

Life history traits, bioclimate, and migratory systems of accipitrid birds of prey (Aves: Accipitriformes)

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Received 21 July 2016; accepted for publication 1 November 2016

Although migration is a widespread phenomenon across a range of taxa, the evolution of migratory behaviour remains insufficiently understood. Therefore, the aim of this study was to examine the relationships between migratory behaviour and life history traits of diurnal birds of prey (Accipitriformes) in a phylogenetic context and also to investigate the bioclimatic suitability of geographical ranges for migratory raptors. We performed phylogenetic generalized least square analysis, using a previously published phylogenetic tree of 179 accipitrid raptors, to identify relationships among distribution patterns, diet, hunting strategies, body measurements, clutch size, and migratory behaviour. Bioclimatic data were employed into computer learning maximum entropy modelling (Maxent) to specify differences between climatic conditions on breeding and wintering grounds. Clutch size and hunting strategies have been proved to be the most important variables in shaping distribution areas, and also the geographic dissimilarities may mask important relationships between life history traits and migratory behaviours. However, this result supports the need for distinctions among the three major migratory routes in raptors. Indeed, the West Palearctic-Afrotropical and the North-South American migratory systems are fundamentally different from the East Palearctic-Indomalayan system, owing to the presence versus absence of ecological barriers. This suggests that the migratory behaviours differ among the three main migratory routes for these species. Future studies could uncover the causes of differences among the three main flyways in more detail.

ADDITIONAL KEYWORDS: biogeography – clutch size – comparative phylogenetic methods – ecology barriers – habitat – hunting strategies – maximum entropy modelling – raptors.

INTRODUCTION

Few comparative and species-rich studies are known to provide detailed explanations for the evolutionary origins and ecology of migratory systems in birds. Two mutually non-exclusive theories seek to explain the evolution of migration (Rappole & Jones, 2002; Bruderer & Salewski, 2008; Milner-Gulland, Fryxell & Sinclair, 2011). First, the ‘tropical origin’ hypothesis proposes that long-distance migration evolved from sedentary, tropical populations (Cox, 1985; Salewski & Bruderer, 2007), whereas the second one is that changes in the breeding territories of northern-distributed species support the ‘northern origin’ hypothesis that predicts that climatic constraints, such as winter

conditions, are predominantly responsible for the evolution of migratory systems (Bell, 2000, 2005; Bruderer & Salewski, 2008). Long-distance and short-distance/partial migration could have been originated in very different ways. While the former is fixed or could be fixed over time under genetic controls (Alerstam *et al.*, 2003; Helm, 2006; Newton, 2008; Milner-Gulland *et al.*, 2011), the latter is more plastic (*ad hoc*); thus, regularity is even harder to be formed in it (Newton, 2008; but see also Biebach, 1983).

Either way, the basal diversification of raptors was predicted to have originated in Africa (Ericson, 2012; Nagy & Tökölyi, 2014), which implies that there was likely to have been independent and multiple evolution of long-distance migratory routes among different lineages. However, changes in migratory behaviour might also be a result of geographical

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processes as adaptation to various climatic challenges (Newton, 2003; Germi *et al.*, 2009; Seeland *et al.*, 2012; Polakowski *et al.*, 2014). Therefore, we may also expect essential differences among the West Palearctic-Afrotropic, East Palearctic-Indomalayan, and Nearctic-Neotropic migratory routes, based on bioclimatic considerations, as a result of a high degree of dissimilarity of these biogeographic realms and their different geological histories. For example, the East Asian migratory flyways are quite different from the migratory routes of Europe and Africa or the New World (Greenberg *et al.*, 2008; Germi *et al.*, 2009; Polakowski *et al.*, 2014) due to more gradual temporal changes of landscapes. However, the presence of a land bridge between North and South America and the Caribbean archipelago allows less hazardous migration than in the Old World, where migrants need to cross large areas of both desert and sea (Newton, 2008). However, the Mexican Plateau could serve as an important barrier, because many bird species from northern regions winter just north of it.

According to a recent survey, migration has been shown to have evolved at multiple times in accipitrid raptors and probably originated in tropical biogeographic realms, parallel to the range expansion of species towards northern latitudes (Nagy & Tökölyi, 2014). Previous studies have obtained similar results in a variety of avian groups (e.g. Joseph *et al.*, 1999; Outlaw *et al.*, 2003; Milá *et al.*, 2006). However, little is known about how ecological (e.g. climatic and life history) factors influenced the emergence of migration in birds, especially for birds of prey.

The evolution of birds of prey in different phylogenetic groups was studied previously (Thiollay, 1998; do Amaral *et al.*, 2009; Ericson, 2012). The diversification of migratory behaviour in each group might be a result of the isolation of lineages on different continents, which was induced by the ascension of taxa originated from Australia, South America, and Africa (Ericson, 2012). Although the migration ecology of accipitrid raptors was studied by previous researchers (see, e.g., Newton, 2008; Nagy & Tökölyi, 2014), migratory systems on different geographic scales require further research. Specifically, the role of climatic modulations in migratory patterns of raptors in different migratory systems is not yet fully understood, especially in a phylogenetic context. According to up-to-date and large-scale biogeographic studies, birds of prey (excluding falcons and New World vultures) are thought to be of African origin (Ericson, 2012). The diversification of diurnal raptors began approximately 40 million years ago, which was intensified during the Oligocene–Miocene epoch and continued until recent times (Nagy & Tökölyi, 2014). Similar patterns were detected in buteonine hawks

(do Amaral *et al.*, 2009) and in a wider range of avian families globally (Ericson *et al.*, 2006; Jetz *et al.*, 2012). Due to their life history and ecology, raptors were able to spread and consequently, have adapted to various environmental conditions. The ability to migrate may also have played a fundamental role in this success.

In some evolutionary processes, such as dimorphism in diurnal raptors, dietary specialization is a known life history attribute that may have resulted in significant effects on predator–prey interactions. For instance, a previous study concluded that polymorphic buteos consume more mammalian prey than monomorphic buteos (Roulin & Wink, 2004) although the inclusion of phylogenetically distinct falcons may have influenced the findings. In addition to distribution, dietary generalization and habitat affinity may have also played a fundamental role, as Nagy & Tökölyi (2014) found a correlation between migratoriness and these factors. We therefore predict that reliance on warm-blooded prey or carcasses is more important during wintering for nonmigratory species, whereas migratory taxa are characterized by dietary breadth, which provides the opportunity to find food during migration and on their wintering grounds: for instance, the evolution of a generalist diet is associated with migratory lineages (Nagy & Tökölyi, 2014). Meanwhile, diet may require different hunting strategies and consequently divergently adapted morphological structures, as Roulin & Wink (2004) found divergences in wing length between polymorphic and monomorphic raptors. We thus predict differences in migratory behaviour in relation to body size and wing–tail ratio, which are connected to resource partitioning and thus to niche segregation among coexisting raptors (Brown, 1976).

Our study aims to (1) test which ecological and life history traits show strong connectedness with the evolution of migration in a phylogenetic context in diurnal birds of prey, (2) explain how climatic factors are related to migratoriness – classified as migratory or nonmigratory – of each species, and (3) identify dissimilarities in these factors related to the three migratory systems. Many examples show that clutch sizes are larger in migratory species than in nonmigrants (see, e.g., Bruderer & Salewski, 2009; Jahn & Cueto, 2012; Barve & Mason, 2015; but see also Böhning-Gaese *et al.*, 2000). Because migration may be costly (Newton, 2008), mostly due to the higher mortality of the young, unexperienced individuals during the migratory journey (examples for raptors in Strandberg *et al.*, 2009; Klaassen *et al.*, 2014; Oppel *et al.*, 2015), we expect that it would be compensated by a definable shift in reproductive attempts as measured by clutch size.

MATERIALS AND METHODS

LIFE HISTORY TRAITS

We compiled an extensive database of the life history traits of 179 accipitrid birds of prey, including their migratory and hunting behaviours, body measurements, clutch sizes, and their distribution (Table 1). More specifically, migratory behaviour was divided into three classes (based on, e.g., Kondo & Omland, 2007; do Amaral *et al.*, 2009): (1) nonmigrant, (2) partial migrant (if part of the populations of a species is migratory), or (3) obligatory migrant (species with clearly distinguishable breeding and wintering areas). We merged Classes 2 and 3 as migratory for further analyses to balance the numbers of migratory and nonmigratory species.

We categorized diet (main prey types) into nine classes: (1) bird, (2) mammal, (3) reptile, (4) fish, (5) amphibian, (6) crustacean, (7) insect, (8) worm (invertebrate prey other than insects), and (9) carrion. Each type of prey was assigned a rank as calculated by the frequency of its consumption, whereas dietary breadth and reliance on warm-blooded prey (bird and mammal) or carcasses were calculated for both during and outside the breeding season (e.g. Roulin & Wink, 2004; Nagy & Tökölyi, 2014). For example, the Eastern Imperial Eagle (*Aquila heliaca*) feeds mostly on mammals, birds, reptiles, carrion, occasionally fish, and insects (Ferguson-Lees & Christie, 2001); thus, its dietary breadth amounts to six, calculated as the number of prey item groups. The mean dietary score of mammals, birds, and carrion was used to assess the degree of reliance on warm-blooded prey or carcasses.

Hunting behaviours were classified as hunting (1) in the air, (2) on the ground, or (3) by both ways. As flying skills highly depend on morphological parameters, we collected data on body size measurements (Table 1), in particular on the ratio of wing to tail,

which is a robust metric of aerodynamic performance, because body shape significantly affects the duration, length, or technique of flight during migration (Kerlinger, 1989; Bildstein, 2006; Newton, 2008; Polakowski *et al.*, 2014). We classified species into eight categories based on the direction of the deviation from the average length (in millimetres) of wing and tail: first category is assigned when (1) both wing and tail are shorter than average, (2) shorter wing and longer tail indicate a second category, (3) longer wing and longer tail delimit a third category, and (4) longer wing and shorter tail form a further category. These four categories have been identified for both small- and large-bodied species.

Habitat preferences were classified as forest or open habitat (grassland, savannah, and water surface), which defined a factor including these two categories. The role of types of food or habitat was emphasized by Thiollay (1998) who found that South Asian mainland and islands differ for raptors as indicated by both food and habitat specialization.

PHYLOGENETIC ANALYSES

We used the multivariate phylogenetic generalized least square approach applying Brownian motion fitting (nlme package in R; Pinheiro *et al.*, 2015) to identify which life history factors affect migratory behaviour. The phylogenetic tree published in Nagy & Tökölyi (2014; see Fig. S1 in Appendix S1) was used for our analyses using data for more than a hundred raptor species where information was available for all variables. Significant values of several pairwise models of a simple run (migratory behaviour as a dependent variable and one of the explanatory variables) form the base of a model selection (Bartoń, 2015). Model selection approach evaluates all models (all possible combination of variables) based on Akaike's information criterion (AIC). We considered

Table 1. Variables used for analyses (type of variables in parentheses)

Variable	Number of species	Sources
Migration (categorical)	179	Ferguson-Lees & Christie (2001)
Habitat (categorical)	179	Ferguson-Lees & Christie (2001)
Hunting strategy (categorical)	179	Ferguson-Lees & Christie (2001)
Clutch size (continuous)	154	Jetz <i>et al.</i> (2008)
Distribution (categorical)	179	BirdLife International (2015)
Diet (categorical, rank)	179	Ferguson-Lees & Christie (2001)
Diet breadth		Calculated for this study
Reliance on warm-blooded prey		
Proportion of wing/tail (continuous)	169	Ferguson-Lees & Christie (2001) The Birds of North America Online (2015) (Rodewald, 2015)
Body size dimorphism between sexes (categorical)	179	Calculated for this study

models with the smallest AIC value (delta AICc < 4). All analyses were performed in the R v3.2.2 statistical computing environment (R Development Core Team, 2015).

Although we found a very strong impact of distribution of species on migratory behaviour of raptors showing that only realms differ significantly in model selection (Table 2), we split our data set into three classes of migratory system: (1) species of North and South America ($N = 40$), (2) species of West Palearctic-Afrotropical ($N = 50$), and (3) species of East Palearctic-Indomalayan ($N = 33$). This approach allows the analysis of important factors potentially masked by their geographic distribution. Those few species that are presented in more than one migratory system (*Aquila clanga*, *Aquila nipalensis*, *Circaetus gallicus*, *Circus macrourus*, *Circus pygargus*, *Gypaetus barbatus*, *Hieraetus fasciatus*, and *Hieraetus pennatus* in two and *Buteo lagopus* and *Pandion haliaetus* in three) were included in all data sets.

BIOCLIMATIC VARIABLES AND MIGRATION

We downloaded bioclimatic variables of ten arc-minutes resolution from the WorldClim database (<http://www.worldclim.org/>, last accessed: 25.11.2015). The bioclimatic variables have been made for creating biologically more meaningful variables that indicate annual tendencies, seasonality, and limiting environmental factors. To avoid confounding the results, we calculated correlations between variables (Hijmans, 2015) where clusters were built based on Pearson's correlation coefficient. We used uncorrelated variables for implementing computer learning maximum entropy modelling (Maxent 3.3; Phillips & Dudík, 2008). Only variables resulting from separated branches were retained with a preference for longer time periods (quarters). As a result, we used temperature seasonality, mean temperature of driest quarter, mean temperature of warmest quarter, precipitation seasonality, and precipitation of driest quarter as

predictors. Coordinates were sampled from distribution shape files of migratory species. The appropriate number of sample points for a species was calculated by the percentage of 1000 random points based on the proportion of breeding distribution range of species divided by the largest breeding range. We replicated all runs five times by cross-validation and extended the projection for wintering and year-round areas of species where the latter is applicable.

RESULTS

PHYLOGENETIC ANALYSES

The models selected for North and South America and West Palearctic-Afrotropical regions are summarized in Table 3. The importance of significant variables amounted to 0.99 (clutch size, P -value < 0.001), 0.83 (hunting strategy, P -value < 0.01) for the former, and 1.00 (clutch size, P -value < 0.001), and 0.94 (hunting strategy, P -value < 0.001) for the latter migratory system. Parameter estimates for clutch size (0.42 and 0.46) were similar for both sets of data. The prefix of parameter estimate for hunting strategy was positive (0.42) for North and South America, whereas it was negative (−0.47) for West Palearctic-Afrotropic. Although reliance on warm-blooded prey or carcasses has a low importance value of 0.18 in the data set of North and South America, the related P -value of 0.03 was significant.

None of the variables was significant for the East Palearctic-Indomalayan regions when bioclimate (as categorical variable) was not included in the model selection procedure. However, when the output of bioclimatic analyses (see next section and Appendix S1) was applied in the analyses (Table 4), strongly supported differences were found for this migratory system. Specifically, clutch size had an importance of 0.97 (P -value < 0.001), and a highly significant (P -value < 0.001) difference was shown among bioclimatic variables associated with 1.00 importance.

Table 2. Variables in the first five models of model selection for the whole data set

No.	Variables	Degree of freedom (d.f.)	AIC	Delta	Weight
4	Distribution, continent*	20	−67.6	0.00	0.912
8	Distribution, continent, dimorphism	21	−60.7	6.90	0.029
12	Distribution, continent, habitat	21	−60.6	7.01	0.027
2	Continent	18	−59.4	8.16	0.015
36	Distribution, continent, diet breadth without breeding season	21	−57.4	10.14	0.006

Note: The highly supported model is indicated in **bold**.

* – Distribution equivalent to tropical/nontropical subdivision while continent reflect to geographical realms where a species breed. Importance for both variables was 1.00.

BIOCLIMATIC VARIABLES AND MIGRATION

We analysed bioclimatic data of 110 accipitrid birds of prey. Calculations from maximum entropy modelling based on the breeding distribution of migratory species allowed the prediction of the wintering ranges of species (see Figures in Appendix S1), where the current occurrence of these species is confirmed or highly probable. Regions where migratory species regularly winters are at least suitable for them as their breeding ranges (darker colours indicate increasing suitability).

Our results indicate that environmental variables of distribution areas related to temperature are the most important limiting factors for 12 of the 17 long-distance migratory accipitrid raptors (Table 5). The proportion of limiting variables related to temperature, on the one hand, and precipitation, on the other hand, is 70/40 among all of the species (see Table S1 in Appendix S1 for more details).

DISCUSSION

Although differences among migratory routes in distinct geographical regions have been detected previously (e.g. Newton, 2008), our study is the first to find

substantial dissimilarities in migratory behaviour in relation to life history traits and climatic conditions. We found that clutch sizes are larger in migratory species than in residents (Martin, 1995; Jahn & Cueto, 2012; Barve & Mason, 2015) in each of the three migratory routes, which may be related to the increase of clutch size as a compensation of higher mortality during migration (see the relationship between migration and mortality; e.g. Ketterson & Nolan, 1982; Rappole, Ramos & Winker, 1989; Bell, 1996; Alerstam *et al.*, 2003; Newton, 2008). For instance, Schmutz and Fyfe (1987) found that the majority of migratory ferruginous hawks (*Buteo regalis*) did not survive their first year, and the hazards of migration were emphasized in Klaassen *et al.* (2014) when they demonstrated that mortality during migration is six times higher than in other times of the year. Furthermore, Oppel *et al.* (2015) demonstrated convincing evidence for mortality during migration of Egyptian vultures (*Neophron percnopterus*), which implies actual conservation significance.

Furthermore, the success of raising young depends on hunting and feeding strategies as more successful hunters are expected to provide increased quantities of prey to feed the young. For example, McDonald *et al.* (2004) found that larger female brown falcons (*Falco*

Table 3. List of supported models (delta AICc < 4) as a result of model selection for the species of North and South America (A) and West Palearctic-Afrotropical (B)

A					
No.	Variables	Degree of freedom (d.f.)	AIC	Delta	Weight
6	Clutch size, hunting strategy	4	63.6	0.00	0.582
8	Clutch size, dimorphism, hunting strategy	5	66.0	2.39	0.176
12	Dimorphism, hunting strategy	5	66.7	3.18	0.119
B					
No.	Variables	Degree of freedom (d.f.)	AIC	Delta	Weight
6	Clutch size, hunting strategy	5	61.1	0.00	0.793
8	Clutch size, dimorphism, hunting strategy	6	65.0	3.92	0.112

Note: The highly supported model is indicated in **bold**.

Table 4. List of supported models (delta AICc < 4) as a result of model selection for the species of East Palearctic-Indomalayan

No.	Variables	Degree of freedom (d.f.)	AIC	Delta	Weight
4	Bioclimate, clutch size	6	69.3	0.00	0.455
8	Bioclimate, clutch size, dimorphism	7	70.1	0.84	0.300
20	Bioclimate, clutch size, reliance on warm-blooded prey or carcass without breeding season	7	72.8	3.49	0.080

Note: The highly supported model is indicated in **bold**.

Table 5. The most important variables of maximum entropy modelling for long-distant and semi-long-distant migratory species based on averaged values of maximum entropy modelling (importance (%) of variable in parentheses)

Species	Breeding distribution	Variable
<i>Accipiter gularis</i>	East Palearctic	Mean temperature of driest quarter (33.7)
<i>Accipiter soloensis</i>	East Palearctic	Mean temperature of driest quarter (25.4)
<i>Aquila clanga</i>	Trans-Palearctic	Precipitation seasonality (37.9)
<i>Aquila nipalensis</i>	Trans-Palearctic	Temperature seasonality (29.6)
<i>Aquila pomarina</i>	West Palearctic	Temperature seasonality (60.4)
<i>Butastur indicus</i>	East Palearctic	Mean temperature of driest quarter (36.7)
<i>Buteo lagopus</i>	Holarctic	Mean temperature of driest quarter (35.0)
<i>Buteo platypterus</i>	Nearctic	Mean temperature of warmest quarter (35.7)
<i>Buteo swainsoni</i>	Nearctic, Mexico	Precipitation seasonality (45.0)
<i>Circaetus gallicus</i>	Trans-Palearctic	Precipitation of driest quarter (32.9)
<i>Circus macrourus</i>	Palearctic (Steppic)	Precipitation of driest quarter (33.5)
<i>Circus pygargus</i>	Trans-Palearctic	Mean temperature of driest quarter (38.0)
<i>Elanoides forficatus</i>	Nearctic	Mean temperature of warmest quarter (30.4)
<i>Hieraaetus pennatus</i>	Trans-Palearctic	Mean temperature of driest quarter (44.2)
<i>Ictinia mississippiensis</i>	Nearctic	Precipitation seasonality (29.2)
<i>Pandion haliaetus</i>	Holarctic	Mean temperature of driest quarter (41.8)
<i>Pernis apivorus</i>	West Palearctic	Temperature seasonality (38.3)

berigora), as characterized by them having higher scores of wing–tail ratios, exhibited higher reproductive success. Thus, increased breeding performance may induce enhanced preference for migratory behaviours. Additionally, they are likely to be able to hunt more effectively during migration and on the wintering grounds under different climatic conditions to those experienced on their breeding grounds. Nevertheless, our findings support the idea that the uncertainty of seasonal climatic conditions during breeding may be related to the increased cost of raising young under unpredictable environmental conditions (Jetz & Rubenstein, 2011; Rice *et al.*, 2013; Thomson *et al.*, 2014; Rubenstein, 2015).

Our study highlighted the importance of the proportion of prey classes in predicting different hunting strategies for different distribution areas. Indeed, a number of previous studies have detected morphological adaptations to a wide variety of prey types (e.g. Rutz, Whittingham & Newton, 2006; Hertel *et al.*, 2014) among different groups of raptors (Fowler *et al.*, 2009; Sustaita & Hertel, 2010). For instance, the results of Otterbeck, Lindén & Roualet (2015) imply beneficial effects of prey specialization, as pairs of Eurasian Sparrowhawks (*Accipiter nisus*) were able to raise more young related to higher constancy in prey size, which indirectly indicates higher success in hunting behaviour [see also Pérez-Camacho *et al.* (2015) for a similar study on northern goshawks (*Accipiter gentilis*)].

Meanwhile, the shape of wings and tails of raptors differed among the three migratory routes, which highlight that hunting strategies are substantially

different for birds of prey in the New World than in West Palearctic and Africa (Ferguson-Lees & Christie, 2001). Indeed, hunting strategies have been linked to resource partitioning and to niche segregation among raptors with overlapping ranges (Brown, 1976; Gamauf *et al.*, 1998; Piana, 2013). Specifically, most wintering areas in Africa include mainly open lands such as savannahs, whereas the majority of South America is mostly forested landscapes. Therefore, a higher proportion of West Palearctic-African raptors are connected to open/semi-open landscape, whereas a larger proportion of the Nearctic-Neotropical migrants are confined to woody landscapes (e.g. *Buteo*, *Circus* spp.; see Figures in Appendix S1, BirdLife International, 2015). Such variation in vegetative structure may lead to differences in hunting strategies. Terraube, Guixé & Arroyo (2014) found that dietary specialization was related to higher hunting success in migratory Montagu's harriers (*C. pygargus*).

The results of maximum entropy modelling suggest high differences among migratory species (Figures in Appendix S1) and predictions of our models fit well to the breeding and wintering distributions of raptors. Specifically, conditions experienced on the wintering grounds are equally as suitable for migratory species to those conditions found on their breeding ranges. This partly explains why species overwinter in Africa, while others regularly migrate to South-East Asia.

This has a number of implications for raptor conservation with respect to climate change and to their breeding biology. However, climate change does not only emerge as monotonous warming or cooling, but also as the growing frequency of extreme weather

events, which is increasingly important for migratory species, especially in the timing of arrival to the breeding grounds or finding appropriate number and quality of prey (Fairhurst & Bechard, 2005). Therefore, we suggest the use of maximum entropy modelling to predict future environmental conditions on the breeding ranges of raptors to be able to provide improved species-specific conservation plans.

Significant results obtained for the data set of East Palearctic-Indomalayan species are highly supported by biogeographical considerations as breeding and wintering areas of East Palearctic-Indomalayan species are not separated by geographical and, hence, ecological barriers (Greenberg *et al.*, 2008; Gerami *et al.*, 2009; but see also Polakowski *et al.*, 2014). The apparent continuity of habitats equally allows the development of short- and long-distance migratory strategies, as predicted by the maximum entropy modelling. Conversely, breeding and wintering areas are geographically separated both in North and South-America and in West Palearctic and Africa. On the one hand, the Mexican Plateau, the Gulf of Mexico, and the Caribbean Sea form major barriers for migratory systems of the New World, whereas on the other hand, similar barriers constituted by the Mediterranean Sea and the Sahara emerge for Western Palearctic birds migrating to Africa. In a study of satellite-tracked raptors, Strandberg *et al.* (2009) summarized the difficulties of birds crossing the Sahara and showed a 50–60% mortality rate for first year birds that is largely similar to the findings of Schmutz & Fyfe (1987).

Furthermore, the only significant variable related to diet was reliance on warm-blooded prey or carcasses, which does not support our prediction on differences among consumed prey types between migratory and nonmigratory species because its importance was relatively low. Nevertheless, our findings are applicable on wider taxonomical scales, as the importance of hunting and reproductive strategies in modulating distribution ranges is predictable for migratory raptors. For example, similar distribution patterns and migratory behaviour emerge in insectivorous owls. European populations of common scops owls (*Otus scops*) migrate to Africa across the Sahara. In contrast, its related species, the oriental scops owl (*Otus sunia*) has continuous breeding and wintering areas in South-East Asia and adjacent archipelagos (König & Weick, 2008; BirdLife International, 2015).

In *Falconiformes*, the other diurnal group of raptors, vicariant and migratory species show remarkable geographical segregations. Although this order is phylogenetically not closely related to the species in our study (e.g. Ericson *et al.*, 2006; Jetz *et al.*, 2012; Burleigh, Kimball & Braun, 2015; Jarvis *et al.*, 2014; Prum *et al.*, 2015), it shows a high degree of ecological and morphological similarities. For instance, red-footed falcons

(*Falco vespertinus*) breed in the West Palearctic and winters in Africa, whereas amur falcons (*Falco amurensis*), their sister and vicariant species (Fuchs *et al.*, 2015), inhabits the East Palearctic and also winters in Africa (Ferguson-Lees & Christie, 2001; BirdLife International, 2015). This might be a result of parallel evolutionary histories of the two species because both are insectivorous and inhabit relatively open habitats. Besides, relationship among habitat, migration, and diversification rate of falcons is high, and further, it is remarkable that splits among falconid taxa are frequently younger than the estimated ancestral migratory behaviour (Fuchs *et al.*, 2015).

In summary, we conclude that (1) the dominant differences between the three migratory systems of diurnal birds of prey are related to the connectivity of breeding and wintering ranges, (2) bioclimatic conditions can emerge as limiting factors on varying levels in biogeographic regions that are considered to be homogenous, and finally (3) the importance of life history attributes in predicting distribution is enhanced by distances and discontinuities between breeding and wintering grounds.

ACKNOWLEDGEMENTS

We are grateful to two anonymous referees for their comments and suggestions and to Mark C. Mainwaring for useful comments on the manuscript. J. Nagy was supported by a grant (NTP-EFÖ-P-15-A-0495) of the Human Capacities Grant Management Office (EMET), an institution of the Hungarian Ministry of Human Capacities (EMMI).

REFERENCES

- Alerstam T, Hedenström A, Åkesson S. 2003. Long-distance migration: evolution and determinants. *Oikos* **103**: 247–260.
- do Amaral FR, Sheldon FH, Gamauf A, Haring E, Riesing M, Silveira LF, Wajntal A. 2009. Patterns and processes of diversification in a widespread and ecologically diverse avian group, the buteonine hawks (Aves, Accipitridae). *Molecular Phylogenetics and Evolution* **53**: 703–715.
- Bartoň K. 2015. *MuMIn: multi-model inference*. R package version 1.13.4. Available at: <http://CRAN.R-project.org/package=MuMIn>, last accessed: 13.03.2016.
- Barve S, Mason NA. 2015. Interspecific competition affects evolutionary links between cavity nesting, migration and clutch size in Old World flycatchers (Muscicapidae). *Ibis* **157**: 299–311.
- Bell CP. 1996. The relationship between geographic variation in clutch size and migration pattern in the yellow wagtail. *Bird Study* **43**: 333–341.
- Bell CP. 2000. Process in the evolution of bird migration and pattern in avian ecogeography. *Journal of Avian Biology* **31**: 258–265.

- Bell CP. 2005.** The origin and development of bird migration: comments on Rappole and Jones, and an alternative evolutionary model. *Ardea* **93**: 115–123.
- Biebach H. 1983.** Genetic determination of partial migration in the European robin (*Erithacus rubecula*). *The Auk* **100**: 601–606.
- Bildstein KL. 2006.** *Migrating raptors of the world: their ecology & conservation*. Ithaca: Cornell University Press.
- BirdLife International. 2015.** *IUCN Red List for birds*. Available at: <http://www.birdlife.org>, last accessed: 25.11.2015.
- Böhning-Gaese K, Halbe B, Lemoine N, Oberrath R. 2000.** Factors influencing the clutch size, number of broods and annual fecundity of North American and European land birds. *Evolutionary Ecology Research* **2**: 823–839.
- Brown L. 1976.** *Birds of prey: their biology and ecology*. New York: A&W Publishers.
- Bruderer B, Salewski V. 2008.** Evolution of bird migration in a biogeographical context. *Journal of Biogeography* **35**: 1951–1959.
- Bruderer B, Salewski V. 2009.** Lower annual fecundity in long-distance migrants than in less migratory birds of temperate Europe. *Journal of Ornithology* **150**: 281–286.
- Burleigh JG, Kimball RT, Braun EL. 2015.** Building the avian tree of life using a large-scale, sparse supermatrix. *Molecular Phylogenetics and Evolution* **84**: 53–63.
- Cox GW. 1985.** The evolution of avian migration systems between temperate and tropical regions of the New World. *The American Naturalist* **126**: 451–474.
- Ericson PG, Anderson CL, Britton T, Elzanowski A, Johansson US, Källersjö M, Ohlson JI, Parsons TJ, Zuccon D, Mayr G. 2006.** Diversification of Neoaves: integration of molecular sequence data and fossils. *Biology Letters* **2**: 543–547.
- Ericson PGP. 2012.** Evolution of terrestrial birds in three continents: biogeography and parallel radiations. *Journal of Biogeography* **39**: 813–824.
- Fairhurst GD, Bechard MJ. 2005.** Relationship between winter and spring weather and northern goshawk (*Accipiter gentilis*) reproduction in Northern Nevada. *Journal of Raptor Research* **39**: 229–236.
- Ferguson-Lees J, Christie DA. 2001.** *Raptors of the World*. Boston: Houghton Mifflin Company.
- Fowler DW, Freedman EA, Scannella JB. 2009.** Predatory functional morphology in raptors: interdigital variation in talon size is related to prey restraint and immobilisation technique. *PLoS One* **4**: e7999.
- Fuchs J, Johnson JA, Mindell DP. 2015.** Rapid diversification of falcons (Aves: Falconidae) due to expansion of open habitats in the Late Miocene. *Molecular Phylogenetics and Evolution* **82**(Pt A): 166–182.
- Gamauf A, Preleuthner M, Winkler H. 1998.** Philippine birds of prey: interrelations among habitat, morphology, and behaviour. *The Auk* **115**: 773–726.
- Germi F, Young GS, Salim A, Pangimangen W, Schellekens M. 2009.** Over-ocean raptor migration in a monsoon regime: spring and autumn 2007 on Sangihe, North Sulawesi, Indonesia. *Forktail* **25**: 104–116.
- Greenberg R, Kozlenko A, Etterson M, Dietsch T. 2008.** Patterns of density, diversity, and the distribution of migratory strategies in the Russian boreal forest avifauna. *Journal of Biogeography* **35**: 2049–2060.
- Helm B. 2006.** Zugunruhe of migratory and non-migratory birds in a circannual context. *Journal of Avian Biology* **37**: 533–540.
- Hertel F, Maldonado JE, Sustaita D. 2014.** Wing and hindlimb myology of vultures and raptors (Accipitriformes) in relation to locomotion and foraging. *Acta Zoologica* **96**: 283–295.
- Hijmans RJ. 2015.** raster: geographic data analysis and modeling. *R package version 2.4–15*. Available at: <http://CRAN.R-project.org/package=raster>, last accessed: 13.03.2016.
- Jahn AE, Cueto VR. 2012.** The potential for comparative research across New World bird migration systems. *Journal of Ornithology* **153**: 199–205.
- Jarvis ED, Mirarab S, Aberer AJ, Li B, et al. 2014.** Whole-genome analyses resolve early branches in the tree of life of modern birds. *Science* **346**: 1320–1331.
- Jetz W, Rubenstein DR. 2011.** Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Current Biology* **21**: 72–78.
- Jetz W, Sekercioglu CH, Böhning-Gaese K. 2008.** The worldwide variation in avian clutch size across species and space. *PLoS Biology* **6**: 2650–2657.
- Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012.** The global diversity of birds in space and time. *Nature* **491**: 444–448.
- Joseph L, Lessa EP, Christidis L. 1999.** Phylogeny and biogeography in the evolution of migration: shorebirds of the Charadrius complex. *Journal of Biogeography* **26**: 329–342.
- Kerlinger P. 1989.** *Flight strategies of migrating hawks*. Chicago: Chicago University Press.
- Ketterson ED, Nolan V. 1982.** The role of migration and winter mortality in the life history of a temperate-zone migrant, the dark-eyed junco, as determined from demographic analyses of winter populations. *The Auk* **99**: 243–259.
- Klaassen RH, Hake M, Strandberg R, Koks BJ, Trierweiler C, Exo KM, Bairlein F, Alerstam T. 2014.** When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. *The Journal of Animal Ecology* **83**: 176–184.
- Kondo B, Omland KE. 2007.** Ancestral state reconstruction of migration: multistate analysis reveals rapid changes in New World orioles (*Icterus* spp.). *The Auk* **124**: 410–419.
- König C, Weick F. 2008.** *Owls of the world*. London: Christopher Helm Publishers.
- Martin TE. 1995.** Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* **65**: 101–127.
- McDonald PG, Olsen PD, Cockburn A. 2004.** Selection on body size in a raptor with pronounced reversed sexual size dimorphism: are bigger females better? *Behavioral Ecology* **16**: 48–56.
- Milá B, Smith TB, Wayne RK. 2006.** Postglacial population expansion drives the evolution of long-distance migration in a songbird. *Evolution* **60**: 2403–2409.

- Milner-Gulland EJ, Fryxell JM, Sinclair ARE. 2011.** *Animal migration: a synthesis*. Oxford University Press, Oxford.
- Nagy J, Tökölyi J. 2014.** Phylogeny, historical biogeography and the evolution of migration in accipitrid birds of prey (Aves: Accipitriformes). *Ornis Hungarica* **22**: 15–35.
- Newton I. 2003.** *The speciation and biogeography of birds*. London: Academic Press.
- Newton I. 2008.** *The migration ecology of birds*. London: Academic Press.
- Oppel S, Dobrev V, Arkumarev V, Saravia V, Bounas A, Kret E, Veleviski M, Stoychev S, Nikolov SC. 2015.** High juvenile mortality during migration in a declining population of a long-distance migratory raptor. *Ibis* **157**: 545–557.
- Otterbeck A, Lindén A, Roualet É. 2015.** Advantage of specialism: reproductive output is related to prey choice in a small raptor. *Oecologia* **179**: 129–137.
- Outlaw DC, Voelker G, Milá B, Girman DJ. 2003.** Evolution of long-distance migration in and historical biogeography of Catharus thrushes: a molecular phylogenetic approach. *The Auk* **120**: 299–310.
- Pérez-Camacho L, García-Salgado G, Rebollo S, Martínez-Hestekamp S, Fernández-Pereira JM. 2015.** Higher reproductive success of small males and greater recruitment of large females may explain strong reversed sexual dimorphism (RSD) in the northern goshawk. *Oecologia* **177**: 379–387.
- Phillips SJ, Dudík M. 2008.** Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* **31**: 161–175.
- Piana RP. 2013.** *Ecology and conservation of a diurnal raptor community within a protected area in northwestern Peru*. PhD thesis, Manchester Metropolitan University.
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Development Core Team. 2015.** *nlme: linear and nonlinear mixed effects models. R package version 3.1–121*. Available at: <http://CRAN.R-project.org/package=nlme>. last accessed: 13.03.2016
- Polakowski M, Jankowiak L, Kasprzykowski Z, Bela G, Kosmicki A, Janczyszyn A, Niemczyk A, Kilon D. 2014.** Autumn migratory movements of raptors along the southern Baltic coast. *Ornis Fennica* **91**: 39–47.
- Prum RO, Berv JS, Dornburg A, Field DJ, Townsend JP, Lemmon EM, Lemmon AR. 2015.** A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature* **526**: 569–573.
- Rappole JH, Jones P. 2002.** Evolution of Old and New World migration systems. *Ardea* **90**: 525–537.
- Rappole JH, Ramos MA, Winker K. 1989.** Wintering wood thrush movements and mortality in Southern Veracruz. *The Auk* **106**: 402–410.
- R Development Core Team. 2015.** *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Available at: <http://www.R-project.org/>. last accessed: 25.11.2015
- Rice AM, Vallin N, Kulma K, Arntsen H, Husby A, Tobler M, Qvarnström A. 2013.** Optimizing the trade-off between offspring number and quality in unpredictable environments: testing the role of differential androgen transfer to collared flycatcher eggs. *Hormones and Behavior* **63**: 813–822.
- Rodewald P. 2015.** *The birds of North America*. Ithaca, NY: Cornell Laboratory of Ornithology Available at: <http://birds.cornell.edu/BNA/>. last accessed: 25.11.2015
- Roulin A, Wink M. 2004.** Predator-prey relationships and the evolution of colour polymorphism: a comparative analysis in diurnal raptors. *Biological Journal of the Linnean Society* **81**: 565–578.
- Rubenstein DR. 2015.** Superb starlings: cooperation and conflict in an unpredictable environment. In: Koenig WD, Dickinson JL, eds, *Cooperative breeding in vertebrates: studies of ecology, evolution, and behavior*. Cambridge: Cambridge University Press, 181–196.
- Rutz C, Whittingham MJ, Newton I. 2006.** Age-dependent diet choice in an avian top predator. *Proceedings of the Royal Society of London B* **273**: 579–586.
- Salewski V, Bruderer B. 2007.** The evolution of bird migration – a synthesis. *Die Naturwissenschaften* **94**: 268–279.
- Schmutz JK, Fyfe RW. 1987.** Migration and mortality of Alberta ferruginous hawks. *The Condor* **89**: 169–174.
- Seeland HM, Niemi GJ, Regal RR, Peterson A, Lapin C. 2012.** Determination of raptor migratory patterns over a large landscape. *Journal of Raptor Research* **46**: 283–295.
- Strandberg R, Klaassen RHG, Hake M, Alerstam T. 2009.** How hazardous is the Sahara Desert crossing for migratory birds? Indications from satellite tracking of raptors. *Biology Letters*. <http://rsbl.royalsocietypublishing.org/content/early/2009/11/25/rsbl.2009.0785.short>
- Sustaita D, Hertel F. 2010.** In vivo bite and grip forces, morphology and prey-killing behavior of North American accipiters (Accipitridae) and falcons (Falconidae). *The Journal of Experimental Biology* **213**: 2617–2628.
- Terraube J, Guixé D, Arroyo B. 2014.** Diet composition and foraging success in generalist predators: are specialist individuals better foragers? *Basic and Applied Ecology* **15**: 616–624.
- Thiollay J. 1998.** Distribution patterns and insular biogeography of South Asian raptor communities. *Journal of Biogeography* **25**: 57–72.
- Thomson RL, Griesser M, Laaksonen T, Korpimäki E. 2014.** Brood size manipulations in a spatially and temporally varying environment: male Tengmalm's owls pass increased reproductive costs to offspring. *Oecologia* **176**: 423–430.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:
Appendix S1. Detailed summary of the maximum entropy modelling for 110 raptor species.