

The possible occurrence of cranial asymmetry in three harrier (Accipitridae: *Circus*) species

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Received: May 21, 2021 – Revised: June 02, 2021 – Accepted: June 03, 2021



Pecsics, T., Marx, A. & Csörgő, T. 2021. The possible occurrence of cranial asymmetry in three harrier (Accipitridae: *Circus*) species. – Ornis Hungarica 29(1): 139–148. DOI: 10.2478/orhu-2021-0011

Abstract The harriers (Accipitridae: *Circus*) represent a unique group of raptorial birds due to their hunting behaviour and their facial ruff and prominent facial disc. During previous studies it was suggested that harrier species may have other convergent features shared with owls like asymmetric or enlarged ear openings related to sensitive hearing capabilities. In this study, cranial asymmetry was done using SAGE (Symmetry and Asymmetry of Geometric Data) software. 32 skulls of 3 species (Western Marsh Harrier (*Circus aeruginosus*) n=8, Montagu's Harrier (*Circus pygargus*) n=10, Hen Harrier (*Circus cyaneus*) n=14) were photographed, digitized and assigned with 2D landmarks with TpsDig software. The variables were analysed based on Generalized Procrustes analysis. The morphometric data showed cranial asymmetry of harriers. This asymmetry should rather be explained by foraging strategies as the results are corresponding to the exceptionally good hearing of these species among diurnal raptors.

Keywords: cranial morphology, morphometrics, anatomy, skull, shape, convergent evolution, harrier, auditory system

Összefoglalás A rétihéják (Accipitridae: *Circus*) egyedi képviselői a ragadozó madaraknak, köszönhetően sajátos vadászati technikájuknak és megjelenésüknek, a tollak által alkotott gallérral és arcfátyollal. A korábbi kutatások során felvetődött, hogy utóbbiakon kívül más konvergens tulajdonságokon is osztozhatnak a baglyokkal, mint amilyen az aszimmetrikus vagy megnagyobbodott fülnyílás, amely érzékeny hallásukra utal. Jelen tanulmányban a koponya aszimmetria vizsgálatát a SAGE (Symmetry and Asymmetry of Geometric Data) szoftver segítségével végeztük. Összesen 3 faj 32 koponyájának (barna rétihéja – *Circus aeruginosus*, n=8, hamvas rétihéja – *Circus pygargus*, n=10, kékes rétihéja – *Circus cyaneus*, n=14) fényképét digitalizálva, kétdimenziós landmarkokkal láttuk el azokat a TpsDig programban. A változókat Prokrusztész analízis segítségével vizsgáltuk, ahol a morfológiai adatok aszimmetriát mutattak a rétihéja koponyákon. Ez az aszimmetria a táplálkozásmóddal és viselkedéssel köthető össze és megerősíti azt a megállapítást, miszerint nappali ragadozókhöz mérten ezek a madarak kifinomult hallással rendelkeznek.

Kulcsszavak: koponyasajátosságok, morfometria, anatómia, koponya, alak, konvergens evolúció, rétihéja, táplálékpreferencia, auditív érzékelés

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Introduction

The harriers (Accipitridae: *Circus*) represent a unique group of raptorial birds due to their particular hunting behaviour (Redpath 1992), low, quartering flight, exceptionally light wing loading, their mating pattern of polygyny. In their external appearance, harriers are one of the most easily recognisable Accipitrinae raptors due to their external features such as facial ruff and prominent facial disc (Simmons 2000). Harriers have traditionally been placed within the subfamily Circinae (Peters 1931), but recent molecular studies have revealed that harriers are more closely related to *Accipiter* (Nagy & Tökölyi 2014, Oatley *et al.* 2015). The feeding strategies are highly diverse and the morphological adaptations for feeding are a notable feature of avian evolution (Zusi 1993, Zweers *et al.* 1994). As in many other avian groups, food supply is one of the main factors influencing the ecology of raptors. Population densities of raptors are often limited by food supply (Newton 1980, Franklin *et al.* 2000), which also influences the number of specialist hunters being more likely to fluctuate annually when dependent on a fluctuating food source (Hamerstrom 1969, Korpimäki & Norrdahl 1991, Butet & Leroux 1993).

Previously, the adaptive significance of the anatomical and behavioural convergence between the harriers and some owl species was examined (Clark *et al.* 2020). Anatomically, both groups evolved a sound collecting facial ruff, a curved structure of skin and feathers surrounding the ears, and forage very close to the ground, harriers are very vocal birds while gliding over the hunting area (Rice 1980). The harriers circle an area several times listening and looking for prey, as they have exceptionally good hearing among diurnal raptors. It suggests that these species have a highly developed auditory system. The ears are covered by the feathers of the facial disc (Rice 1982). Some owl species also have a pronounced facial disc, guiding sounds into the ear openings. In owls, the beak is pointed downward, increasing the surface area over which the soundwaves are collected by the facial disc (Nishikawa 2002). Many owl species are remarkable for the bilateral asymmetry of the ears which attributes support a highly developed sense of directional hearing (Coles & Guppy 1988, Pecsics *et al.* 2018). However, the differences are represented by different tissues of the head (feathers, earflaps, ear holes, etc.), ear asymmetry basically caused by cranial structures only, due to the different positions and orientations of the *squamoso-occipital* wings. Ear morphology is different in structure and geometry between species (Norberg 1978). The symmetrical ears are representing a most basal form and cranial structure (Nishikawa 2002).

Bilateral symmetry is a subject of widespread interest, and structures with such symmetry are particularly considered when these consist of two mirror copies on opposite sides of the body (Klingenberg *et al.* 2002). Bilateral symmetry analysis focuses on identifying and measuring the location and extent of symmetry departures in structures, like in the context of matching symmetry, where the two mirror images are considered separated parts of the structure (Torcida *et al.* 2016).

Ear adaptations are a well-known feature of owl evolution. Also there are some documented size and shape asymmetries in birds (Norberg 1978, Aparicio & Bonal 2002, Güntürkün *et al.* 2000, Parés-Casanova & Salas-Bosch 2020). It was suggested that harrier species may have

asymmetric or enlarged ear openings for accurately pinpointing sound (Van Grouw 2012), but our knowledge is still limited regarding the degree and the direction of these skeletal asymmetries.

In this preliminary study, we investigated the cranial diversity among three harrier species. Our objective was to increase our knowledge in the relationship between skull shape and the possible asymmetric skeletal features. For this reason, we investigated shape asymmetries related to hearing capabilities.

Materials and Methods

Specimens

This study is based on 32 skulls of 3 species: Western Marsh Harrier (*Circus aeruginosus*) n=8, Montagu's Harrier (*Circus pygargus*) n=10, Hen Harrier (*Circus cyaneus*) n=14. All skulls are from adult specimens belonging to the collection of Eötvös Loránd University (Budapest, Hungary), the collection of the Hungarian Natural History Museum (Budapest, Hungary), Mátra Museum (Gyöngyös, Hungary) and the digital archives of Natural Sciences Museum of Barcelona (Barcelona, Spain). No bird has been killed to obtain its skull; all birds died either of natural causes, whether accidental death or whether death in captivity.

Landmarks and procedures

The variation of cranial morphology was analysed using landmark-based geometric morphometry. In this study, we tried to find landmarks for this analysis to cover the geometric form of the *regio oticalis*. Ideal landmarks are discrete and noticeable anatomical features that do not alter their topological positions, providing adequate coverage of the morphology (Zelditch *et al.* 2004). The landmarks were taken from high resolution (1200×1600 pixels) photos. We took 3 photographs from each specimen

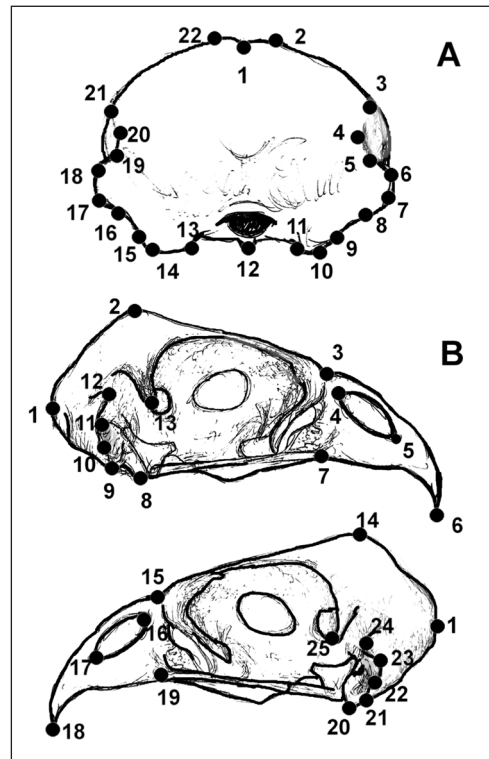


Figure 1. Position and number of landmarks. A: fixed landmarks in caudal view, B: fixed landmarks in lateral (left-right) view (numbers correspond to Table 1)

1. ábra A vizsgálatban használt landmarkok száma és pozíciója. A: fix landmarkok hátulnézetből, B: fix landmarkok oldalnézetből (bal-jobb) (a számok megnevezését lásd a 1. táblázatban)

(caudal, lateral – right and left). Images were standardised for the *foramen magnum occipitale* and the tip of the mandible. Testing for fluctuating asymmetry, three measurements were taken (replicates) per individual. For each specimen, 22 fixed landmarks were recorded in caudal view and 25 fixed landmarks in lateral view (right and left) (Figure 1) (Table 1). The coordinates of the landmarks were digitised using TpsDig 2.16 software (Rohlf 2010) and were transformed using the Procrustes superimposition method. We used Mann-Whitney U two-tailed test for comparing the sides. To detect the components of variances

Table 1. Number and description of landmarks in caudal (A) and lateral (B) view (terminology according to Baumel 1993, Sun *et al.* 2018)

1. táblázat Az egyes landmarkok száma és leírása, hátulnézetben (A) és oldalnézetben (B) (terminológia Baumel 1993 és Sun *et al.* 2018 alapján)

A) Number of landmark	Description of landmark
1	mid section of the <i>neurocranium</i>
2, 22	highest point of the <i>neurocranium</i>
3, 21	top of curvature at the <i>superior</i> end of the <i>M. add. mandibular externus</i> scar
4, 20	top of curvature at the <i>caudal</i> end of the <i>M. add. mandibular externus</i> scar
5, 19	top of curvature at the <i>inferior</i> end of the <i>M. add. mandibular externus</i> scar
6, 18	highest edge of the temporal wing
7, 17	top of curvature at the <i>superior</i> end of the temporal wing
8, 16	top of curvature at the <i>caudal</i> end of the temporal wing
9, 15	top of curvature at <i>inferior</i> end of the temporal wing
10, 14	lowest edge of the temporal wing
11, 13	most inner edge of the temporal wing at the inferior end
12	lowest point of <i>condylus occipitalis</i>

B) Number of landmark	Description of landmark
1	<i>prominentia cerebellaris</i>
2, 14	highest point of the <i>neurocranium</i>
3, 15	mid-point of the <i>cranio-facial</i> hinge
4, 16	top of curvature at the <i>caudal</i> end of the external nares
5, 17	top of curvature at the <i>rostral</i> end of the external nares
6, 18	tip of the beak
7, 19	articulation point of jugal bar and <i>maxilla</i>
8, 20	the <i>processus</i> of the <i>opisthotic</i>
9, 21	lowest edge of the temporal wing
10, 22	top of curvature at the <i>inferior</i> end of the temporal wing
11, 23	top of curvature at the <i>superior</i> end of the temporal wing
12, 24	highest edge of the temporal wing
13, 25	<i>processus postorbitalis</i>

and deviations, Procrustes ANOVA was used (Klingenberg *et al.* 1998, Marquez 2006). Consensus configurations and relative warps were conducted. Variability in shape was assessed using the scores obtained for each individual on the first two relative warps. Cranial asymmetry was estimated using SAGE (Symmetry and Asymmetry of Geometric Data) software (Marquez 2006). We conducted principal component analyses (PCA) on these morphological variables in caudal view. The relative warps are corresponding to the principal components (PCs) and define the shape space in which individuals are replaced. We used PAST v.1.7 software (Hammer *et al.* 2001) for principal component analysis and to extract deformation grids. We only considered those PCs which are explaining >10% of the variance.

Results

Mann-Whitney U two-tailed test showed significant differences between the two sides of the skull regarding the temporal region ($U=838.5$; $z=-8.22$, $P<0.001$ at the significance level 0.01).

Procrustes ANOVAs revealed that directional asymmetry was greater than fluctuating asymmetry (Table 2) reflecting the coordinates in caudal and lateral view.

During the second analysis, we used 22 fixed landmarks recorded in caudal view. The first two PCs explained 38%, and 22% of the variance in shape. The first PC described the variation in shape, the second the relative orientation of the temporal wing which showed that *Circus* species differ considerably in their degree of asymmetry (Figure 2). The Western Marsh Harrier showed less cranial asymmetry than the other two species, Montagu's Harrier was in intermediate position in the analysis and Hen Harrier showed the most asymmetric scores (Figure 3).

Table 2. Results of ANOVA for the registered coordinates in caudal (above) and lateral view (bottom), with the effect of "side" (directional asymmetry) and "side*individual" effect (fluctuating asymmetry)

2. táblázat Az ANOVA eredményei a regisztrált koordináták tekintetében hátulnézetben (fent) és oldalnézetben (alul), az "oldal" (direkcionális aszimmetria) és az "oldal*egyed" (fluktuáló aszimmetria) hatásával

effect / hatás	SS	MS	df	F	p
individual / egyed	0.0566	0.0004	160	4.6948	0.001
side / oldal	0.0045	0.0002	20	2.9694	0.001
side*individual / oldal*egyed	0.0121	0.0001	160	16.7492	0.001
error / hiba	0.0032	0.0002	720		

effect / hatás	SS	MS	df	F	p
individual / egyed	0.0646	0.0004	184	4.7844	0.0001
side / oldal	0.0073	0.0003	23	4.346	0.0001
side*individual / oldal*egyed	0.0135	0.0001	184	93.4848	0.001
error / hiba	0.0006	0.0001	828		

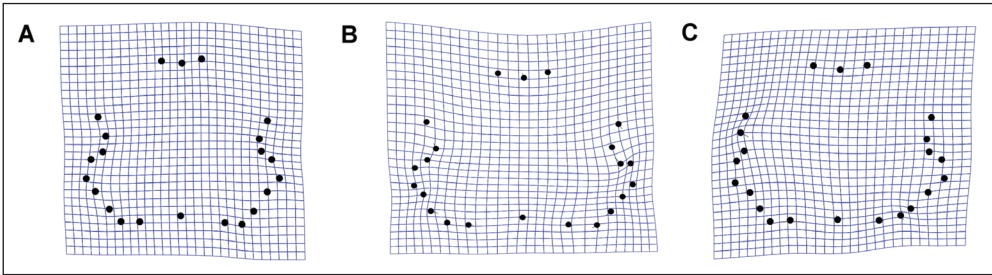


Figure 2. Various harrier species differ considerably in their degree of asymmetry (in caudal view). A: Western Marsh Harrier (*Circus aeruginosus*), B: Montagu's Harrier (*Circus pygargus*), C: Hen Harrier (*Circus cyaneus*)

2. ábra Az egyes rétihéja fajok különböznek az aszimmetria mértékében (hátnézetben). A: barna rétihéja (*Circus aeruginosus*), B: hamvas rétihéja (*Circus pygargus*), C: kékes rétihéja (*Circus cyaneus*)

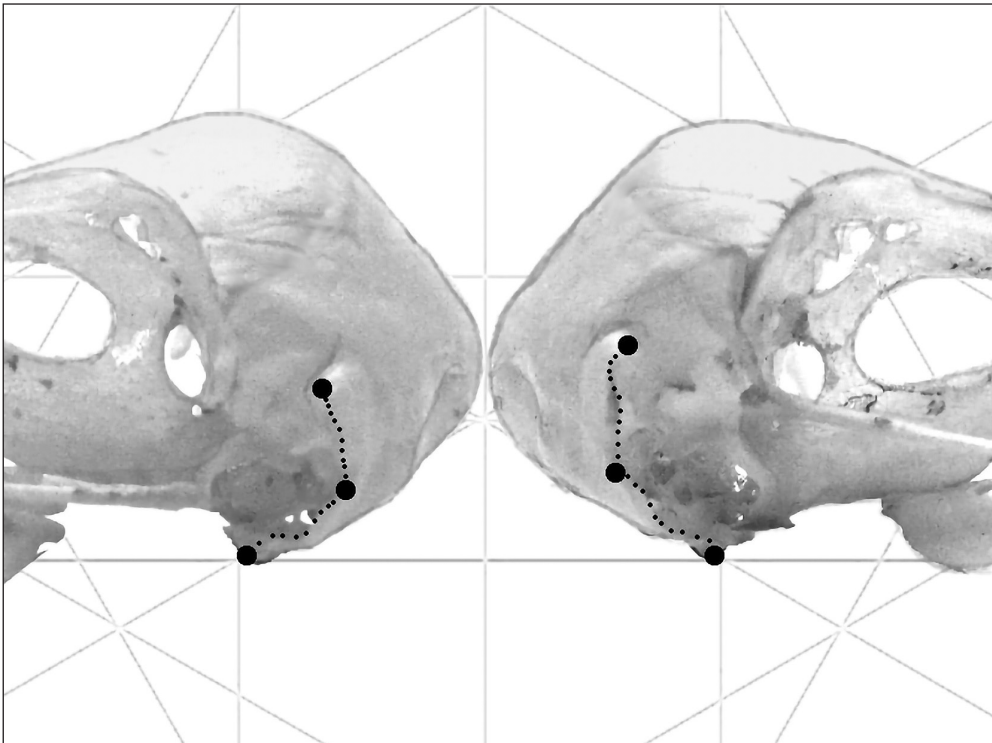


Figure 3. Differences in position and shape of left and right tympanic wings on the skull of a Hen Harrier (*Circus cyaneus*) specimen

3. ábra A kékes rétihéja (*Circus cyaneus*) egy példányának koponyáján lévő különbségek a bal és jobb oldali halántékcsontról *tympanicus* nyúlványainak helyzetében és alakjában

Discussion

We found that the influence of directional asymmetry was greater than fluctuating asymmetry which suggests that these asymmetrical features probably evolved to support directional hearing and sound localization. In lateral and caudal view, there are differences in the size and orientation of the temporal wing between the species. However, the anatomical similarities between harriers can be explained by their slightly different foraging methods and hunting behaviour.

Comparisons between sympatric raptor species with similar ecological needs and preferences but different body size and social behaviour are helpful in assessing the influence of energy needs or dominance on foraging strategies and food partitioning (Fedriani *et al.* 2000, Buij *et al.* 2011). The Montagu's Harrier and the Hen Harrier are breeding and foraging sympatrically in many areas. The diet of these species is very similar (Millon *et al.* 2002). The species differ in size, Hen Harrier being larger and also there are differences in their breeding system (Cramp 1980). Food partitioning by size between species that differ in food requirements is expected and has been observed in other species too (Gerstell & Bednarz 1999). Accordingly, within the large spectrum of prey types indicated that Hen Harriers preyed more frequently on larger prey and Montagu's Harriers on smaller prey (including more insects). This kind of segregation was observed in the main prey (small lagomorphs and rodents), and in the sizes of the most important alternative prey (Garcia & Arroyo 2002, Arroyo & Garcia 2006, Arroyo 2008).

The competition between Western Marsh and Hen Harriers for hunting space in the same area was also observed, i.e. Western Marsh Harriers hunted mainly over the marsh (Buij 2012, Tornberg & Haapala 2013) resulting in niche separation between the two species. Western Marsh Harrier has proportionately shorter wings and tail, its flight is slower and less manoeuvrable compared to Hen Harrier. Western Marsh Harrier has longer tarsi which should be an adaptation to reach deep into tall marsh vegetation preferred to hunt, maybe because this gave it more opportunity for surprise during hunting (Clarke *et al.* 1993, Cardador *et al.* 2012).

Differences in foraging efficiency between generalist and specialist species could be explained by neural limitations. This means that generalists need learning to be able to narrow their resource choices (Bernays *et al.* 2004). Specialization may be also associated with morphological or behavioural adaptations to handle certain resources. Harriers are diurnal raptors but evolved a parabolic collar of feathers surrounding the eyes, suggesting that hearing is enhanced to locate small mammal prey hiding in dense vegetation (Rice 1982, Redpath 1992, Simmons 2000). The facial disc is more pronounced in those harrier species which are feeding on mainly small rodent prey like the Pallid Harrier (*Circus macrourus*) (Buij 2012). The facial disc encircling the ears and meeting below the beak, in contrast, the facial disc of the Montagu's Harrier is confined to an arc just behind the ear openings, suggesting its hearing capacities might be less well developed than that of the rodent specialist species (Clarke *et al.* 2008, Terraube *et al.* 2011). This is also in accordance with our results. The Western Marsh Harrier is a great opportunist with lack of specialization (which means very wide range of prey, varying with local availability)

showed less asymmetrical features. The Montagu's Harrier is feeding on small ground birds, small mammals, reptiles and large insects (Thiollay 1994) but the Hen Harrier (which preys on mostly small rodents, like voles, mice, cotton rats, ground squirrels) (Garcia & Arroyo 2004) showed greater asymmetries in temporal region than the other two species. It suggests that feeding mainly on small rodents requires more sensitive auditory capabilities to detect the movement of the prey item. It is also possible that the relative size of the facial disc is in relationship with asymmetrical cranial structures, which also connected with hearing and auditory capabilities in owls (Norberg 2002). In the case of Hen Harrier some kind of nocturnal behaviour (Russell 1991) may have also effect on this feature.

Our results show relationships between cranial asymmetry and hunting behaviour but also highlight the morphological complexity and diversity of raptor skulls. Future studies should rather examine the possible interspecific and intersexual differences that may have effect on the cranial morphology and asymmetry of these birds. With a larger sample size (including more harrier species) and using parameters of soft tissues of the ear and temporal region will create a more complex vision regarding the evolution of asymmetrical features which are supporting directional hearing. New investigations reflecting on cranial asymmetries may increase our knowledge to understand how these special features are functioning in living specimens.

Acknowledgements

We are grateful to Gergely Babocsay, Miklós Laczi, Tamás Kondor, Martin Segesdi and Péter Urtz for the technical assistance. The text was supervised by Bridgette Dennett, Emese Bodor and Jenő Nagy.

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