species in PC 1 and PC 3 described differences in bill shape, in contrast to PC 2. Furthermore, PC 1 and PC 3 separate corvid species as opposed to PC 2, which only separates Eurasian jay from jackdaw. Therefore, our results might suggest that the inability to detect a significant correlation is due to the low number of species studied, rather than to a non-existent relationship.

Probably the most promising hypothesis to explain differences in the establishment success in urban environments has been termed the brain size – environmental change hypothesis. According to this hypothesis, large brains might have evolved to cope with novel or altered conditions through innovative behavior.

In Chapter 5, we therefore tested the prediction that large brained and more innovative birds more readily settle in urban areas. Relative brain size of the Corvidae were estimated from a three-dimensional reconstruction of the endocrania basing upon CT-scans of corvid skulls and in addition, the effect of pneumatization on the endocranial volume was explored. We then tested whether relative brain size and innovation frequency is associated with four estimates of urban success within Corvidae and Passerida, i. e. absolute and relative population density, as well as population increase and decrease. Three-dimensional reconstruction of the endocranium from CT-scans is particularly suited to account for – rather frequent – damages to the endocranium and the pneumatization of the cranial vault. The difference in the endocranial volume caused by pneumatization averages in the studied corvid species between 12 and 19 %. Within Corvidae, relative brain size correlates neither with feeding innovation frequency, nor with any estimates of urban success. Innovation frequency in contrast, correlates with three out of four estimates of urban success. Within Passerida relative brain size correlates significantly with feeding innovation frequency when controlled for phylogenetic effects. Relative brain size and feeding innovation frequency correlate with population density with and without phylogenetic control. In a multiple linear regression – with and without control for phylogeny – however, only innovation frequency remained significant. Our results indicate that both, relative brain size and feeding innovations predict urban establishment success of birds and therefore support the brain size – environmental change hypothesis. Our results also suggest that innovation frequency is a better predictor for urban success than relative brain size.

However, the relationship between relative brain size and feeding innovation frequency is only significant, when phylogeny is controlled for. Two, not mutually exclusive explanations were posed that might explain this result. First, while major variation in feeding innovation frequency is located on the species level, major variation in relative brain size is concentrated at higher taxonomic levels. It indicates that differences in relative brain size might have evolved in the early diversification of avian lineages. Second, it is thought that the modularity of birds minds and brains might be limited and hence, different cognitive systems might be traded off against one another. For example, the degree of food caching and innovation frequency are negatively correlated in European Paridae and North American Corvidae. Therefore, one might conclude that cognitive traits reflect the flexibility and specialization of a species, particularly because feeding innovations are considered as a measure of behavioral flexibility. Furthermore, the results of this thesis suggest that flexibility is also reflected in morphology. Hence, one might assume that measures of morphology might directly predict urbanization potential. This hypothesis is discussed in Chapter 1.

7. Zusammenfassung

Städtische Ballungsräume in Europa werden von Rabenvögeln mit unterschiedlichem Erfolg besiedelt. Das Ziel dieser Arbeit ist es deshalb, Eigenschaften zu ermitteln, die den unterschiedlichen Besiedlungserfolg erklärbar machen. Die in Europa sympatrisch vorkommenden Corviden eignen sich dabei besonders dieser Fragestellung nachzugehen, da sich diese Arten in ihrem Verhalten, ihrer Ökologie und in ihren kognitiven Fähigkeiten unterscheiden.

Urbane Lebensräume lassen sich durch spezifische Habitattypen charakterisieren, die den Ansprüchen bestimmter Vogelarten entsprechen können. Viele morphologische Untersuchungen an Vögeln zeigen, dass die Morphologie mit dem Verhalten und den Habitatpräferenzen der Vögel kovariiert. Deshalb haben wir in Kapitel 2 die Schädelmorphologie im Hinblick auf den Nahrungserwerb und in Kapitel 3 die Flügel-, Bein- und Fußmorphologie hinsichtlich eines Zusammenhanges mit den angestammten Habitaten untersucht. In Kapitel 1 wird eine mögliche Übertragung auf städtische Habitattypen diskutiert.

In Kapitel 2 haben wir bei den Untersuchungen zur Schädelmorphologie erwartet, dass diejenigen Arten, die sich häufig stochernd im Substrat ernähren, einen längeren Schnabel und seitwärts orientiertere Augenhöhlen besitzen als solche Arten, die die Nahrung auf dem Substrat absammeln. Die Corvidenschädel wurden computertomographisch (CT) gescannt und mittels dreidimensionaler geometrisch morphometrischer Methoden analysiert. Dabei haben wir erstens Muster in der Hauptvariation, zweitens den inner- und zwischenartlichen Zusammenhang zwischen der Form und Körpergröße und drittens die morphologische Integration zwischen Schnabel und Gehirnschädel untersucht. Die größte Formenvariation findet sich am Schnabel, in der Orientierung der Orbita, in der Positionierung des Foramen magnums und in dem Winkel zwischen Schnabel und Gehirnschädel. Die größte Kovariation zwischen dem Schnabel und dem Cranium findet sich in der Orientierung der Orbita im Verhältnis zur Schnabellänge und in dem Winkel zwischen Schnabel und Gehirnschädel. Wir haben festgestellt, dass sich die Schädelform der Rabenvögel stark unterscheidet und sich diese Differenz in den unterschiedlichen Strategien im Nahrungserwerb wiederspiegelt. Dabei begünstigt ein langer, gekrümmter Schnabel und seitwärts orientierte Augen das Stochern im Substrat (und umgekehrt beim Absammeln der Nahrung auf dem Substrat). Die Ergebnisse zur morphologischen Integration legen den Schluss nahe, dass der größte Anteil der Kovariation zwischen Schnabel und Cranium sich auf die Topografie des binokularen Sichtfeldes auswirkt. Zusätzlich verändert sich die Projektion der Schnabelspitze im binokularen Feld und weist damit darauf hin, wie wichtig das Sichtfeld für den Nahrungserwerb der Rabenvögel ist.

In Kapitel 3 wurden Flügel-, Bein- und Fußmorphologie analysiert. Allgemein wird angenommen, dass sich die Flügelform im Gradienten vom Wald zum offenen Habitat wiederspiegelt. Von der Bein- und Fußmorphologie wird hingegen vermutet, dass sie Gradienten vom Hüpfen zum Laufen und der Nahrungssuche in Bäumen bis auf den Boden reflektiert. Die Untersuchungen zur Flügelform zeigen deutliche Unterschiede zwischen den Rabenvogelarten. Runde Flügel begünstigen ein Vorkommen im Wald, während spitze Flügel eher ein Vorkommen in offenen Habitaten unterstützen. Die Analyse der Bein- und Fußmorphologie ergeben keine deutlichen Unterschiede zwischen den Arten. Es ist wahrscheinlich, dass dieses Ergebnis der allgemeinen Flexibilität im Verhalten und der Habitatpräferenzen geschuldet ist. Alle Arten rasten und/oder brüten in Bäumen und suchen ihre Nahrung auf dem Boden. Außerdem bewegen sich die Rabenvögel sowohl hüpfend als auch laufend. Der Unterschied zwischen den Arten ist also vielmehr die Frequenz, mit denen sie unterschiedliche Habitattypen nutzen und/oder Verhaltensweisen zeigen.

Man nimmt an, dass diejenigen Arten, die sich flexibel ernähren können, mit größerer Wahrscheinlichkeit anthropogene Nahrungsressourcen ausnutzen können. Demnach sollten diese Arten in urbanen Lebensräumen denjenigen, welche an ihre ursprünglichen Nahrungsquellen gebunden sind, überlegen sein. Von der Innovationsrate (Innovationen im Nahrungserwerb) wird angenommen, dass sie die Erschließung neuer Nahrungsquellen und die Verhaltensflexibilität einer Art messen. Gemäß der „behavioral drive“ Hypothese breiten sich Innovationen durch individuelles und soziales Lernen in einer Population aus. Dadurch ist die Art neuen Selektionsdrücken ausgesetzt, die wiederum die morphologische Variabilität erhöhen.

In Kapitel 4 haben wir deshalb den Zusammenhang zwischen der innerartlichen morphologischen Variabilität und der Innovationsrate untersucht. Die innerartliche Variabilität in der Schädelform wurde durch eine Hauptkomponentenanalyse eines dreidimensionalen Landmarken-Datensatzes abgeschätzt, welchem die CT-Scans zugrunde lagen. Die größte zwischenartliche Variation in der ersten und dritten Hauptkomponente (HK) findet sich am Schnabel, während die zweite HK die größte Variation in dem Winkel zwischen Schnabel und Cranium, sowie in der Orientierung der Orbita zeigt. Keine der innerartlichen Variabilitäten in den ersten drei Dimensionen der Hauptkomponentenanalyse zur Schädelform korreliert signifikant mit der Innovationsrate. Allerdings zeigt die innerartliche Variabilität in der ersten und dritten Hauptkomponente einen nahezu signifikanten Trend. Dieses Ergebnis ist sehr bemerkenswert, da sich die größte zwischenartliche Variation in HK 1 und HK 3 – im Gegensatz zu HK 2 – in der Schnabelform finden. Außerdem ergeben sich in HK 1 und HK 3 deutliche Unterschiede zwischen den Arten, während sich in HK 2 nur Unterschiede zwischen dem Eichelhäher und der Dohle und finden. Diese Ergebnisse legen den Schluss nahe, dass das Unvermögen, eine signifikante Korrelation zu ermitteln, eher an der geringen Anzahl untersuchter Arten als an einem nicht existierenden Zusammenhang liegt.

Die wahrscheinlich vielversprechendste Hypothese, die den unterschiedlichen Besiedlungserfolg in urbanen Lebensräumen erklärbar machen könnte, wurde als „brain size – environmental change“ Hypothese bezeichnet. Dieser Hypothese zufolge, haben sich große Gehirne evolviert, um auf neue Umweltbedingungen mit innovativen Verhalten reagieren zu können.

In Kapitel 5 haben wir deshalb die Hypothese überprüft, dass Vögel mit größeren Gehirnen und einer größeren Neigung für innovatives Verhalten mit größerem Erfolg urbane Lebensräume besiedeln. Die Endocranien der Corviden wurden mittels CT-Scans dreidimensional rekonstruiert und dadurch deren relative Gehirngröße abgeschätzt. Zudem haben wir den Effekt der Pneumatisation auf das Endocranialvolumen untersucht. Innerhalb der Corvidae und Passerida wurde getestet, ob die relative Gehirngröße und die Innovationsrate mit vier Indices des urbanen Besiedlungserfolg zusammenhängen – der absoluten und relativen Populationsdichte, sowie der Populationszunahme und -abnahme. Wir haben festgestellt, dass sich die dreidimensionale Rekonstruktion der Endocranien durch CT-Scans besonders eignet, um die relativ häufigen Beschädigungen am Endocranium und die Pneumatisation zu berücksichtigen. Der durch die Pneumatisation bedingte Unterschied im endocranialen Volumen beträgt im Artmittel zwischen 12 und 19 %. Innerhalb der Corviden korreliert die relative Gehirngröße weder mit der Innovationsrate, noch mit den Indices für den urbanen Besiedlungserfolg. Die Innovationsrate hingegen ist signifikant mit drei der vier Indices für den urbanen Besiedlungserfolg korreliert. Innerhalb der Passerida korreliert die relative Gehirngröße signifikant mit der Innovationsrate, wenn die unterschiedliche Phylogenie berücksichtigt wird. Die relative Gehirngröße und die Innovationsrate korrelieren signifikant mit der absoluten Populationsdichte, sowohl mit als auch ohne Berücksichtigung der unterschiedlichen Stammesgeschichte. In einem multiplen linearen

Modell bleibt aber nur die Korrelation mit der Innovationsrate signifikant. Unsere Ergebnisse legen den Schluss nahe, dass sowohl die relative Gehirngröße, als auch die Innovationsrate den Besiedlungserfolg vorraussagt und damit die „brain size – environmental change“ Hypothese unterstützen. Unsere Ergebnisse zeigen aber auch, dass die Innovationsrate den Zusammenhang mit dem urbanen Besiedlungserfolg besser erklärt als die relative Gehirngröße.

Wie bereits erwähnt, ist der Zusammenhang zwischen der relativen Gehirngröße und der Innovationsrate nur signifikant, wenn die unterschiedliche Phylogenie berücksichtigt wird. Zwei sich nicht gegenseitig auschließende Hypothesen wurden angeführt, die dieses Ergebnis erklären könnten. Erstens, während sich die größte Variation in der Innovationsrate auf dem Artniveau findet, ist die Variation in der relativen Gehirngröße auf höherem taxonomischen Niveau konzentriert. Dieses Ergebnis deutet an, dass sich die Unterschiede in der relativen Gehirngröße in der frühen Stammesgeschichte der Vögel evolviert haben könnten. Zweitens wird angenommen, dass die Modularität von Verstand und Gehirn der Vögel limitiert ist. Demnach könnten unterschiedliche kognitive Systeme einem „Tradeoff“ unterliegen. So wurde z. B. nachgewiesen, dass innerhalb der der europäischen Paridae und der nord-amerikanischen Corvidae die Nahrungsspeicherung negativ mit der Innovationsrate korreliert. Dieser negative Zusammenhang legt den Schluss nahe, dass kognitive Fähigkeiten den Grad der Flexibilität und Spezialisierung einer Art widerspiegeln, insbesondere weil die Innovationsrate als Maß für Verhaltensflexibilität angesehen wird. Zudem deuten die Ergebnisse dieser Arbeit an, dass sich die Flexibilität einer Art ebenso in der Morphologie widerspiegelt. Demzufolge könnte die Morphologie das Urbansierungspotential einer Art direkt vorraussagen. Diese Hypothese wird in Kapitel 1 diskutiert.

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Erklärung

Hiermit bestätige ich, dass ich die vorliegende Dissertation selbstständig verfasst und keine anderen als die angegebenen Quellen und Hilfsmitteln verwendet habe.

Berlin, den 20. 04. 2009

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