Postcranial skeletal pneumaticity in non-aquatic neoavians: Insights from accipitrimorphae

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Abstract

Postcranial skeletal pneumaticity, air-filled bones of the trunk and limbs, is exclusive to birds among extant tetrapods and exhibits significant variation in its expression among different species. Such variation is not random but exhibits relationships with both body mass and locomotor specializations. Most species-level comparative research to date has focused on aquatic-oriented taxa (e.g., Anseriformes). The lack of data from non-aquatic birds constrains our ability to characterize global (i.e., avian-wide) patterns of this trait complex. To address this gap, the study conducted herein quantified postcranial pneumaticity in Accipitrimorphae, a mostly terrestrial clade composed of species that span a range of body sizes and exhibit diverse flight/foraging behaviors. All examined species (n = 88) invariably pneumatized the postaxial through precaudal vertebrae, sternum, coracoid, humerus, vertebral and sternal ribs, and pelvic girdle, a pattern herein referred to as the accipitrimorph baseline. Of the 88 sampled species, 41 expanded upon this pattern, whereas 10 species exhibited a reduction. No species deviated from the accipitrimorph baseline by more than two anatomical regions. A phylogenetically-informed regression analysis failed to identify a significant relationship between body mass and pneumaticity. However, specific pneumaticity phenotypes deviating from the baseline were correlated with aspects of wing morphology, tail length, and home range size. Results from this and previous studies provide clarity on two hypotheses: (1) aquatic taxa display distinct pneumaticity expression patterns relative to non-aquatic birds, notably with reductions in the proportion of the skeleton filled with air in diving specialists and (2) contemporary comparative studies, including the one herein, that explicitly account for phylogenetic relationships consistently fail to support the oft-cited positive relationship between pneumaticity and body mass. Instead, historical relationships and functional/ecological attributes (e.g., diving, specialized flight behaviors) appear to be the primary drivers underlying patterns of variation in this trait complex.

KEYWORDS
Accipitrimorphae, bird, pneumaticity, skeleton
1 | INTRODUCTION

Modern birds possess several extraordinary skeletal modifications (e.g., tooth and bone reduction or loss), but one wholly unique among extant tetrapods is postcranial skeletal pneumaticity. Postcranial skeletal pneumaticity is a condition in which extensions from the respiratory system (lungs and air sacs) called pneumatic diverticula enter bones and replace marrow and other internal bone tissues (e.g., inner cortical bone) with a thin lining of epithelium and air (O’Connor, 2006). This trait has an extensive evolutionary history, with the first inferred occurrence roughly 200 million years ago among nonavian dinosaurs (Wedel, 2006). Three now extinct groups (non-avian theropods, sauropodomorphs, and pterosaurs) exhibit robust osteological correlates associated with postcranial skeletal pneumaticity (Butler et al., 2009, 2012; O’Connor, 2006; O’Connor & Claessens, 2005; Wedel, 2003, 2006). Focused research has begun to characterize expression patterns of postcranial pneumaticity in both neornithine birds (Gutherz & O’Connor, 2021; Moore, 2020; O’Connor, 2004, 2009; Smith, 2012) and their now extinct relatives (e.g., non-avian theropod dinosaurs; Benson et al., 2012). Such studies have primarily examined the presence/absence of the trait in individual bones of the skeleton and documented significant variation, with some species exhibiting pneumaticity in almost every single element and others lacking a single pneumatic postcranial bone (O’Connor, 2004, 2009; Smith, 2012). Furthermore, the variation is often not random, as pneumaticity exhibits a strong phylogenetic signal and observed variations are frequently related to body mass and/or other aspects of ecology (Benson et al., 2012; Gutherz & O’Connor, 2021; O’Connor, 2004, 2009; Smith, 2012). For example, the number of individual elements pneumatized generally increases with body mass, whereas certain locomotor behaviors are consistently associated with extreme pneumaticity phenotypes (e.g., subsurface divers either lacking or exhibiting greatly restricted pneumaticity, static soaring exhibiting hyperpneumaticity) (O’Connor, 2004, 2009; Smith, 2012). A recent study focused on cervicothoracic vertebrae in storks analyzed the air space proportion or relative pneumaticity of each bone using quantita μCT and identified that pneumaticity patterns were correlated with the size, shape, and serial position of an individual vertebra, suggesting that the local biomechanical loading environment may also influence the expression of pneumaticity (Moore, 2020).

One important consideration regarding postcranial skeletal pneumaticity in crown birds is that the majority of detailed (i.e., bone-specific) data collected thus far focused on three clade-centric surveys (Gutherz & O’Connor, 2021; O’Connor, 2004; Smith, 2012). Furthermore, two of these studies focused on Anseriformes and Aequorilornithes (“Aequornithes” of Smith, 2012), two clades that include taxa that spend significant time inhabiting, if not exclusively foraging, within the aquatic environment (O’Connor, 2004; Smith, 2012). Given the well-characterized differences in skeletal structure (e.g., dense, compact bone) in birds and other amniotes that regularly exploit, if not live entirely within, aquatic environments (Amson et al., 2014; Habib & Ruff, 2008; Hinic-Frllog & Motani, 2009; Houssaye et al., 2016), it is possible, if not likely, that the expression of skeletal pneumaticity is significantly altered in aquatic specialists. For example, several subsurface foraging specialists (e.g., penguins, cormorants) that exhibit osteosclerosis in limb bones (Habib & Ruff, 2008; Ksepka et al., 2015) are also apneumatic or exhibit significantly reduced pneumaticity (Smith, 2012), presumably to reduce buoyancy and conserve energy while underwater (Lovvorn et al., 1999; Nopcsa, 1923; Wall, 1983). This thus limits our ability to extrapolate patterns of pneumaticity exhibited in aquatic clades to non-water-oriented birds, not to mention extinct organisms, potentially confounding our ability to characterize the evolution of this trait more generally.

To assess if patterns observed in previous studies are more generally applicable to modern birds, we quantified pneumaticity in the mostly non-aquatic Accipitrimorphae. Accipitrimorphae is composed of several groups of birds of prey including “Old and New World” vultures, the Secretary Bird, the Osprey, eagles, hawks, harriers, and kites (Jarvis et al., 2014; Mindell et al., 2018). Molecular divergence estimates place the origin of this large clade at approximately 60–70 million years ago (De Panis et al., 2021; Jarvis et al., 2014; Johnson et al., 2016), with most phylogenetic hypotheses supporting the Strigiformes (owls)–Coraciiformes (rollers, woodpeckers, hornbills, etc.) pairing as its sister clades among Telluraves (Jarvis et al., 2014). Accipitrimorphae has one of the largest body mass ranges (i.e., 85g to 14,000g) of any group of neognath birds, and despite a generally predatory nature, members of the clade exhibit a diversity of foraging (e.g., piscivory, obligate scavenging) and locomotor behaviors (static soaring, flapping flight) (del Hoyo et al., 2013). The diversity contained within this group, particularly in terms of body mass disparity and behavior, makes it an ideal candidate to evaluate current hypotheses related to the species-specific expression and evolution of postcranial skeletal pneumaticity among crown birds.

The broad goals of this contribution are to: (1) characterize species-specific expression patterns of pneumaticity in Accipitrimorphae, (2) assess the relationship between body mass and relative pneumaticity, (3) evaluate the associations among pneumaticity phenotypes and locomotor/foraging behaviors, and (4) compare the results from Accipitrimorphae with previously sampled groups of neornithine birds. To accomplish these goals, we first collected presence/absence data for skeletal pneumaticity in a sample of Accipitrimorphae. In addition to providing robust primary data for analysis, our sub-clade-specific sampling strategy allowed us to assess the influence of phylogeny on patterns of pneumaticity expression throughout the entire group. We then quantitatively assessed the relationship between body mass and pneumaticity. Next, we used a literature-based compilation of morphological and home range data for selected species across the taxonomic sample and explored how these factors covary with pneumaticity expression in different parts of the skeleton. Lastly, we contextualized the results of this study with those from Anseriformes, Aequorilornithes, and Cuculidae in order to explore pneumaticity expression patterns in neornithine birds. We address the following specific hypotheses in this study: (1)
patterns of pneumaticity expression in Accipitrimorphae (e.g., most common phenotype, degree of variation) will be more similar to Cuculidae (i.e., another non-aquatic neornithine group) than to either Anseriformes or Aequorlitornithes; (2) larger/heavier members of Accipitrimorphae will exhibit pneumaticity in a greater proportion of the skeleton than smaller/lighter species; (3) distal forelimb pneumaticity will be correlated with greater home range sizes and larger wingspan/area.

2 | METHODS

Skeletal specimens (Table S1) of Accipitrimorphae from museum collections were examined, with individual bones of the postcranial skeleton scored for the presence of pneumaticity using the osteological correlates established in O’Connor, 2006, namely the presence of an external bony foramen through which large internal cavities are visible. In total, 248 specimens were examined, representing 88 species (31.2% of all Accipitrimorphae) and 48 genera (64%). All morphological measurements were obtained from del Hoyo et al., 2013 and Ferguson-Lees & Christie, 2001, whereas home range data were compiled from a literature review (Table S2).

Once skeletal data were compiled, two different measures were used to quantify and compare pneumaticity among species: a pneumaticity index and binary characterization (0/1) for specific anatomical regions. A pneumaticity index was calculated following the methods of O’Connor, 2004, in which the skeleton is partitioned into 17 anatomical regions, with an index score calculated by dividing the number of pneumatic regions by the total number (i.e., 17) possible for each species. Whereas this measure provided a convenient means for assessing general pneumaticity trends and comparing patterns with previous studies, we feel that the pneumatic index failed to capture all biologically informative differences in pneumaticity expression. For example, two birds could exhibit an identical pneumaticity index score but express pneumaticity in different regions of the skeleton. Thus, to assess the potential impact of pneumaticity in specific regions of the skeleton, we also treated pneumaticity expression as a binary character in regions of the skeleton that exhibited variability among the sampled species, namely the caudal vertebrae, scapula, and distal forelimb. Both the pneumaticity index (PI) and binary characterization measures were used to assess the phylogenetic signal in the data. Additionally, the former was used for establishing body mass-PI regressions, with the latter used in phylogenetic logistic regression analyses.

We utilized Pagel’s lambda to assess phylogenetic signal and determine if closely related taxa exhibited more similar body masses and pneumaticity phenotypes or if each trait evolved in a stochastic manner (Pagel, 1999). All phylogenetic hypotheses for Accipitrimorphae interrelationships and outgroups used in this study were derived from subsets of the Jetz et al., 2012 global phylogeny of birds. Lambda values were calculated in R using the phylosig function from the phytools package (R Core Team, 2020; Revell, 2012) for pneumaticity index and body mass, whereas the fitDiscrete function of the Eiger package (Pennell et al., 2014; R Core Team, 2020) was used to assess the binary traits.

To quantitatively assess the relationship between body mass and pneumaticity, we performed a generalized least squares analysis that incorporates a Brownian motion model covariance matrix to account for the phylogenetic relationships of the included taxa (Phylogenetic Generalized Least Squares, PGLS). For the PGLS, we used the corBrownian function of the ape package (Paradis & Schliep, 2019) for the covariance matrix and the gls function of the nlm package (Pinheiro et al., 2020) to perform the regression analysis (R Core Team, 2020).

To address the relationship between pneumaticity and flight/foraging behavior, we elected to use six log transformed morphological measures (body mass, wingspan, wing chord, tail length, body mass corrected tail length, and wing loading [g/cm²]) and one log-transformed ecological measure (home range size [km²]). The morphological measures generally capture the size of the airfoil for a given species, attributes thought to ultimately affect both flight and foraging characteristics. We avoided categorical measures of diet, foraging, and flight style due to the high degree of subjectivity, potential overlap, and difficulties in partitioning species cleanly. We conducted a series of phylogenetic logistic regression analyses (Ives & Garland Jr., 2010) assessing the ability of the morphological and ecological variables to predict individual species’ expression of the caudal vertebral, scapular, and distal forelimb pneumaticity. We employed a forward and backward stepwise model selection tool using the phylostep function of the phylolm package (Ho & Ane, 2014; R Core Team, 2020) to select the best regression model containing the most appropriate independent variables based on the Akaike Information Criterion (AIC) score. The corresponding phylogenetic logistic regression was run using the phylom function of the phylolm package with 2500 independent bootstrap replicates to produce confidence intervals and test for statistical significance of independent variables (Ho & Ane, 2014; R Core Team, 2020). It is important to note that analyses including home range and wing loading measures utilized a more limited data set (i.e., less than the full 88 species) due to the absence of data for certain species (noted in Table S2). Thus, analyses were run in three series, a morphology-only series, a wing loading + morphology series, and a home range + morphology series.

3 | RESULTS

The majority (86/88 taxa) of sampled Accipitrimorphae exhibited pneumaticity in the following bones (Figure 1): all postaxial and precaudal vertebrae, humerus, coracoid, sternum, furcula, femur, all vertebral and sternal ribs, and all elements of the pelvis. The remaining two species (2/88) exhibited this pattern with one exception each: the furcula was apneumatic in Pernis apivorus (European Honey Buzzard) and the femur was apneumatic in Pandion haliaetus (Osprey). There were four additional regions that were variably pneumatic: caudal vertebrae, second cervical vertebra (i.e., axis), scapula,
and distal (i.e., distal to the humerus) forelimb. Given that the axis exhibits intraspecific variability but most commonly exhibits pneumaticity, both in this clade and previously sampled groups, we consider the variable expression of pneumaticity in this individual vertebra to be the result of stochastic processes and fundamentally of limited biological significance. Thus, it will not be discussed further. The scapula was generally pneumatic, but 10 species lacked pneumaticity in this element (Table 1). Caudal vertebrae in Accipitrimorphae were most commonly apneumatic; however, 32 species exhibited at least one pneumatic caudal vertebra (Figure 2). Due to incomplete preservation in this region in many skeletal specimens, however, it is difficult to determine which and how many vertebrae were pneumatic for several taxa. Additionally, because several specimens lacked a complete caudal series, it is possible that additional taxa may have expressed pneumaticity in the caudal vertebral series but were not available for this study. Lastly, distal forelimb pneumaticity was exclusively present in all sampled members of two vulture clades, Cathartidae ("New World" vultures), and Gypiiinae (or Aegypiinae, one of the two subfamilies of "Old World" Vultures).

We performed several phylogenetic signal analyses of both body mass and pneumaticity. For body mass and pneumaticity index, we calculated a lambda value of 0.9999 \((p = 4.561 \times 10^{-16})\) and 0.9480 \((p = 8.228 \times 10^{-15})\), respectively, with both values supporting a Brownian motion model for the evolution for these traits. For the phylogenetic signal of specific pneumaticity phenotypes, we calculated lambda values of 1, 1, and 0.7178 for scapular, distal forelimb, and caudal vertebral pneumaticity, respectively, with all values indicating moderate to strong support for a Brownian motion model for the evolution for these traits. A phylogenetic generalized least squares (PGLS) analysis reveals a non-significant positive relationship between body mass and pneumaticity with a slope of 2.674 \((p = 0.3207)\) and a residual standard error of 1.513.

For each variably pneumatic region, we ran three phylogenetic logistic regressions using a different data set (morphology only, morphology + wing loading, and morphology + home range) for each as we were unable to obtain values for every measure (i.e., wing loading and home range) for the entire 88 species dataset (Table 2). For distal forelimb pneumaticity, a model containing only wingspan was best supported for our morphological and wing loading data (Table 2), with both regressions returning a significant positive relationship between wingspan and expression of distal forelimb pneumaticity (i.e., birds that express distal forelimb pneumaticity generally have larger wingspans). For our home range analysis, the home range was the only independent variable in our best-supported model, which identified a significantly positive relationship between home range size and distal forelimb pneumaticity. That the home range analysis did not also identify wingspan as a significant predictor of distal limb pneumaticity status may be due to a limited data set or the greater
**TABLE 1** List of taxa surveyed for this study

| Species                               | Number of specimens examined | Pneumaticity Index | Body Mass (g) |
|---------------------------------------|-----------------------------|-------------------|---------------|
| Accipiter cirrocephalus               | 1                           | 0.941176471       | 180           |
| Accipiter cooperii                    | 6                           | 0.941176471       | 444           |
| Accipiter fasciatus                   | 2                           | 0.941176471       | 454           |
| Accipiter gentilis                    | 5                           | 0.941176471       | 1041          |
| Accipiter gularis                     | 2                           | 0.941176471       | 129           |
| Accipiter gundlachi                   | 1                           | 0.941176471       | 675           |
| Accipiter imitator                    | 1                           | 0.882352941       | 228           |
| Accipiter nisus                       | 3                           | 0.941176471       | 286           |
| Accipiter novaehollandiae             | 2                           | 0.941176471       | 202           |
| Accipiter rufitorques                 | 1                           | 0.882352941       | 209           |
| Accipiter striatus                    | 2                           | 0.941176471       | 141           |
| Accipiter tachiro                     | 3                           | 0.941176471       | 238           |
| Aegypius monachus                     | 2                           | 1                 | 8170          |
| Aquila audax                          | 5                           | 0.941176471       | 3466          |
| Aquila chrysaetos                     | 3                           | 0.941176471       | 4112          |
| Aquila fasciata                       | 1                           | 0.941176471       | 2000          |
| Aquila pomarina                       | 1                           | 0.941176471       | 1393          |
| Aquila rapax                          | 3                           | 0.882352941       | 2250          |
| Aquila verreauxii                     | 1                           | 0.941176471       | 4195          |
| Aquila wahlbergi                      | 1                           | 0.882352941       | 640           |
| Aviceda cuculoides                    | 1                           | 0.882352941       | 277           |
| Busarellus nigricollis\(^a\)         | 4                           | 0.882352941       | 871           |
| Buteo albonotatus                     | 2                           | 0.882352941       | 775           |
| Buteo auguralis                       | 2                           | 0.882352941       | 670           |
| Buteo buteo                           | 4                           | 0.882352941       | 884           |
| Buteo galapagoensis                   | 5                           | 0.882352941       | 1082          |
| Buteo jamaicensis                     | 11                          | 0.882352941       | 1122          |
| Buteo lagopus                         | 4                           | 0.882352941       | 943           |
| Buteo lineatus                        | 2                           | 0.882352941       | 623           |
| Buteo magnirostris                    | 5                           | 0.882352941       | 269           |
| Buteo nitidus                         | 1                           | 0.882352941       | 495           |
| Buteo platypterus                     | 1                           | 0.882352941       | 454           |
| Buteo polyosoma                       | 1                           | 0.882352941       | 733           |
| Buteo regalis                         | 1                           | 0.882352941       | 1502          |
| Buteo rufouscus                       | 1                           | 0.882352941       | 1530          |
| Buteogallus meridionalis              | 4                           | 0.941176471       | 808           |
| Buteogallus unubitinga                | 2                           | 0.882352941       | 1183          |
| Cathartes aura                        | 3                           | 0.941176471       | 2006          |
| Cathartes burrovianus                 | 2                           | 0.941176471       | 935           |
| Circus aeruginosus                    | 2                           | 0.941176471       | 683           |
| Circus cyaneus                        | 5                           | 0.941176471       | 434           |
| Circus pygargus                       | 1                           | 0.941176471       | 295           |
| Coragyps atratus                      | 1                           | 0.941176471       | 2150          |
| Elanoides forficatus\(^a\)            | 5                           | 0.823529412       | 420           |
| Elanus axillaris\(^a\)                | 1                           | 0.823529412       | 263           |

(Continues)
| Species                        | Number of specimens examined | Pneumaticity Index | Body Mass (g) |
|-------------------------------|-----------------------------|-------------------|---------------|
| Elanus caeruleus              | 1                           | 0.823529412       | 260           |
| Gampsongyx swainsonii         | 5                           | 0.823529412       | 93            |
| Geranoaetus melanoleucus      | 6                           | 0.882352941       | 2547          |
| Gymnogyps californianus       | 2                           | 0.941176471       | 8425          |
| Gypaetus barbatus             | 3                           | 0.882352941       | 5690          |
| Gypohierax angolensis         | 7                           | 0.882352941       | 1600          |
| Gyps africanus                | 1                           | 1                 | 5433          |
| Gyps fulvus                   | 5                           | 0.941176471       | 7436          |
| Haliaeetus albicilla          | 1                           | 0.882352941       | 4949          |
| Haliaeetus leucocephalus      | 5                           | 0.882352941       | 4757          |
| Haliaeetus leucogaster        | 3                           | 0.882352941       | 2907          |
| Haliaeetus vocifer            | 5                           | 0.882352941       | 2806          |
| Haliastur indus               | 4                           | 0.882352941       | 529           |
| Haliastur sphenurus           | 2                           | 0.882352941       | 753           |
| Harpy arpyja                  | 5                           | 0.941176471       | 4800          |
| Hieraaetus morphnoides        | 1                           | 0.941176471       | 815           |
| Ictinia mississippiensis      | 1                           | 0.882352941       | 266           |
| Ictinia plumbea               | 2                           | 0.882352941       | 247           |
| Kaupifalco monogrammicus      | 3                           | 0.823529412       | 281           |
| Leucopternis albicollis       | 4                           | 0.882352941       | 732           |
| Leucopternis melanops         | 1                           | 0.941176471       | 319           |
| Lophoictinia isura            | 2                           | 0.941176471       | 1067          |
| Machirampus alcinus           | 3                           | 0.882352941       | 650           |
| Milvus migrans                | 4                           | 0.882352941       | 567           |
| Morphnus guianensis           | 1                           | 0.941176471       | 1750          |
| Necrosyrtes monachus          | 3                           | 0.941176471       | 2043          |
| Neophron perconopterus        | 3                           | 0.882352941       | 2082          |
| Pandion haliaetus             | 6                           | 0.764705882       | 1499          |
| Parabuteo unicinctus          | 3                           | 0.882352941       | 825           |
| Pernis apivorus               | 1                           | 0.764705882       | 750           |
| Polemaetus bellicosus         | 3                           | 0.941176471       | 4063          |
| Rostrhamus sociabilis         | 3                           | 0.882352941       | 402           |
| Sagittarius serpentarius      | 5                           | 0.882352941       | 4017          |
| Sarcogyps calvus              | 3                           | 1                 | 5400          |
| Sarcoramphus papa             | 3                           | 0.941176471       | 3400          |
| Spilornis cheela              | 2                           | 0.882352941       | 900           |
| Spizaetus ornatus             | 1                           | 0.941176471       | 1192          |
| Stephanoaetus coronatus       | 3                           | 0.941176471       | 3640          |
| Terathopius ecaudatus         | 5                           | 0.882352941       | 2200          |
| Torgos tracheliotes          | 1                           | 0.941176471       | 6969          |
| Trigonoceps occipitalis       | 1                           | 0.941176471       | 3016          |
| Vultur gryphus                | 3                           | 0.941176471       | 11,300        |

*Indicates species exhibiting an apneumatic scapula.
strength of the relationship with the home range. For expression of pneumaticity in caudal vertebrae, the morphological data set best-supported model contained body mass and body mass corrected tail length as independent variables, with the expression of caudal vertebral pneumaticity positively associated with both measures. For the wing loading data set, the best model contained body mass, wingspan, and tail length, with only wingspan (negative association) and tail length (positive association) exhibiting a significant relationship with pneumaticity expression. The home range data set best model contained wingspan and wing chord, but the regression failed to identify a significant relationship between either of the variables and pneumaticity expression in caudal vertebrae. Lastly, for the scapula, only the home range data set produced a model with any independent variables, with a significant positive association between body mass and scapular pneumatic expression, whereas wing chord was negatively associated with scapular pneumatic expression. The lack of significant regression variables in these analyses may indicate that other unassessed traits impact the expression of scapular pneumaticity or that pneumaticity in this bone occurs in a stochastic manner.

4 | DISCUSSION

We propose the following bones as the accipitrimorph baseline, given that all but two sampled species (86/88) exhibited
pneumaticity in these elements: all postaxial and pre-caudal vertebral, all dorsal and sternal ribs, the pectoral and pelvic girdles, humerus, and femur. These elements were pneumatic in all but two sampled taxa, the femur being pneumatic in the Osprey and the furcula being pneumatic in the European Honey Buzzard. This pattern of pneumaticity expression characterizes a number of medium to large-sized birds across several avian clades (e.g., galloanserae, cuculidae) (Guthertz & O’Connor, 2021; O’Connor, 2004, 2009). Fifty species of Accipitrimorphae deviated from this baseline level, with 11 species exhibiting a reduction in pneumaticity and 42 species expanding on the pattern (Figure 2). None of the sampled taxa deviated from the Accipitrimorphae baseline by more than two anatomical regions. Despite previous documentation of extensive variation in certain aquatic clades (O’Connor, 2004; Smith, 2012), more recent work indicates that pneumaticity expression is relatively stable in non-aquatic groups (Guthertz & O’Connor, 2021, the data presented herein).

Historically, body mass has been hypothesized to be a significant factor influencing the expression of postcranial pneumaticity (Buhler, 1992; Currey & Alexander, 1985; McLelland, 1989). Whereas this has been supported in extinct non-avian theropod dinosaurs (Benson et al., 2012), data from extant birds indicate that other factors (e.g., foraging ecology; flight style) may be more significant drivers of the variable expression observed in this system. Whereas all studies assessing pneumaticity and body mass have found a positive relationship between the two variables, most, including the study herein, have reported that the significance of the relationship is lost when considered in an explicit phylogenetic context (e.g., when examined using phylogenetic comparative methods). Moreover, certain behaviors (e.g., subsurface diving) are associated with specific pneumaticity phenotypes regardless of body mass (O’Connor, 2004, 2009; Smith, 2012). This suggests that while body mass may account for some proportion of the variation in pneumaticity expression, it may not exert strong enough selection pressure to alter ancestral phenotypes or overcome the influence of other factors such as dominant locomotor/foraging behavior.

More directly, biomechanical loading regimes related to specific behaviors may be more useful predictors of pneumaticity expression in a given element and/or species of bird than body mass alone. Whereas pneumatic bone has been shown to perform worse than apneumatic bone in generalized stiffness and bending tests (Cubo & Casinos, 2000), its structure may be more efficient at resisting torsional loads (Cubo & Casinos, 2000). The ability of a beam, in this case, an individual bone, to resist torsional stresses (J) is directly proportional to its cross-sectional area. Thus, expanding the diameter or cross-section of a beam (or bone) will increase J or torsional resistance. Pneumaticity may achieve an enlarged cross-section indirectly in a relatively low-cost manner by inflating the volume of a given bone. Prior research in birds has indicated that torsional loads are experienced by the forelimb during flight (Biewener & Dial, 1995; Buhler, 1992; de Margeria et al., 2005) and the femur during avian terrestrial locomotion (Carrano & Biewener, 1999; de Margeria et al., 2005).

Furthermore, large wing chords, those often associated with static soaring birds, are predicted to impose higher torsional stresses on the forelimb (Frongia et al., 2018; Simons et al., 2011). Perhaps the most striking observation from this study is the convergent evolution of distal forelimb pneumaticity between Gypiinae and Cathartidae, combined with the absence of this trait in the other subfamily of vultures, Gypaetinae. Distal limb

| TABLE 2 | Results of the best phylogenetic logistic regression model after the model selection process |
|-----------------|---------------------------------|-----------------|-----------------|-----------------|-----------------|
| Pneumonic expression region | Independent variable | Estimate | 95% confidence interval | p-value | AIC Score | Log likelihood |
|-----------------|---------------------------------|-----------------|-----------------|-----------------|-----------------|
| Morphological expression region | | | | | | |
| Distal Forelimb | Log Wingspan | 15.222 | 14.894 to 15.912 | 0.00949 | 36.29 | −15.14 |
| Caudal Vertebrae | Log Body Mass | 2.517 | 1.66 to 3.474 | 0.0295 | 102.73 | −47.37 |
| | Body-Mass Corrected Tail Length | 42.974 | 42.529 to 44.061 | 0.04097 | | |
| Morphology + Wing Loading Data | | | | | | |
| Distal Forelimb | Log Wingspan | 14.552 | 10.613 to 15.92 | 0.0105 | 29.97 | −11.99 |
| Caudal Vertebrae | Log Body Mass | 2.593 | −0.0369 to 4.484 | 0.2392 | 53.96 | −21.98 |
| | Log Wingspan | −17.57 | −19.305 to 11.96 | 0.0207 | | |
| | Log Wing Loading | 14.11 | 6.442 to 18.851 | 0.01246 | | |
| Morphology + Home Range Data | | | | | | |
| Distal Forelimb | Log Transformed Home Range | 0.695 | 0.3541 to 2.589 | 0.0234 | 22.59 | −8.296 |
| Caudal Vertebrae | Log Wingspan | −14.647 | −16.1796 to 13.102 | 0.2328 | 51.05 | −21.52 |
| | Log Wing Chord | 13.401 | 7.5401 to 17.287 | 0.2948 | | |
| Scapula | Log Body Mass | 11.7 | 8.622 to 13.836 | 0.021 | 30.6 | −10.3 |
| | Log Wing Chord | −31.241 | −33.166 to 27.403 | 0.0254 | | |
| | Body-Mass Corrected Tail Length | 11.918 | 10.45 to 12.724 | 0.795 | | |

Note: Bolded results are statistically significant.
Pneumaticity is an extremely rare phenotype among modern avian taxa (to date, observed in only 9 of ~249 families of neovians) and when present, is typically only expressed in the largest species of the respective clades (O’Connor, 2009). When distal forelimb pneumaticity is present, it exhibits a modular expression wherein all elements distal to the humerus are pneumatic, even the distalmost phalanges.

To quote del Hoyo et al. (2013: p. 29, Vol. 2) “every aspect of the ecology and behavior of vultures is aimed at saving energy.” Perhaps unsurprisingly, vultures rely on soaring as their primary mode of flight, not only for energy efficiency but to cover large distances at a great height. Flying at high altitude for extended periods (>50% of the individual’s daily activity; Xirouchakis & Andreou, 2009) and being able to traverse long distances relatively quickly is a necessity given the unpredictable location, timing, and fierce competition typically associated with a vulture’s primary food source, carrion (Pennycuick, 1971; Shepard & Lambertucci, 2013). We observed a significant positive relationship between home range and distal limb pneumaticity, providing a potential feeding ecology connection between pneumaticity and long-distance soaring. A large airfoil relative to body size is required to maintain effective long-distance static soaring, with larger wing chords predicted to generate relatively high torsional stresses on the forelimb (Frongia et al., 2018; Simons et al., 2011).

Thus, pneumaticity expression in the distal forelimb may be a mechanism to redistribute the bone over a larger area (circumference) that would increase resistance to torsional loads applied to a forelimb skeleton in taxa with broader wings. This hypothesis is supported by the significant positive relationship between distal limb pneumaticity and wingspan in our morphological and wing loading data sets. It is worth noting that two members (G. angolensis and N. percornpterus) of Gypaetinae, the vulture clade that does not exhibit distal forelimb pneumaticity, consume a diversity of food items, whereas the third member, G. barbatus, consumes primarily bone marrow, an infrequently consumed part of the carcass due to the increased challenge of accessing marrow. This deviation in dietary preference from other vulture species may reduce the selection pressure to evolve extreme phenotypes needed for access to a highly competitive food resource.

One additional potential benefit of pneumaticity in the distal forelimb is that by extending the wingspan (supported by the significant positive relationship between distal forelimb pneumaticity and wingspan in our regression analyses), the attachment for forelimb extensor musculature is positioned further distally on the metacarpal I (Fisher, 1946). This serves to increase the lever arm and potentially decrease the energy requirements of extensor musculature necessary to maintain wrist joint extension. Given that soaring/gliding accounts for up to 99% of vulture flight time (Williams et al., 2020), during which the forelimb must be held in extension, this could provide large energy savings. Indeed, a morphological study of accipitriform forelimb skeletons observed a consistent pattern wherein the extensor process is more proximally located in taxa that more frequently employ flapping flight, whereas birds that utilized soaring typically exhibited a more distal location of the extensor process (Fisher, 1946).

Caudal pneumaticity was present in roughly 1/3 of the species sampled. Caudal pneumaticity was the most difficult region to confidently assess as several specimens in collections preserved incomplete tails, and a few did not include any caudal vertebrae. Thus, it is possible that caudal pneumaticity has a greater distribution in Accipitriformes than currently assigned. When caudal pneumaticity was present (at least one pneumatic vertebra), the number and serial position of the pneumatic caudal vertebrae varied considerably, both intra- and interspecifically. The large degree of variation in the expression of caudal pneumaticity may support the hypothesis that its presence is merely a consequence of stochastic developmental processes and lacks any adaptive significance (Witmer, 1997), similar to our comment above regarding the expression of pneumaticity in the second cervical vertebra. However, caudal pneumaticity did exhibit some phylogenetic signal (lambda = 0.718) in Accipitriformes, and other groups of birds (e.g., cuckoos) have shown consistent expression patterns in this region (Gutherz & O’Connor, 2021).

Whereas the adaptive benefit of pneumaticity expression in caudal vertebrae is uncertain, the presence of pneumaticity in other anatomical regions suggests that the expression of this trait occurs to potentially increase the volume (and therefore length) of the tail. Given that both raw tail length and body mass corrected tail length were positively associated with expression of caudal pneumaticity in the wing loading and morphological regression analyses, respectively, caudal pneumaticity is correlated with longer tails in Accipitriformes. Long tails are a common trait of Accipiter species, a genus of hawks known to inhabit forests that also frequently express caudal pneumaticity. Whereas in some open habitats, soaring accipitriforms do possess elongate tails (e.g., Gypaetus barbatus and Milvus milvus (del Hoyo et al., 2013)), the majority of open habitats, soaring birds have short tails and lack caudal pneumaticity (e.g., “New World” Vultures, Buteo hawks). Perhaps pneumaticity expression in caudal vertebrae may serve to inflate the volume of each element, indirectly increasing the surface area for attachment of muscles utilized in the agile flight necessary to navigate complex forested environments or support a heavier individual, given the positive relationship between caudal pneumaticity expression and body mass observed herein. This hypothesis is lent some support by Mosto et al. (2019) who found a greater volume of caudal musculature in the forest-dwelling, agile falcons as compared to the closely related, terrestrial, and relatively poor flying caracaras.

One last example of pneumaticity expression potentially related to behavior is observed in the femur of the Osprey. Osprey is the only species to exhibit apneumatic femora within the entire sample. Osprey dives at relatively high angles, impacting the water feet first (Johnsguard, 1990), applying potentially significant and less predictable loading through the hind limbs during prey acquisition. As stated previously, pneumatic bones may not be well suited for resisting less predictable loading environments (Cubo & Casinos, 2000).
Thus, the absence of pneumaticity expression in the Osprey femur suggests that a relatively high safety factor offered by the absence of pneumaticity may be related to preventing injury during this specific prey capture technique.

Examining pneumatic expression in Aves more generally, three patterns become apparent: (1) non-aquatic birds (e.g., Accipitrimorphae, Cuculidae) exhibit distinct and less variable pneumaticity expression patterns compared to clades that either contain obligate or predominantly aquatic taxa (e.g., Anseriformes, Aequorlitornithes); (2) body mass and pneumaticity exhibit a positive relationship, although this relationship is often overridden by other life histories (e.g., locomotor specializations), and/or phylogenetic factors; (3) whereas pneumaticity expression in many groups is relatively constant, deviations from common expression patterns occur when a lineage evolves specialization toward a particular locomotor activity (e.g., apneumaticity and subsurface diving, hyperpneumaticity, and long-distance static soaring).

Both accipitrimorphs and cuculids exhibit relatively high baseline pneumaticity patterns with minimal variation, with no single species varying from their respective clade’s basic profile by more than two anatomical regions. This contrasts greatly with both Anseriformes and Aequorlitornithes, wherein almost the entire range of possible postcranial pneumaticity phenotypes is present, (i.e., from nearly complete postcranial pneumaticity to skeletons that are entirely devoid of pneumaticity). To highlight the contrasts in expression patterns, the standard deviations in the pneumaticity index for our non-aquatic birds (Cuculidae: 0.0427, 42 species; Accipitrimorphae: 0.0441, 88 species) are nearly identical and significantly smaller than for the two aquatic clades (Anseriformes: 0.210, 99 species; Aequorlitornithes: 0.363, 48 species). One explanation for this discrepancy may be that members of the two aquatic clades evolved higher rates of pneumaticity trait change as compared to other groups of birds, a hypothesis that remains to be tested. Another possible explanation is that the extensive diversity in pneumatic phenotypes present in aquatic clades is related to the broad range of locomotor ecologies exhibited by the taxa within these groups. These clades exhibit significantly reduced pneumaticity patterns relative to non-aquatic groups. Pneumatic bones, which contain air instead of marrow, may increase the buoyancy of an animal and make underwater foraging more effortful. Thus, reducing pneumaticity may reduce buoyancy and represent an energy-saving mechanism in subsurface diving taxa (Currey & Alexander, 1985; Fajardo et al., 2007; O’Connor, 2004; Wall, 1983).

Finally, one additional explanation for reduced pneumaticity should be considered and relates to an increased safety factor of individual bones in response to a decrease in biomechanical loading predictability. Moore (2020) noted that differences in air space proportion (i.e., relative pneumaticity) of individual vertebrae in storks corresponded with the predictability of loading environment, with bones that experienced more predictable loads having higher air space proportions. Given that many members of Anseriformes and Aequorlitornithes frequently interact with both air and water, media that have vastly different physical properties, the direction and magnitude of forces exerted on the skeleton may vary broadly at any given moment. Thus, a decrease in biomechanical loading predictability may ultimately drive an overall decrease in pneumaticity expression to prevent the possibility of injury.

The two dense sampling pneumaticity surveys of non-aquatic birds (Cuculidae, Accipitrimorphae) indicate that pneumatic expression is relatively stable with low levels of variability (Gutherz & O’Connor, 2021). When variation does occur in these clades, it frequently co-occurs with locomotor specializations (cursorial locomotion and femoral pneumaticity in roadrunners [Gutherz & O’Connor, 2021]), long-distance static soaring, and distal forelimb/hyperpneumaticity in vultures [O’Connor, 2009, this study]. This provides context for the more complex patterns observed in aquatic groups, in which a diverse array of pneumaticity phenotypes and locomotor behaviors from static soaring to subsurface foraging occur (O’Connor, 2004; Smith, 2012). It thus appears that pneumaticity co-varies with a broad range of behavioral ecologies exhibited in crown birds. By altering the skeletal mass-volume relationship of bone, pneumaticity allows efficient construction of skeletons for the exploration of new locomotor behaviors without significantly altering the basic avian Bauplan. Being the heaviest tissue type in the body, region-specific alterations of mass-volume relationships in bone have significant implications for the center-of-mass of an organism and may explain the near ubiquity of vertebral pneumaticity in medium-large birds. As continued taxonomic sampling explores patterns of pneumaticity expression in crown birds, research on the evolutionary drivers of pneumaticity is necessary not only to understand its impact on the broad diversity of living forms but the successful radiation of now-extinct groups in which postcranial skeletal pneumaticity has been inferred.

5 Conclusion

Postcranial skeletal pneumaticity was assessed in a dense taxonomic sample of Accipitrimorphae. We observed a relatively consistent expression pattern consisting of all postaxial and precaudal vertebrae, humerus, coracoid, sternum, pelvic girdle, and all ribs. Whereas deviations from this pattern occurred in roughly half of the sampled taxa, no single species varied from the Accipitrimorph baseline by more than two anatomical regions. We note a positive trend between body mass and relative pneumaticity, though this relationship was not significant when explicitly analyzed in a phylogenetic framework. We also observed that two clades of “Old” and “New World” vultures exclusively expressed pneumaticity in the distal forelimb, a phenotype best interpreted as convergent. The data collected in this study indicate that major differences in pneumaticity expression co-occur with locomotor specializations. Further research into the biomechanical impact of skeletal pneumaticity, as well as the potential for pneumaticity to fundamentally alter mass-volume relationships at both the individual bone and whole skeleton levels, is necessary to understand how
changes in pneumaticity may have driven the expansive diversity of modern birds and now extinct taxa such as nonavian dinosaurs and pterosaurs.

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DATA AVAILABILITY STATEMENT

All data and analysis (e.g., R code, .nex trees) files will be made available upon reasonable request.

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