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REVIEW

A surrogate forelimb: Evolution, function and development of the avian cervical spine

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Abstract

The neck is a critical portion of the avian spine, one that works in tandem with the beak to act as a surrogate forelimb and allows birds to manipulate their surroundings despite the lack of a grasping capable hand. Birds display an incredible amount of diversity in neck morphology across multiple anatomical scales—from varying cervical counts down to intricate adaptations of individual vertebrae. Despite this morphofunctional disparity, little is known about the drivers of this enormous variation, nor how neck evolution has shaped avian macroevolution. To promote interest in this system, I review the development, function and evolution of the avian cervical spine. The musculoskeletal anatomy, basic kinematics and development of the avian neck are all documented, but focus primarily upon commercially available taxa. In addition, recent work has quantified the drivers of extant morphological variation across the avian neck, as well as patterns of integration between the neck and other skeletal elements. However, the evolutionary history of the avian cervical spine, and its contribution to the diversification and success of modern birds is currently unknown. Future work should aim to broaden our understanding of the cervical anatomy, development and kinematics to include a more diverse selection of extant birds, while also considering the macroevolutionary drivers and consequences of this important section of the avian spine.

KEYWORDS
avian, axial, biomechanics, development, evolution, neck, vertebrae

1 | INTRODUCTION

The neck is a critical portion of the vertebral column and serves two primary functions: to support the weight of the head and to provide it with a degree of movement that is independent from the trunk (Gans, 1992; Wilkinson & Ruxton, 2012). This degree of trunk-independent movement has allowed the neck to be involved in a multitude of tasks that range from feeding to observance, vigilance displays and conspecific displays of dominance (Boas, 1929; Gans, 1992; Kress et al., 2015; Pete et al., 2015; van der Leeuw et al., 2001; Wilkinson & Ruxton, 2012). Many of these tasks are repeated daily and are performed regularly by most clades of tetrapods (Gans, 1992; Wilkinson & Ruxton, 2012). This universal basic function of the neck has given rise to the hypothesis that the tetrapod neck is adapted for the 'economics of continuous movement' rather than to any specific function or behaviour (van der Leeuw et al., 2001; Wilkinson & Ruxton, 2012).

Given this hypothesis one might expect that morphological variation of cervical vertebrae across Tetrapoda may be conservative, yet vertebral morphology, vertebral counts, cervical musculature and neck length all vary considerably among different clades (Arnold, 2021; Li et al., 2023; Marek et al., 2021; Müller et al., 2010). However, this diversity is disparate in its distribution across tetrapods owing to the presence of, or release from, developmental and biomechanical constraints (Müller et al., 2010). Such constraints exist in mammals due to the posterior migration of cells from the paraxial mesoderm (tissue that gives rise to muscles) to form new muscle tissue, including the diaphragm during the evolution of the clade (Arnold et al., 2017; Buchholtz et al., 2012; Hirasawa et al., 2016; Jones et al., 2018). This evolutionary process gave rise to a keystone mammalian synapomorphy, the muscularized diaphragm. As a consequence, this connection between the forelimb and neck [along with other developmental restraints (Galis, 1999)] has restricted the count of cervical vertebrae across Mammalia (with very few exceptions) to seven (Buchholtz et al., 2012; Hirasawa et al., 2016; Jones et al., 2018).

Whereas diversity of cervical counts is restricted in mammals, neck vertebral morphology nonetheless remains extremely variable (Arnold et al., 2017; Jones et al., 2021; Li et al., 2023). Differing counts of vertebrae between species often hinder the study of intraspecific morphological variation due to uncertain homology of vertebrae at differing points in the axial column. The fixed cervical count that is homologous across most mammals has allowed the morphological diversity of the mammalian cervical column to be extensively studied over recent years. This has led to a form of renaissance in the study of the mammalian neck, whereby we now understand how the development and evolution of this structure has shaped its current diversity, as well as its contribution to the success of Mammalia via the muscularisation of the diaphragm (Arnold et al., 2017; Buchholtz et al., 2012; Hirasawa et al., 2016; Jones et al., 2018; Jones et al., 2021, 2021; Jones et al., 2020; Li et al., 2023; Randau & Goswami, 2018).

Other tetrapod clades are not restrained by such factors and neck morphological diversity within these groups is much more abundant (Head & David Polly, 2007; Müller et al., 2010; O'Keefe & Hiller, 2006) and among extant tetrapods, birds display some of the highest diversity in neck form and function (Figure 1; Boas, 1929; Böhmer et al., 2019; Boumans et al., 2015; Kambic et al., 2017; Marek et al., 2021; van der Leeuw et al., 2001). Unlike their mammalian counterparts, counts of cervical vertebrae in birds can vary between 10 in parrots and up to 23 in some swans (Figure 1; Benoit et al., 1950; Marek et al., 2021). This morphological diversity is matched by the functional diversity of the avian neck, as it is utilized in a wide variety of habitual and specialized behaviours from feeding and prey capture (Boas, 1929; Böhmer et al., 2020; van der Leeuw et al., 2001; Zweers, Bout, & Heidweiller, 1994) to tool use, and even powering tripedal locomotion in some parrot species (Reader et al., 2022; Young et al., 2022). The neck and head of birds often work in tandem as an appendage that is able to precisely manipulate its surroundings. This adaptation, a so-called 'surrogate forelimb' (Bhullar et al., 2012, 2016; Clarke & Middleton, 2008; Marek et al., 2021), is especially important in birds as the wing is primarily adapted for powered flight leaving it unable to grasp or manipulate objects. Both the morphofunctional variability and the extensive use of the neck as a surrogate arm appears to be a key evolutionary trait as the avian neck has undergone extensive changes across the theropod-bird transition (Marek et al., 2021; Zanno & Makovicky, 2011). Despite recent advances in our understanding of the factors that determine morphofunctional variation in extant avians (Böhmer et al., 2019, 2020; Marek et al., 2021; Terray et al., 2020), we still do not understand the tempo and mode of neck evolution, nor the forces that shaped the evolution of neck in their dinosaurian antecedents.

Our understanding of the morphofunctional variation, tempo and mode of avian neck evolution does not currently match the body of work that exists for the mammalian cervical column. By gaining such knowledge of the underlying mechanics of cervical variability in birds, we may allow for a deeper understanding of how Hox genes (genes responsible for segment identity along the body axis) adapt and change between lineages and over evolutionary time. However, recent advances in developmental biology, biomechanics and geometric morphometrics are allowing researchers, for the first time, to understand the factors that shape the astounding morphofunctional diversity of the avian neck (Böhmer et al., 2019; Böhmer et al., 2015; Marek et al., 2021; Terray et al., 2020). To promote the study of this diverse and fascinating musculoskeletal system, I will provide an overview of the current literature available that pertains to the development, function and evolution of the avian neck. I will also offer insight into the areas where future study of the avian neck would provide the most critical knowledge advancements.

2 | DEVELOPMENT

Variation of the axial column across vertebrates (including birds) occurs along two axes—the number and shape of vertebrae, and are each controlled by separate developmental processes. The number of vertebrae in the entire axial column and within each individual axial region is determined by a process called somitogenesis (Dequéant & Pourquié, 2008; Dubrulle & Pourquié, 2002; Tam et al., 1999). During development, somites (segmental units and vertebral precursors) form on each side of the neural tube and notochord from the presomitic mesoderm (Gomez et al., 2008; Richardson et al., 1998). Somitogenesis is then the periodic formation of these somites from the presomitic mesoderm, the periodicity of which is controlled by a molecular 'segmentation clock' (Dequéant & Pourquié, 2008; Pourquié, 2003). The speed of this segmentation clock determines the number of somites produced during somitogenesis—a slower clock will produce fewer somites while a fast clock will produce more (Gomez et al., 2008). As somites are vertebral precursors, somitogenesis and the segmentation clock together are responsible for changes in the number of vertebrae produced during vertebrate development (Gomez et al., 2008). The speed of this segmentation clock can also

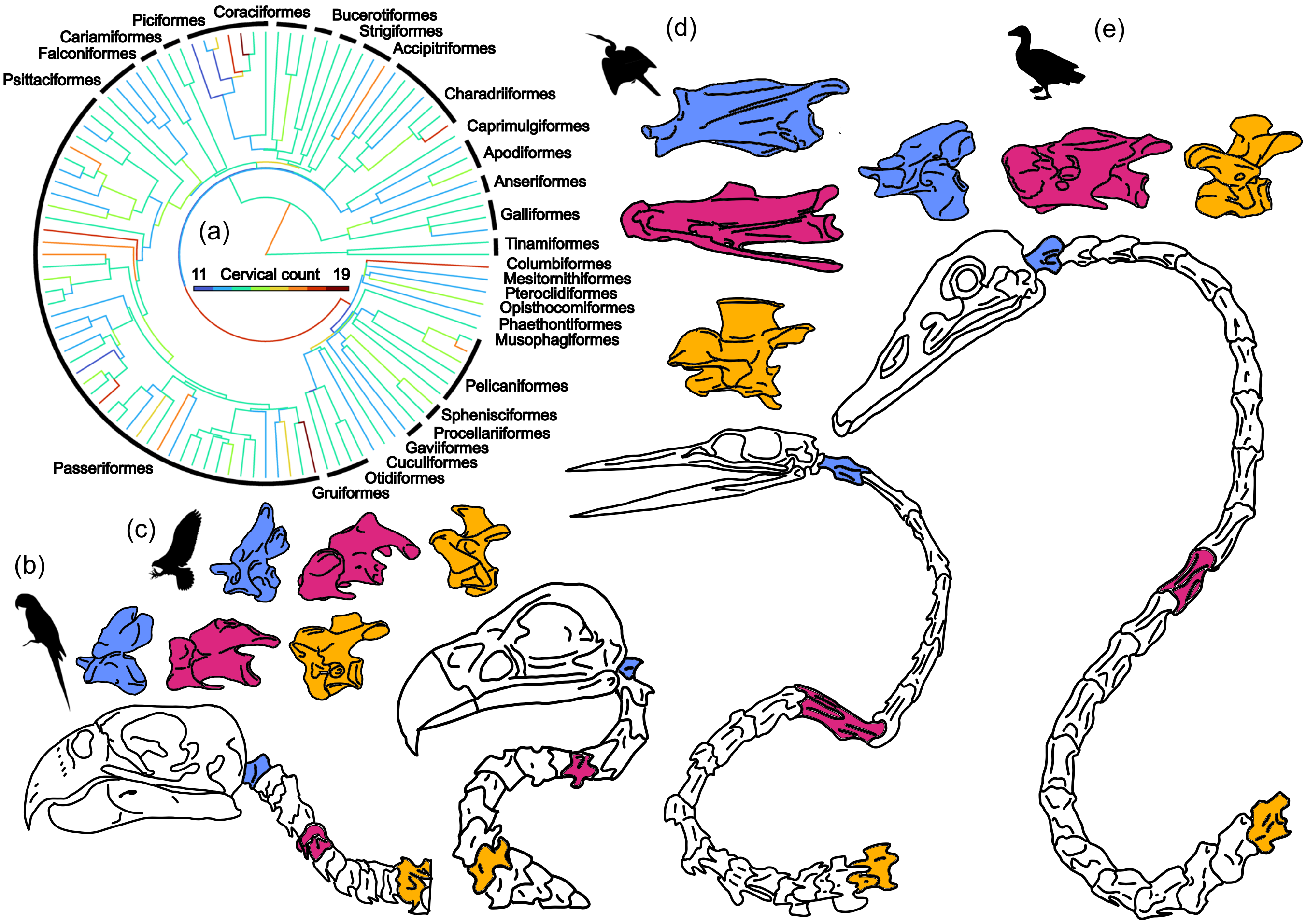

FIGURE 1 A visual summary of the diversity of avian cervical morphology. (a) Variation in counts of cervical vertebrae across 112 species of extant birds due to be included in an upcoming study of avian cervical morphological evolution. Tree topology follows Jetz et al. (2012), branches are coloured according to the number of cervical vertebrae. (b–e) Morphological vertebral variation across the cervical spine of *Strigops habroptilus* (b), *Pandion haliaetus* (c), *Anhinga anhinga* (d), and *Anser fabalis* (e) is represented by C2 (blue), a vertebrae occupying the exact midpoint of the cervical column (pink) and the last cervical vertebrae (gold). Sillouhuettes taken from PhyloPic.org.

change between vertebrate lineages, leading to meristic changes (changes in the vertebral formula) across Vertebrata (Gomez et al., 2008; Müller et al., 2010).

Changes to the shape of vertebrae along the axial column are controlled by sequential *Hox* gene expression in the somitic mesoderm. Over the course of development, multiple overlapping *Hox* genes are expressed, which results in the development of multiple vertebral morphologies across an entire axial column or even within specific axial regions (Burke et al., 1995; Carroll, 1995; Chen et al., 2013; Krumlauf, 1994; Mallo et al., 2010; Wellik, 2009). The boundaries between axial regions are delineated by the expression limits of these *Hox* genes, and create an axial column that is divided into regions of morphologically (and often functionally) distinct vertebrae. Vertebral morphology is not homogeneous within each of these axial regions, and within the avian cervical column, it can vary greatly along the length of the neck (Boas, 1929; Böhmer et al., 2015; Marek et al., 2021; Terray et al., 2020). Again, it is the expression boundaries of *Hox* genes that control this granular variation in cervical morphology, but on a smaller subregional scale. At the time of writing, the expression boundaries of *Hox* genes that delineate vertebral morphology within the neck have only been examined in one bird species, the domesticated chicken, *Gallus gallus domesticus* (Figure 2) (Böhmer et al., 2015; Burke et al., 1995). Expression limits of *Hox A-4*, *B-4*, *C-4*, *D-4*, *A-5*, *B-5* and *C-5* delineate five regions within the cervical column of *G. g. domesticus* (Figure 2). The anterior expression limit of *Hox B-4* and *D-4* form the boundary of region 1 which consists of just cervical vertebrae 2 (C2; Böhmer et al., 2015; Burke et al., 1995). Region 2 is formed from the three immediately proceeding vertebrates (C3–C5) and the posterior regional boundary is formed by the anterior expression limits of *Hox A-4* and *C-4* which is located at the level of C5 (Böhmer et al., 2015; Burke et al., 1995). The next boundary-forming anterior expression limit is formed by *Hox A-5* is located at the level of C7, making C6 and C7 part of the third cervical region (Böhmer et al., 2015; Burke et al., 1995). The fourth region is the largest, consisting of C8–C12 and it is the anterior expression limit of *Hox C-5* at the level of C12 which forms

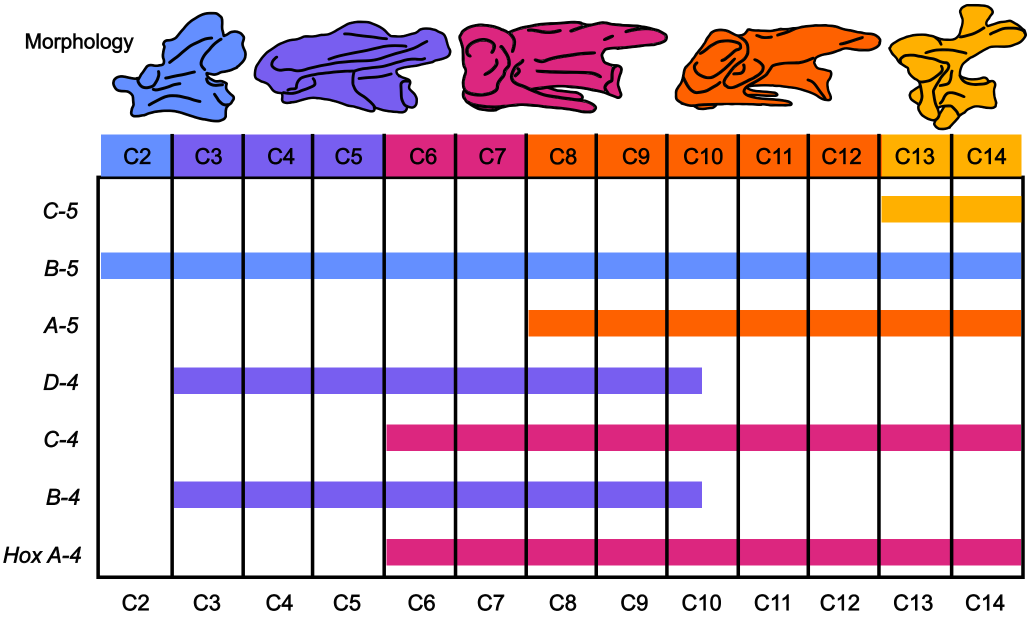

FIGURE 2 *Hox* gene expression limits found within the developing cervical spine of *Gallus gallus domesticus*. These expression limits give rise to a cervical spine that is divided into five morphological regions, the morphology of which is represented above the chart. Colours respond to distinct regional identities: blue for region 1, purple for region 2, pink for region 3, orange for region 4 and gold for region 5. Modified from Böhmer et al. (2015).

the posterior boundary of this region (Böhmer et al., 2015; Burke et al., 1995). Finally, C13 and C14 form the fifth region and the anterior expression limits of *Hox C-6* form the boundary between the cervical and thoracic portion of the axial column (Böhmer et al., 2015; Burke et al., 1995).

The ability to precisely assign *Hox* gene expression boundaries to the morphological variation of specific cervical vertebrae allows us to understand how biotic and abiotic factors influence the underlying genetic patterning of the avian axial column (Böhmer et al., 2015). Unfortunately, the methodological framework to directly assess *Hox* gene expression limits is time and resource expensive, therefore future work should focus upon expanding our knowledge of *Hox* gene expression boundaries within the cervical column to a broader range of extant birds. However, these limitations to study may be soon alleviated as current techniques combine geometric morphometrics with a likelihood-based segmented regression approach (Head & David Polly, 2007; Jones et al., 2018). This new approach provides the most likely number of axial regions as well as the boundaries between these regions and has been used to quantify axial regionalisation in both extinct and extant taxa (Jones et al., 2018; Jones et al., 2020). Applying this new technique to the avian neck will allow researchers to more efficiently model regionalisation patterns across a much larger range of birds and their extinct relatives, allowing for the assessment of what specific factors influence both the morphological variation and underlying genetic pattern of the avian neck. This morphological approach to studying patterns of regionalisation is gaining traction, (Head & David Polly, 2007; Jones et al., 2018; Jones et al., 2020; Marek et al., 2021), however, few studies have investigated how these patterns relate to the underlying *Hox* gene expression boundaries (Böhmer et al., 2015; Criswell et al., 2021), and this relationship should be studied further, in a wide array of vertebrates.

3 | FUNCTION

The musculoskeletal anatomy of the avian neck is highly complex with up to 23 cervical vertebrae (Figure 1) and over 200 paired muscle slips (Figure 3; Baumel, 1993; Benoit et al., 1950; Kuroda, 1962; Marek et al., 2021). Such a large quantity of joints and muscles within a musculoskeletal system leads to an enlarged number of degrees of freedom. This immediately presents a problem when studying the movement and function of the avian neck–kinematic redundancy, where an enormous set of possible combinations of muscle forces and neck joint angles can produce any particular head movement. Fortunately, many of these movements, although mathematically possible, can be excluded as they would result in a biologically unfeasible angle between two adjacent cervical vertebrae (Bout, 1997). By removing biologically unfeasible joint angles from kinematic models, previous studies have calculated that the characteristic 'S'-shaped neck resting posture of birds is maintained by evenly distributing rotation angles across all cervical joints (Bout, 1997).

The complexity of the cervical musculoskeletal system is only equalled by its variability, with adaptations to certain ecological behaviours leading to subtle changes to the neck musculature and vertebral morphology (Böhmer et al., 2020; Boumans et al., 2015; Kuroda, 1962; Zusi & Storer, 1969; Zusi, 1985). However, neck

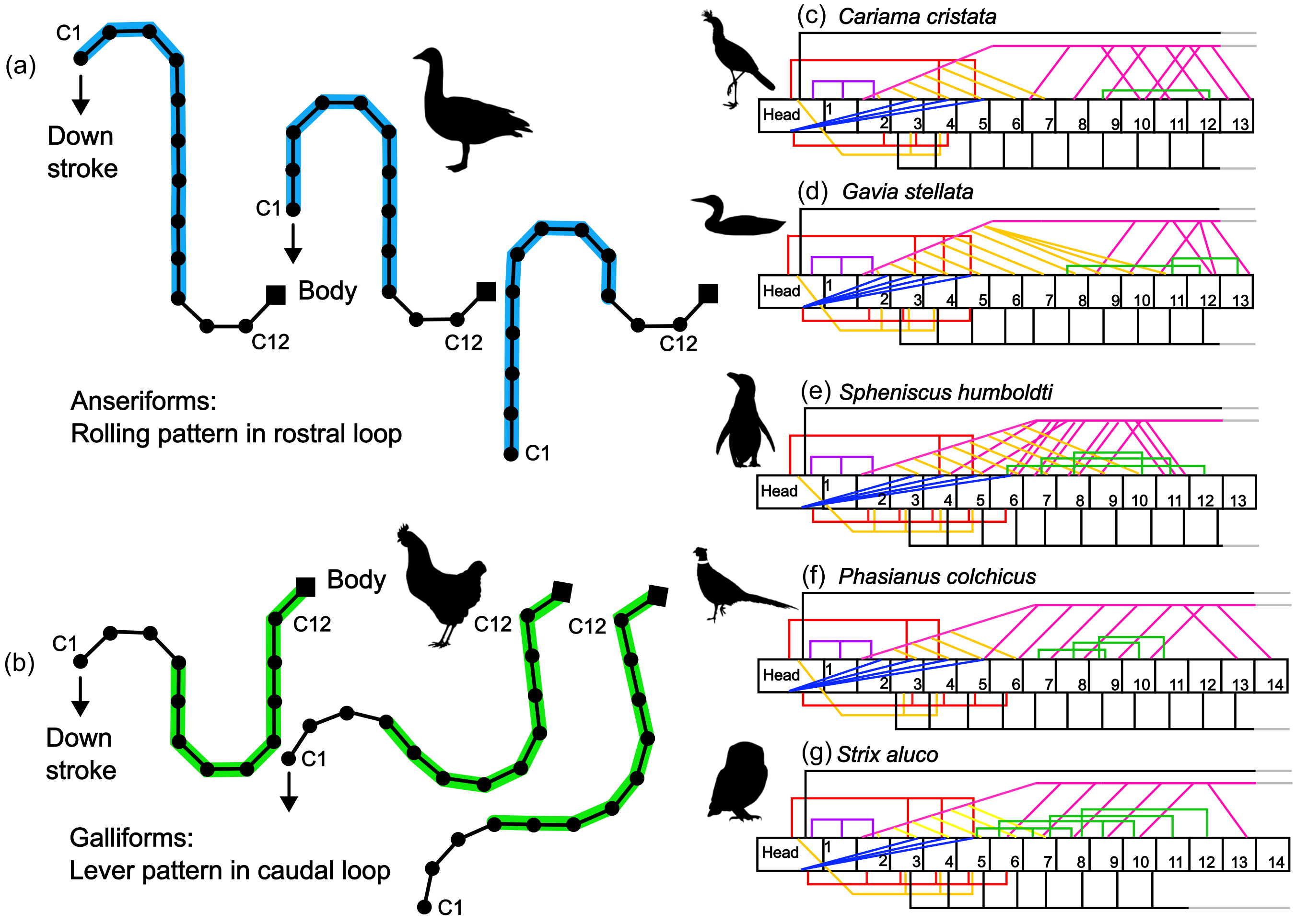

FIGURE 3 Kinematic and myological variation across extant avians. Diagrammatic depiction of kinematic differences between the neck movements of Anseriformes (a) and Galliformes (b), modified from Van der Leeuw et al. (2001). (c–g) Muscle attachment diagrams for five species of birds. Numbered boxes represent the head and cervical vertebrae. Coloured lines are representations of muscles. Dorsal musculature: M. complexus (red), M. biventer cervicis (black), M. splenius capitis (purple), M. longus colli dorsalis pars caudalis (pink), M. longus dorsalis pars cranialis (gold), M. longus colli dorsalis pars profunda (green). Ventral musculature: M. rectus capitis ventralis (red, M. rectus capitis lateralis (Yellow), M. rectus capitis dorsalis (blue), M. longus colli ventralis (black). Dashed lines for M. longus colli dorsalis pars caudalis represent discrete origination slips. Thicker grey bars represent aponeurotic insertions. Animal silhouettes taken from PhyloPic.org.

utilisation in birds is often generalised, with many species using the neck for the same habitual tasks such as eating, drinking, preening and prey, predator/aggressor awareness (Pete et al., 2015; van der Leeuw et al., 2001; Wilkinson & Ruxton, 2012). In this way, the avian neck has been previously stated to adapt to the 'economics of continuous movement' and is classically subdivided into three morphofunctional regions (Boas, 1929; Kambic et al., 2017; van der Leeuw et al., 2001; Wilkinson & Ruxton, 2012; although see Terray et al., 2020). The first region forms the cranial-most curve of the S-shape and allows for predominantly ventral flexion, the middle region occupies the portion of the neck between the cranial and caudal curves and accommodates predominantly dorsal flexion, while the caudal region facilitates both dorsal and ventral flexion to some degree (Boas, 1929; Kambic et al., 2017; van der Leeuw et al., 2001).

Studies that seek to quantify the kinematics of avian neck movement are rare, and studies that compare intraspecific neck function are rarer still. Despite these limitations, prior studies have been able to distinguish patterns of neck kinematics and factors that influence their variation in extant avians (van der Leeuw et al., 2001; Zweers et al., 1994). Two predominant patterns of neck movement have been observed in vivo in relation to pecking and drinking (Figure 3), which are two of the most common and habitual tasks among all birds (van der Leeuw et al., 2001). A lever-like motion pattern exists in Galliformes (Figure 3), whereby some vertebrae in the caudal curve are involved in rotation, and others remain straight in relation to adjacent vertebrae (Heidweiller et al., 1992). The other pattern of neck movement is observed primarily in Anseriformes and consists of a rolling pattern of motion (Figure 3; van der Leeuw et al., 2001). This movement consists of two waves of vertebral rotation that result in a rolling pattern of the cranial curve of the neck during which the external outline of the curve remains similar despite vertebral movements through the outline of the curve (Figure 3; van der Leeuw et al., 2001). Kinematic patterns of neck movement during pecking and drinking have also been observed in vivo in ratites, in which both motion patterns are utilized depending on the task (van der Leeuw et al., 2001). Ratites utilise the anseriform-like rolling pattern of neck motion for multiple neck movements, and employ the galliform-like lever pattern when more horizontal head trajectories are required, that is, during pecking (van der Leeuw et al., 2001). Despite a small sample size, this in vivo work on the kinematics of neck motion in Galloanserae and ratites suggests that generalised neck kinematics is an avian plesiomorphy, and it suggests that cervical kinematics may only adapt to ecologies that require entirely different kinematic regimes such as the transition from terrestrial to aquatic feeding (Heidweiller et al., 1992; van der Leeuw et al., 2001). Recent work analysing the factors that influence variation in avian neck vertebral morphology have supported this suggestion (Marek et al., 2021).

Prior work into the function of the avian neck has largely been restricted to commercially available taxa such as Galloanserae and ratites (Heidweiller et al., 1992; van der Leeuw et al., 2001; Zweers et al., 1994), and it is only within the last decade that the cervical kinematics of neoavians have been investigated (Reader et al., 2022; Snively et al., 2014; Young et al., 2022). Neoaves accounts for almost 95% of extant bird species diversity (Ericson et al., 2006), and contained within this clade is a myriad of specialised functions (Böhmer et al., 2020; Boumans et al., 2015; Chang et al., 2016; Reader et al., 2022; Young et al., 2022). Previous studies on non-neoavian neck kinematics have focused on neck motions and tasks that primarily involve the neck itself (Heidweiller et al., 1992; van der Leeuw et al., 2001; Zweers et al., 1994), when in reality the neck is often utilised in tandem with the hindlimb in a variety of tasks that are more specialised than pecking or drinking (Böhmer et al., 2019; Reader et al., 2022; Young et al., 2022). Raptorial birds present a prime example of how the neck is involved in task-based whole-body kinematics (Snively et al., 2014).

Extant raptors utilise the head, neck and hindlimb in tandem to de-flesh caught prey items and recent in vivo videography studies have observed that multiple stages are involved in the coordinated movements of the neck and the hindlimb (Snively et al., 2014). Upon sighting the prey the raptor will ventroflex the neck and prepare for striking by raising the trunk relative to the femur, or by extending the posterior curve of the neck while further flexing the head ventrally (Snively et al., 2014). The prestrike preparation is followed by a pecking phase whereby the anterior and posterior curves of the neck along with the lowering of the trunk relative to the femur bring the head closer to the prey (Snively et al., 2014). Next, the beak forms initial contact with the prey and the anterior portion of the neck moves to position the head to the appropriate orientation to engage the prey (Snively et al., 2014). Following this the trunk is then raised relative to the femur and the posterior curve of the neck is flexed dorsally during a 'pull' phase (Snively et al., 2014). In the final phase, the head is then raised by dorsiflexion of the anterior portion of the neck and shifts the gaze away from the prey (Snively et al., 2014). In addition to detailing the kinematic regime involved with live prey feeding, these authors also noted some interspecific kinematic variations between raptor species that is based on the varying levels of involvement of the hindlimb in all of the stages before the penultimate 'pull' phase (Snively et al., 2014).

The combined use of the neck and hindlimb is found in another neoavian clade, Psittaciformes (parrots) and is utilised during climbing (Brockway, 1964; Dilger, 1960; Reader et al., 2022; Young et al., 2022). Many birds perform vertical climbing—members of Certhoidea (nuthatches and treecreepers) and Picidae (woodpeckers) climb using synchronous movements of the hindlimb (Fujita et al., 2007; Norberg, 1986), and Chukar partridges (*Alectoris chukar*) ascend surfaces via 'wing-assisted incline running' (Dial, 2003) as do many other species of birds (Heers et al., 2022). However, it is only members of Psittaciformes (parrots) that combine movements of the head, neck and hindlimbs to climb vertically (Reader et al., 2022; Young et al., 2022). Recent in vivo work has focused on this phenomenon in parrots and has found that they have evolved a form of tripedal locomotion whereby the head is used in conjunction with the hindlimb in a tripedal gait cycle during vertical climbing (Reader et al., 2022; Young et al., 2022). During this cyclical tripedal gait, the beak and head provide stability and the necessary propulsive force to ascend vertically. This ascension also involves neck flexor muscles, which have been calculated to be operating at an isometric flexion force of 71% bodyweight, over twice that observed for humans (Valkeinen et al., 2002; Young et al., 2022). The evolution of the head and neck as a propulsive limb in a tripedal locomotory scheme is an evolutionary novelty among Vertebrata that is only present within Psittaciformes (Reader et al., 2022; Young et al., 2022)—this adaptation of the head and neck truly represents the extent of morphofunctional variation that is present with the avian cervical column.

Whereas relatively simple biomechanical principles may govern the overall posture of the avian neck (Boas, 1929; Bout, 1997), it is a complex musculoskeletal system that is required to perform a large variety of tasks to act as an effective surrogate forelimb. As in other vertebrates, complex tasks are achieved by the combination of the kinematic patterns of multiple bodily appendages. These intricacies have made the study of avian cervical kinematics a complex process, however, future work should focus on first principles by quantifying the musculoskeletal (particularly myological) variation found across extant Aves as well as documenting the cervical kinematics of a broader range of neck movements and their associated tasks. This knowledge of the diversity of avian cervical form and function will be useful in informing future work on the tempo, mode and drivers of avian neck evolution.

4 | EVOLUTION

Unlike in mammals (Arnold, 2021; Arnold et al., 2017; Jones et al., 2020), our understanding of the avian neck does not currently extend to its evolutionary history nor how it has contributed to avian diversity and success. The surrogate forelimb hypothesis states that the neck is a key avian trait due to its widespread role in many behaviours and also indicates that avian cervical evolution is correlated with the forelimb and head to accommodate the evolution of a flight-focused wing (Bhullar et al., 2016, p.201; Bhullar et al., 2012; Clarke & Middleton, 2008; Marek et al., 2021). It is only recently that the relationship between avian cervical diversity and ecology has been quantified (Böhmer et al., 2019; Marek et al., 2021). How the evolution of the neck has been shaped by interactions with other anatomical systems, such as potential head–neck–forelimb integration, is as yet unstudied (although see Böhmer et al., 2019). Using 3D geometric morphometrics, recent work has quantified the ecological signal in the morphological variation of the avian neck and found it to be an evolutionary versatile appendage (Marek et al., 2021). This evolutionary versatility is expressed in the neck's hierarchical organisation of functional morphology; that is, differences exist in the magnitudes of phenotypic variation across different morphological scales (Marek et al., 2021). At the macroscale, shape variation across the entire neck is morphologically conservative, and significant excursions from this general model only occur in taxa with mechanically demanding ecological functions (Marek et al., 2021). This widespread conservatism of neck construction suggests that in many cases, the avian neck is adapted to the 'economics of continuous movement', allowing it to perform well as a surrogate forelimb (Marek et al., 2021; van der Leeuw et al., 2001; Wilkinson & Ruxton, 2012).

Mechanically demanding functions that are associated with major changes in neck morphology include specialized feeding behaviours (e.g., carnivory, insectivory) and specialized locomotor behaviours (e.g., soaring, continual flapping; Marek et al., 2021). Carnivory and insectivory are demanding for the neck as they require juxtaposing mechanical demands; the former requires forceful, slow retraction forces to tear flesh from prey (Snively & Russell, 2007) and the latter require fast extension and protraction forces to capture small, rapid prey (Yanega, 2007). Insight into potential constraints on the morphological variation of the avian neck can be gleaned from observing the differences between the two locomotor ecologies which show significantly different macroscale neck morphology, that is, soarers and continual flappers. Soaring birds display increased morphological differentiation of cervical vertebrae at the macroscale compared with continual flapping birds (Marek et al., 2021), and since the neck must counteract the movements of the wingbeat during flight to provide a stable visual acuity (Kress et al., 2015; Pete et al., 2015), this may suggest that flapping flight constrains morphological variation of cervical vertebrae. At the scale of individual cervical vertebrae, morphological variation is correlated with both intrinsic and extrinsic factors (Marek et al., 2021). These factors include neck length, dietary ecology (carnivory) and locomotor ecology (intermittent bounding and terrestriality) and suggest birds have modified certain portions of the neck to allow for specific neck functions while still retaining a generalised pattern of overall neck morphology to perform habitual tasks (Marek et al., 2021).

Very few musculoskeletal systems act in isolation, and often many anatomical modules work in tandem to produce a certain motion or function. Anatomical modules may become integrated when they operate together, and thus may covary with each other as they adapt to disparate mechanical functions (Goswami et al., 2014; Olson & Miller, 1999). The avian neck is often used in conjunction with other anatomical modules, such as the head during feeding, drinking and observance, and the hindlimb during feeding and even tripedal locomotion (Heidweiller et al., 1992; Reader et al., 2022; Snively et al., 2014; van der Leeuw et al., 2001; Wilkinson & Ruxton, 2012; Young et al., 2022). With this knowledge we must not study the evolution of the avian neck in isolation, however little in the way of avian neck integration literature currently exists. Our current understanding of neck integration extends to head–neck and neck–hindlimb integration, however, both of these are restricted to simple metrics of morphology, such as linear and weight measurements (Böhmer et al., 2019; Marek et al., 2021). Neck length scales isometrically with both head mass and total leg length (Böhmer et al., 2019; Marek et al., 2021). Head mass often acts as a major constraint on neck morphology across vertebrates, with neck length being negatively correlated with head mass in other major groups of vertebrates (Arnold et al., 2017; Cardini & Polly, 2013; Cardini et al., 2015). However, this constraint appears to be lifted in birds as the relationship between head mass and neck length is isometric (Marek et al., 2021). The isometric relationship between neck length and total leg length suggests that the neck and hindlimb module are integrated, and this may allow birds to reach the ground with their beaks with an increased leg length (Böhmer et al., 2019). Unlike their dinosaurian antecedents, birds lack a counterbalancing tail and cannot rotate the trunk relative to the hindlimb to move the head and neck to forage at ground level (Böhmer et al., 2019; Grossi et al., 2014), therefore a co-elongation between neck length and the hindlimb length is necessary for the feasibility of ground foraging. However further work is needed to investigate other intuitive integration scenarios for the avian neck, such as neck–forelimb integration. The neck of birds provides compensatory movements to counteract each wingbeat to provide a stable image field (Kress et al., 2015; Pete et al., 2015), and so neck and forelimb morphology may be integrated and could covary to provide stable vision across a broad range of locomotor ecologies. Head shape, size and usage is extremely disparate across extant Aves (Bhullar et al., 2016; Cooney et al., 2017, 2017; Felice & Goswami, 2018), and despite the potential removal of head mass constraint on avian neck morphology (Marek et al., 2021), many avian habitual and specialised tasks still involve the linked use of the head and neck (Heidweiller et al., 1992, 1992; Wilkinson & Ruxton, 2012). It is extremely likely that head–neck integration occurs in birds and future study must quantify this further.

Changes to patterns of integration and modularity over evolutionary timescales can influence the macroevolutionary dynamics of a clade (Goswami et al., 2014). Integration and modularity are key components of avian evolution, as the shift from two locomotor modules (forelimb and hindlimb+tail) to three (forelimb, hindlimb, tail) across the dinosaur-bird transition contributed to the evolution of powered flight (Clarke & Middleton, 2008; Eliason et al., 2023; Gatesy & Dial, 1996). Following this, a decrease of integration between the fore- and hindlimbs allowed for a dramatic increase in locomotor behaviour disparity in extant birds (Eliason et al., 2023). These key transitions have allowed birds to become one of the most successful and speciose extant vertebrate clades, yet the changes in axial morphology and integration that facilitated these modifications have not yet been investigated. The neck of birds is a critical portion of the axial skeleton, as it allows birds to interact with their environment despite a lack of grasping-capable forelimbs (Bhullar et al., 2012, 2016; Marek et al., 2021). Recent work has hinted that this surrogate forelimb hypothesis may provide insight into how the avian neck evolved, through changes to neck–head–forelimb integration (Marek et al., 2021). To truly test the surrogate forelimb hypothesis, future work must quantify the effects of both head size and forelimb shape on neck morphology across the evolution of dinosaurs and early birds. Modern birds display an expanded repertoire of cervical morphology potentially due to the reduced constraint of head mass (Marek et al., 2021), thus we would expect to see cervical morphological variation and rates of neck evolution increase in response to decreasing head masses throughout the evolution of dinosaurs to birds. We would also expect evolutionary rates and morphological variation of the neck to be correlated with changes to forelimb proportions over the evolution of powered avian flight. By quantifying the relationship between the head, neck, and the postcervical skeleton across avian evolution we can quantify this importance and refer to the neck as a key evolutionary trait that, like powered flight, allowed birds to become so speciose and prevalent in modern ecosystems.

5 | CONCLUSION AND FUTURE PERSPECTIVES

By synthesizing almost a century's worth of this work during this review (Boas, 1929; Eliason et al., 2023), it is apparent that although we understand the fundamental principles of neck development, function and evolution in birds there is still much work to be done. Future work must include studies that investigate the anatomical variation of the musculoskeletal system of the avian neck as well as innovative studies that quantify processes on macroevolutionary timescales. The study of model systems and commercially available taxa allows us to study the anatomy, development and function of various vertebrate clades under repeatable conditions. Commercially available taxa have allowed us to understand the fundamental mechanisms behind the development and operation of the avian neck (Böhmer et al., 2015; Heidweiller et al., 1992; Pete et al., 2015; van der Leeuw et al., 2001; Zweers et al., 1994), but much of the diversity of musculoskeletal anatomy and genetic underpinnings of neck morphology remains undocumented across birds. Expanding our understanding of this diversity will help to inform larger studies that seek to understand the macroevolutionary dynamics behind the enormous diversity of avian neck form and function. This review also aimed to celebrate the current breadth of knowledge surrounding the neck of birds. During the last 5 years alone we have observed how the avian neck is an evolutionary versatile appendage, that covaries with multiple other anatomical modules, and can even display functionally relevant musculoskeletal adaptations within a single ecological niche (Böhmer et al., 2019, 2020; Marek et al., 2021; Terray et al., 2020). Across almost an entire century researchers have repeatedly remarked upon the astonishing diversity and complexity of the avian neck (Boas, 1929; Böhmer et al., 2015, 2019; Marek et al., 2021; Terray et al., 2020; van der Leeuw et al., 2001), by continuing to study this remarkable anatomical system we will gain further insight into the evolutionary versatility of the vertebrate axial skeleton. By delving deeper into how the avian neck became a surrogate forelimb, we can elucidate how integration can transfer functional burden to other parts of the skeleton to retain and expand an organism's functional repertoire.

AUTHOR CONTRIBUTIONS

Ryan D. Marek: Conceptualization; writing—review and editing; visualization; writing—original draft.

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CONFLICT OF INTEREST STATEMENT

The author declares no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed in this study.

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PEER REVIEW

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