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Nasal conchae function as aerodynamic baffles: Experimental computational fluid dynamic analysis in a turkey nose (Aves: Galliformes)

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ABSTRACT

We tested the aerodynamic function of nasal conchae in birds using CT data from an adult male wild turkey (*Meleagris gallopavo*) to construct 3D models of its nasal passage. A series of digital "turbinectomies" were performed on these models and computational fluid dynamic analyses were performed to simulate resting inspiration. Models with turbinates removed were compared to the original, unmodified control airway. Results revealed that the four conchae found in turkeys, along with the crista nasalis, alter the flow of inspired air in ways that can be considered baffle-like. However, these baffle-like functions were remarkably limited in their areal extent, indicating that avian conchae are more functionally independent than originally hypothesized. Our analysis revealed that the conchae of birds are efficient baffles that—along with potential heat and moisture transfer—serve to efficiently move air to specific regions of the nasal passage. This alternate function of conchae has implications for their evolution in birds and other amniotes.

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1. Introduction

Conchae are projections of the nasal mucosa lining the nasal passages of most extant amniotes. They vary in complexity from species to species, ranging from simple, hill-shaped evaginations of the nasal capsule to scrolled or variably branching structures arising from either a cartilaginous or mineralized skeleton (i.e., turbinates; Negus, 1956, 1958). Conchae increase the surface area of the nasal mucosa, which aids in physiologically relevant functions such as olfaction and thermoregulation (Hillenius, 1992).

The function of conchae garnered extensive interest in the 1960s and 1970s with the seminal works of Jackson and Schmidt-Nielsen (1964), Schmidt-Nielsen et al. (1970), and Collins et al. (1971) laying the groundwork for nasal passage function and the role of respiratory conchae in maintaining heat and water balance. Several studies later validated these conchal functions across a broad range of species within Amniota (Schmidt-Nielsen et al., 1969; Murrish and Schmidt-Nielsen, 1970; Murrish, 1973; Langman et al.,

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http://dx.doi.org/10.1016/j.resp.2016.09.005 1569-9048/© 2016 Elsevier B.V. All rights reserved. 1979; Schmidt-Neilsen et al., 1981; Schroter and Watkins, 1986). The role of conchae in maintaining body temperature and reducing respiratory evaporative water loss (REWL), coupled with the generally more complicated conchae observed in mammals and birds has led to the hypothesis that respiratory conchae—and the turbinates on which they rest—may be a necessity for the evolution of tachymetabolic endothermy (Hillenius, 1992, 1994; Ruben, 1995; Ruben et al., 1996; Hillenius and Ruben 2004). Whereas this hypothesis has received continued support from studies on mammals (e.g., Van Valkenburgh et al., 2004, 2011; Green et al., 2012), support in birds has been less consistent (Tieleman et al., 1999; Geist, 2000; Michaeli and Pinshow, 2001; Owerkowicz et al., 2015). This inconsistency led us to question if avian conchae had an alternate function beyond just heat and water exchange.

Although there is some variation in their number and placement, most avian nasal passages consist of three conchae: a rostral, middle, and caudal concha (Fig. 1, Bang, 1971; Bang and Wenzel, 1985; Witmer, 1995). The physiological functions of conchae in olfaction and thermoregulation are made possible by the increased surface area that they provide for these diffusion-based processes (Schmidt-Nielsen et al., 1970; Getchell et al., 1980; Hillenius, 1992). However, by simply residing in the path of the respired vector field (air field), conchae have the potential to function as baffles, redirecting air to specific regions of the nasal capsule. This







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Fig. 1. Segmented airway cast of wild turkey (*Meleagris gallopavo*, OUVC 10599) showing the location of the various meatuses within the nasal capsule as shown in (A) lateral and (B) dorsal views. (C) Axial cross sections showing the location of false-colored conchae, and crista nasalis, within the nasal capsule. Abbreviations: at co, atrial concha; caud co, caudal concha; caud meat, caudal meatus; ch, choana; cnp, cavum nasi proprium; cr nas, crista nasalis; mid co, middle concha; mid meat, middle meatus; olf, olfactory recess; ros co, rostral concha; ros meat, rostral meatus; vest, nasal vestibule.

aerodynamic baffling function can be particularly beneficial for olfaction as odorant absorption requires slower airflow speeds for odorant particles to bind to odorant receptors (Mozell and Jadodowicz, 1973; Craven et al., 2010). In contrast, oxygen requirements of the body necessitate faster air speeds that reduce air transport time between the environment and lungs. These dichotomous demands of the nasal passage can be met by anatomically separating the respired air field into a low-pressure, fast-moving respiratory stream and a higher-pressure, slower-moving olfactory stream. Having anatomical structures in the nose that can direct air to various regions of the nasal capsule can thus be advantageous. Prior work on mammalian noses have observed that the nasoturbinate in carnivorans and the inferior turbinate of humans and other primates both function as airway baffles, redirecting air to the olfactory recess and middle meatus respectively (Elad et al., 1993; Churchill et al., 2004; Wexler et al., 2005; Craven et al., 2010). Bang (1971) proposed that the atrial (when present) and rostral conchae were chiefly airway baffles in birds. We sought to test this hypothesis functionally and see if it could be extended to other conchae within the nose of a representative bird.

To test the function of avian conchae in redirecting airflow, we produced a series of 3D models based on CT scans of the airway in an adult turkey (*Meleagris gallopavo*). As members of the basal-branching group Galliformes, turkeys serve as useful model organisms for avian nasal passages. The conchae shape of turkeys are representative of many avian orders (Bang, 1971) and may be close to the ancestral neognathan nasal conchae arrangement. Results obtained from this study can thus be generalized to a variety of different bird groups, making turkeys ideal candidates for nasal passage airflow analysis. We constructed multiple airway models that differed only in which conchae were removed. Models were subjected to a computational fluid dynamic (CFD) analysis that simulated the flow of air through the nasal passage during restful inspiration. If conchae played an appreciable role in redirecting airflow, then the removal of those conchae should produce detectable—and presumably physiologically detrimental—effects on air field characteristics.

2. Materials and methods

2.1. Specimen

To test the effects of conchae on nasal airflow, we used the nasal passage of an adult wild turkey (*Meleagris gallopavo*). The animal was legally harvested in southeastern Ohio completely independently from the authors or Ohio University, and the head of the turkey was later obtained from the hunter as a salvage specimen. It was accessioned into a public repository, the Ohio University Vertebrate Collections (OUVC), as OUVC 10599 under the terms of permit #14-2762 issued by the Ohio Division of Wildlife. The animal had



Fig. 2. Workflow of model creation for OUVC 10599. (A) Axial CT slice through portion of nose located on skull at right, to show the segmentation methodology used to make each model. Note how the rostral concha is ignored during segmentation, producing the R model. (B) Cast of left nasal capsule segmented out in 3D. (C) Model is cleaned of segmentation artifacts and given a series of boundary conditions prior to volumetric mesh generation. Vertical dashed-red line indicates the location of the axial cross section in (D), showing the tetrahedral-hexahedral (tet-hex) hybrid mesh interior. Abbreviations as in Fig. 1.

an approximate mass of 4.94 kg. The specimen was determined to be a young male (Jake) based on the length of the preserved snood (Dickson, 1992).

2.2. CT scanning

The head of OUVC 10599 was CT scanned using Ohio University's MicroCT scanning facility (OU μ CT). The scanner used was an eXplore Locus MicroCT scanner by General Electric. The specimen was scanned at 60 kV at 450 μ A with a slice thickness of 90 μ m. Data were exported in Digital Imaging and Communications in Medicine (DICOM) format for 3D segmentation and extraction in the program Avizo 7.1 (FEI Visualization Sciences Group, Burlington, MA.). Nasal passage data were compared to those of other turkeys found in the collections (OUVC 10624, 10362) where it was determined that OUVC 10599 had conchae representative of turkeys in general.

2.3. Model creation

DICOM data from the microCT scan of OUVC 10599 were used to segment out (i.e., to digitally "fill in") the left airway of the animal (Fig. 2). We segmented only one side of the nasal passage as the presence of a complete nasal septum ensured that each nasal passage would act independently of the other. Thus, airflow movement in one side of the nose should not affect the flow of air in the other side. The segmented airway served as a cast, indicating all of the potential space that air could enter within the nasal passage. The soft-tissue nasal conchae were segmented out so as to better visualize air movement past these structures. Segmented 3D models were converted into volumetric meshes using the program ICEM CFD (ANSYS Inc., Canonsburg, PA). The volumetric models used in this study incorporated a tetrahedral-hexahedral (tet-hex) hybrid mesh (Fig. 2). Hexahedral meshes are preferred over tetrahedral meshes for CFD analyses as they are capable of obtaining the same results as their tetrahedral counterparts at a fraction of the element number, thus reducing computational costs (Aftosmis et al., 1994; Biswas and Strawn, 1998). Unfortunately, hexahedral mesh generation is more time consuming and meticulous than tetrahedral meshing. It is often very difficult to fit hexahedra to unstructured grids such as those that compose organic structures (Blacker, 2001; Ruiz-Gironés, 2011). To alleviate this problem, we used a tet-hex hybrid mesh. The outer shell of the model was comprised of tetrahedra to better capture the anatomical detail whereas the inner core, incorporating most of the air field, was comprised of hexahedral cells (Fig. 2D). This hybrid design allowed for automated mesh generation with only a marginal increase in computational cost compared to a hexahedral-only mesh.

Boundary conditions were assigned to each model. They consisted of a pressure inlet located at the nostril, a pressure outlet located at the choana, and an impermeable wall boundary. Boundary conditions were used to induce physiologically-realistic (i.e., pressure-based) airflow through the models (Fig. 2B).

To ensure grid independence, we performed a solution-based adaptive mesh refinement on each airway model (Table 1, Prakash, 1999; Prakash and Ethier, 2001). This process uses data from a fairly converged solution (see Section 2.7) to determine regions of the mesh where cell count is too low to accurately resolve the flow field. These regions are marked and refined by the program

Table 1

Initial cell resolution and final cell resolution from solution-based Adaptive Mesh Refinement (AMR).

Model	Initial cell resolution	Final (AMR) cell resolution
Original airway	946,441	992,514
A model	879,000	939,065
R model	885,316	1,482,662
AR model	684,801	807,671
M model	1,081,371	1,093,607
C model	1,306,554	1,846,181
MC model	1,085,445	1,098,911
CN model	300,298	867,919

(e.g., by splitting each tetrahedral or hexahedral cell into eight daughter cells). The refined model is then re-run using the same criteria as in the original mesh, and the results are compared between meshes. This process is repeated until the refined mesh returns values that are approximately the same (falling below a predeter-mined margin of error), at which point they are considered to be mesh-independent (Prakash and Ethier, 2001). This method of grid refinement is similar to a standard multi-grid convergence index (Roache, 1994; Craven et al., 2009). However, by using fluid flow criteria and localized refinement, it reduces the need to re-mesh the entire model multiple times, which greatly reduces processing time and saves on computational costs by only refining poorly resolved regions of the model. Using mean velocity magnitude we ran a solution-based AMR until our grids had returned errors <5%.

2.4. Digital "turbinectomies"

To test the effects that the various conchae had on airflow, we digitally removed each concha, accounting for most possible permutations as we proceeded caudally through the nasal passage until we had completely removed all the conchae, resulting in an airway that was only bounded by the walls of the cartilaginous nasal capsule, producing a large empty space somewhat akin to the "bony-bounded" airway of Bourke et al. (2014). For our study, this completely empty nasal passage was referred to as the empty nasal passage (Table 2). Digital removal was accomplished by ignoring the soft-tissues of the conchae in question and "painting" over them using the segmentation tools in Avizo 7.1 (Fig. 2A).

2.5. Respiratory variables

To date there are no data available on resting respiratory variables in wild turkeys. We obtained reasonable resting inspiratory variables from the phylogenetically corrected allometric equations on resting respiratory variables in birds provided by Frappell et al. (2001). Using their equations for inspiration and breathing frequency, we calculated that our 4.94 kg turkey would have inspired 47.2 ml/s (23.6 ml/s for one nostril) and respired at 9.8 breaths/min.

Table 2

Nasal passage permutations tested in this study.

2.6. Analysis

CFD analysis was performed on each model using the commercial software Fluent (ANSYS Inc., Canonsburg, PA.). To determine the appropriate model for analysis (i.e., steady state vs. transient, laminar vs. turbulent), we performed a cross sectional analysis on the nasal passage. Following the methods of Bourke et al. (2014), we took axial cross sections across the length of the nasal passage. From these cross sections, we calculated the average Reynolds and Womersley numbers for the nasal passage. The results of our cross sectional analysis indicated that the nasal passage could be modeled using a time-independent, steady-state analysis (Womersley numbers = 0.14-0.52) and a laminar viscous model (Reynolds numbers = 71-312). Air material properties reflected air at sea level and 30 °C. We used the Semi-Implicit Method for Pressure-Linked Equations-Consistent (SIMPLEC) algorithm in Fluent for our pressure-velocity coupling. We used second-order accurate discretization terms for momentum and pressure along with a node-based gradient for our individual models.

2.7. Convergence

CFD analysis is an iterative process. As such, the values of the variables being calculated will change from iteration to iteration. The difference in these values between iterations reflects imbalances in the calculation, or the residuals of error (Tu et al., 2012). The lower the residual of error for the variables of interest, the more refined the solution and the closer it is to its "true" value (i.e., residual of error = 0). Depending on the variable being measured, the acceptable amount of error will vary. In general, global errors for momentum and pressure are considered acceptable at a level of 10e⁻³ (Tu et al., 2012). However, for physiological simulations, a level of $10e^{-4}$ is preferred (Craven et al., 2009). When the residuals of error have reached a designated level of acceptability, the simulation is considered converged. Although global variables such as momentum and continuity can provide a superficial view of how converged an analysis is, it is generally recommended that one directly monitor the convergence of one's flow variables of interest (Fluent, 2006; Tu et al., 2012), which can be accomplished by using custom monitoring surfaces that are designed to record data from a single location (point surfaces).

For our analysis, convergence was determined when the residuals of error for momentum and continuity fell below $10e^{-4}$. Surface point models were placed along the models to further monitor convergence of specific criteria (velocity magnitude and pressure). A "flatlining" of these surface point values indicated a lack of change between iterations and, thus, convergence.

2.8. Data comparisons

Velocity and pressure data were compared using area-weighted average surface integrals of specific regions within the nasal

	Soft tissue present ($$) or absent (X)					
Model	Atrial concha	Rostral concha	Middle concha	Caudal concha	Crista nasalis	
Original airway	\checkmark	\checkmark	\checkmark	\checkmark	\checkmark	
A model	Х	\checkmark	\checkmark	\checkmark	\checkmark	
R model	\checkmark	Х	\checkmark	\checkmark	\checkmark	
AR model	Х	Х	\checkmark	\checkmark	\checkmark	
M model	\checkmark	\checkmark	Х	\checkmark	\checkmark	
C model	\checkmark	\checkmark	\checkmark	Х	\checkmark	
MC model	\checkmark	\checkmark	Х	Х	\checkmark	
CN model	Х	Х	Х	Х	\checkmark	
Empty model	Х	Х	Х	Х	Х	

Table 3Pressure change differences between the various permutations of wild turkey(Meleagris gallopavo OUVC 10599) nasal passage under the same flow rate. Pressureinformation represents mean pressure values (below atmospheric) throughout thenasal passage.

Model	Average pressure (Pa)
original airway	-9.6
A model	-7.5
R model	-7.8
AR model	-5.8
M model	-7.9
C model	-10.2
MC model	-8.0
CN model	-4.8
empty model	-0.8

capsule using the built-in features of Fluent. The CFD module for Avizo (Avizo Wind) was used for post-processing and visual analysis of the fluid dynamics data. For specific velocity magnitude comparisons, a region-of-interest (ROI) box was placed around specific portions of the nasal capsule (e.g., just the nasal vestibule) and the average velocity magnitude was calculated using the built-in functions of Avizo Wind 7.1.

3. Results

3.1. Anatomy

The nasal passage in turkeys houses four nasal conchae (Fig. 1). Just deep to the nostril, inside the nasal vestibule (vestibulum nasi), there is the short, partially coiled (approximately one-half of a scroll) atrial nasal concha. Deep to that is the larger rostral nasal concha. This concha retains the same shape as the atrial concha, albeit at a larger scale such that the atrial concha rests inside the lateral aspect of the rostral concha (Fig. 1). Both conchae reside within the nasal vestibule where they are covered in stratified squamous epithelium similar to-though not as keratinized as-the skin (Bang, 1971). Despite this seemingly dry epithelial coating, the rostral concha may still be well vascularized (Bang, 1971). Immediately caudal to the rostral concha, at the terminus of the nasal vestibule, the floor of the nasal passage (solum nasi) rises up to form a fleshy crest known as the crista nasalis (Bang, 1971). This structure constricts the passage between the nasal vestibule and the cavum nasi proprium (CNP). Inside the CNP resides the more complicated middle nasal concha. The middle concha in turkeys is a well vascularized structure that scrolls 1.5 times before exiting into the short nasopharyngeal duct (ductus nasopharyngeus, Fig. 1). The middle concha is covered by mucociliated respiratory epithelium (Bang, 1971). The final concha found in turkeys is the olfactorybased caudal nasal concha. It resides in the caudodorsal region of the CNP, dorsal to the middle concha. It forms a bubble-shaped hillock within the olfactory recess of the nasal passage (Fig. 1). As expected for a structure located in the olfactory recess, the caudal concha is covered in olfactory epithelium (Bang, 1971).

3.2. Air speed and pressure distribution

Average nasal capsule velocity magnitude stayed fairly constant between treatments, whereas pressure distribution between the various permutations of the turkey nasal capsule revealed appreciable changes in the overall pressure gradient following the removal of different conchae (Table 3). In general, as more softtissues were removed, the increased space within the nasal capsule produced more homogeneous pressure distributions. These reductions reached their zenith in the empty airway model which had the most homogenous pressure distribution and air velocities of all the models tested (Table 3).

3.3. Original airway

In the original airway, air entered from the nostril where it immediately encountered the atrial concha nested within the lateral aspect of the rostral concha. This caused a splitting of the air field into a small lateral air channel and a larger medial air channel (Fig. 3A). Air streams wrapped around the medial aspect of the atrial concha, moving at relatively high velocity across much of the lateral aspect of the rostral concha before proceeding caudoventrally towards the CNP (Fig. 3A). The presence of the large rostral concha ensured that a medial channel of air was maintained throughout the majority of the nasal vestibule. Few medial air streams were observed crossing ventrolaterally under the rostral concha. As air proceeded caudally, a large portion of the air field passed medially around the base of the crista nasalis prior to arcing over it and entering the CNP (Fig. 3B). Air in the CNP was tightly constrained by the shape of the coiled middle concha, which maintained strong separations between slower moving medial and faster moving lateral air streams (Fig. 3C). Most medial air streams entered the caudal meatus where they proceeded across the caudal concha in a caudomedial direction (Fig. 3D). A slightly raised region of the nasal passage on the dorsal surface of the middle concha-which we refer to as the entrance to the olfactory recess (aditus olfactorius)-partially split incoming olfactory air into medial and lateral streams. These air streams later anastomosed deeper within the olfactory recess. Lastly, the entire nasal air field anastomosed at the entrance to the nasopharyngeal duct, producing a single channel of air that exited via the choana.

3.4. Atrial concha removal (A model)

Removal of the atrial concha resulted in a much shallower pressure gradient in this region of the nasal vestibule. Air pressure within the atrial meatus of the A model was 1/4th the magnitude of the atrial meatus in the original airway (Fig. 4). Inspired air formed vortices along the lateral aspect of the rostral concha (Fig. 4). This vorticity, coupled with the shallower pressure gradient, slowed down the velocity of the inspired air in this region of the nose (Table 4), increasing its transit time through the nasal capsule. Unlike with the original airway, airflow across the lateral aspect of the rostral concha was more restricted with the atrial concha removed. An airflow vortex localized air along the center of the lateral aspect of the rostral concha (Fig. 4). Some air streams were observed passing ventrally along the rostral portion of the rostral concha. Air that passed ventrally and caudoventrally along the rostral concha appeared the same regardless of atrial concha removal, indicating that the atrial concha's effect on airflow was limited to its local region.

3.5. Rostral concha removal (R model)

Removing the rostral concha produced a much shallower pressure gradient as compared to the original airway. This resulted in large drop in local velocity magnitude (Table 4) in this region of the nose (Fig. 5). The presence of the atrial concha in the R model resulted in the air field splitting into lateral and medial streams similarly to what was observed in the original airway. However, unlike the original airway model, this splitting of the air field was not maintained. In the R model, air passed medially over the atrial concha where it formed a slight vortex as it continued caudoventrally towards the lateral aspect of the rostral meatus (Fig. 5). This vorticity continued into the entrance of the middle meatus of the CNP. A portion of the air field passed dorsomedially over the atrial concha



Fig. 3. Airflow through the original airway model of a wild turkey (*Meleagris gallopavo*, OUVC 10599). (A) Selected air streams through the nasal vestibule. (B) Airflow around the crista nasalis. (C) Airflow through the middle concha. (D) Airflow through the caudal concha. Arrows represent paths of major air channels.



Fig. 4. Airflow and pressure comparisons between the A model (removal of the atrial concha) versus the original airway model of a wild turkey (*Meleagris gallopavo*, OUVC 10599). Red dashed line on skull indicates location of cross sections. *Upper left*: Axial cross sections showing changes in the pressure gradient across the nasal vestibule after atrial concha ablation. *Bottom insets*: Particle plots within the nasal vestibule showing differences in airflow patterns after atrial concha ablation. Note the formation of a vortex along the lateral aspect of the rostral concha. Abbreviations: at meat, atrial meatus. All other abbreviations as in Fig. 1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

where it hugged the medial wall of the nasal capsule and entered the CNP medially. These medial air streams were most similar to the air streams that represented olfactory flow in the original airway model. Maintenance of these olfactory channels was weak with large portions of the vestibular air field reflecting off the medial wall of the nasal passage and continuing ventrolaterally through

Table 4

Comparison of local air velocities in relevant regions of the ablated models and the original airway model. Measurements were taken from the same region of the air field in the original airway and ablated models.

	Airflow velocity					
Model	Atrial meatus	Rostral meatus	Middle meatus	Caudal meatus		
Original airway	0.62	0.67	0.61	0.39		
A model	0.61	-	-	_		
R model	_	0.64	-	_		
AR model	_	0.47	-	_		
M model	-	-	0.54	_		
C model	-	-	-	0.60		
MC model	_	-	0.55	-		



Fig. 5. Airflow and pressure comparisons between wildtype and R model (removal of the rostral concha) of a wild turkey (*Meleagris gallopavo*, OUVC 10599). Red dashed line indicates location of cross sections. *Top*: Axial cross sections (CS) through the nasal vestibule showing changes in pressure distribution between models. *Bottom*: Rostrolateral view through nasal vestibule showing increased vorticity within the R model as opposed to the original airway. Abbreviations as in Figs. 1 and 3. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the nasal passage. Air streams largely bypassed the base of the crista nasalis during inspiration. Airflow between the original airway and R model became equivalent upon entrance into the CNP, indicating the limits of the rostral concha's effect on air flow.

3.6. Atrial and rostral concha removal (AR model)

Ablation of both atrial and rostral conchae produced a drop in local velocity magnitude that was greater than that observed in either the A or R models (Table 4). The static pressure gradient within the nasal vestibule was very shallow, with static pressure throughout the nasal vestibule of the AR model being only 1/3rd the magnitude of the original airway (Fig. 6). Air in the nasal vestibule of the AR model swirled across the nasal capsule, producing a large vortex (Fig. 6). Air entered the laterally-placed nostril where it banked off the nasal capsule's medial (septal) wall and continued to arc across the rostral meatus. The AR model exhibited homogenous airflow throughout the rostral meatus (Fig. 6) with only a few of the ventral air streams passing by the base of the crista nasalis. As with the A and R models, airflow patterns in the AR model became equivalent to the original airway at the level of the CNP, suggesting limited influence of these conchae on the inspired air field.

3.7. Middle concha removal (M model)

Air exiting the nasal vestibule, traveled through the middle meatus of the M model at lower velocities than air from the same region of the original airway model (Table 4). A minor jetting of the air field was observed as it passed by the crista nasalis and entered into the larger CNP (Fig. 7). This increased velocity was short-lived as the air field spread across the open space of the middle meatus, resulting in slower moving air in this region of the nose as compared to the original airway model. The air field within the nasal vestibule was undisturbed by middle concha ablation.

Despite the increased space provided by middle concha removal, the air field proved to be remarkably limited in its coverage of the middle meatus. We observed velocity stratification within the middle meatus of the M model. Most air channels were localized to the center of the middle meatus (Fig. 7). The ventral portion of the middle meatus contained recirculating air streams. This ventral air recirculation produced a barrier to entry for most of the air



Fig. 6. Airflow and pressure comparisons between the original airway and AR model (removal of both atrial and rostral conchae) of a wild turkey (*Meleagris gallopavo*, OUVC 10599). Red dashed lines indicate location of cross sections. *Left top:* Axial cross sections (CS) through the nasal vestibule showing homogenization of pressure in the AR model compared to the original airway. *Left bottom:* Axial cross section of velocity streamlines passing through the nasal vestibule show enhanced vorticity within the AR model. *Right:* Particle plots showing general airflow patterns in the original airway and AR models during inspiration. Abbreviations as in Fig. 1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

field, resulting in the stratified velocity field within the CNP. Air entering from the nasal vestibule moved in a fairly straight path caudally towards the nasopharyngeal duct. A noticeable mediolateral angling of the air field was noticed as air banked off the medial and ventral aspect of the rostral concha and entered the CNP medially, where it proceeded caudolaterally towards the nasopharyngeal duct. This airflow pattern held true for all of the CNP air field save a few of the most medial streams. These streams drifted caudodorsally into the olfactory recess. Surprisingly, air that entered the olfactory recess traversed it in a near identical fashion to air in the original airway model (Fig. 7), albeit at slower speeds in the M model (25 cm s^{-1} for M model. 36 cm s^{-1} for original airway model).

3.8. Caudal concha removal (C model)

Unlike the other airway models tested, there was a noticeable increase in local air field velocity magnitude upon ablation of the caudal concha (Table 4). Removal of the hillock-shaped caudal concha increased the volume of the olfactory recess by 44%. This increased volume acted as a reservoir for inspired olfactory air, drawing most of the nearby air field into it (Fig. 8). In the ablated model, olfactory air entered the caudal meatus similarly to the original airway model. However, with the increased volume of the olfactory recess, much of the air field filled the now open lateral aspect of the caudal meatus. A more even pressure draw from the nasopharyngeal duct in the C model as compared to the original airway model, resulted in multiple air streams fanning caudoventrally from the lateral aspect of the caudal meatus to the nasopharyngeal duct (Fig. 8). Air stream splitting via the aditus olfactorius, was maintained for a shorter distance in the C model as compared to the original airway. Unlike with the previous models tested, removing the caudal concha actually steepened the pressure gradient, resulting in noticeably lower pressures within the olfactory recess (Fig. 8) for the C model as compared to the original airway. Local pressure in the olfactory recess of the C model increased in magnitude by 13%, resulting in an appreciable increase in olfactory velocity magnitude compared to the original airway model ($60 \text{ cm s}^{-1} \text{ vs.}$ 39 cm s⁻¹, respectively).

3.9. Middle and caudal concha removal (MC model)

The removal of both conchae within the CNP resulted in a decrease in local velocity magnitude (Table 4). Air field patterns were very different from what that observed in the original airway model (Fig. 9). In the MC model, a relatively slow moving air stream ran along the medial wall of the nasal capsule. Air entering from the nasal vestibule continued caudally in a mediolateral spiral towards the nasopharyngeal duct (Fig. 9). Air field stratification was evident and similar to that observed in the M model (Figs. 7 and 9). The majority of the air field remained localized to the center of the middle meatus. Airway stratification was more exaggerated in the MC model than in the M model. Dorsal-most air streams entered the olfactory recess where, as in the C model, the air streams continued laterally across the recess before diving ventrally into the rest of the CNP (Fig. 9). However, unlike in the C model, airflow through the olfactory recess formed a large ventrally-directed vortex. In the absence of both middle and caudal conchae a substantial portion of the ventral air field moved in a counterintuitive direction during inspiration (Fig. 9). As with the M model, this ventral, recirculating air channel was slower-moving and acted as a barrier for much of the inspired air field, keeping air coming from the nasal vestibule from immediately entering the ventral portion of the middle meatus.



Fig. 7. Airflow and pressure comparisons between original airway and M model (removal of the middle concha) of a wild turkey (*Meleagris gallopavo*, OUVC 10599). Red dashed lines indicate location of cross sections. *Left top:* Axial cross sections (CS) showing total pressure in the original airway and M model. *Left bottom:* Axial cross sections showing velocity streamlines of air field shape between the original airway and M model. *Right:* Medial view of nasal capsule with inspiratory airflow in the original airway and M model. Note the distinct jetting and vorticity present in the M model when the middle concha is removed. Arrows color-coded for flow type. Red = Respiratory flow Blue = Olfactory flow. Abbreviations as in Fig. 1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.10. Only crista nasalis present (CN model) and without conchae (empty model)

Airflow through the CN mode and empty model were largely consistent with each other (Fig. 10), with the exception of a large arcing effect that occurred at the junction of the nasal vestibule and CNP. This arcing effect was produced by the crista nasalis (Fig. 10). In the absence of the crista nasalis (empty model), air was able to pass directly through to the nasopharyngeal duct. This resulted in fewer air streams within the olfactory recess of the empty model as compared to the CN model. In contrast, in the CN model more of the air field reached the olfactory recess due to air launching off the crista nasalis (Fig. 10).

4. Discussion

4.1. Critique of methods

The results observed in our analysis of turkey nasal passages are contingent on our initial assumptions of bird respiration and the energetics of the flow field (i.e., laminarity vs. turbulence). Although there are currently no empirical data available for resting respiration rates and tidal volumes in turkeys, we felt that the data provided by Frappell et al. (2001) were suitable for our analysis. Nonetheless, it is pertinent to note that in an analysis of their data, Frappell et al. (2001) found that Galliformes differed from other birds in having a tidal volume that was 2.3 times larger. This larger tidal volume, coupled with their estimated breathing rate (which was not found to differ from other birds) would have increased flow rate by 15%, suggesting that our initial airflow estimate was too low. However, using the confidence intervals provided by Frappell et al. (2001), an upper-most volumetric flow rate for a 4.9 kg turkey was estimated to be 77 ml/s (38.5 ml/s for one nostril), which is 1.6 times higher than our mean estimate of 47 ml/s (23.5 ml/s for one nostril). Cross sectional analysis with this higher flow rate produced only a modest increase in the Reynolds number (Re=174-612). This suggests that laminarity of the flow field would be maintained across all of these flow rates. To further ensure stability of the flow field patterns observed, we tested the original airway model using a series of increasingly higher flow rates until breakdown of the observed air field occurred (Fig. 11). Our results found that flow pattern stability was retained up to 300 ml/s (150 ml/s for one nostril), when turbulence began to develop. Yet even then, turbulence was limited to specific regions of the nasal passage (Fig. 11). This flow rate was 6.4 times higher than the mean estimate from Frappell et al. (2001) and four times as high as the maximum flow rate estimated from their confidence intervals. These results agree well with previous works that found flow field patterns remain stable across a fairly large range of volumetric flow rates (Bourke et al., 2014) and even under different viscosity models (Jiang and Zhao, 2010; O'Brien and Bourke, 2015). As such, we feel confident that our choice of a laminar viscosity model and our estimated flow rate were suitable assumptions for our nasal passage models.



Fig. 8. Airflow and pressure comparison between the original airway and C models (removal of the caudal concha) of a wild turkey (*Meleagris gallopavo*, OUVC 10599). Red dashed line indicates location of cross sections. *Left:* Axial cross sections (CS) through the olfactory recess showing the increased volume of the C model compared to the original airway along with the corresponding pressure decrease in the former. *Right:* Dorsal view of the nasal capsule comparing inspiratory flow in the original airway and C model. Original airway olfactory flow covered a greater mediolateral arc than the C model, which stayed largely in the lateral portion of the olfactory recess. Abbreviations: ad olf, aditus olfactorius. All other abbreviations as in Fig. 1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



Fig. 9. Airflow and pressure distribution within the MC model (removal of both middle and caudal conchae) of a wild turkey (*Meleagris gallopavo*, OUVC 10599) during inspiration. *Left:* Medial sagittal sections through the highlighted region shown on the turkey skull (red dashed line). Cross sections show pressure distribution and air streams through this region of the nasal capsule. Air streams are color coded for velocity (warmer colors = faster flow). Flow is compared to the original airway model. *Right:* Inset showing flow pattern in the MC model from a medial and dorsal perspective. Abbreviations as in Fig. 1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



Fig. 10. Airflow comparison between the original airway, CN model (removal of the crista nasalis), and the empty airway (removal of all soft-tissue structures). Arrows show major flow patterns and are color coded for flow type (Red = respiratory, Blue = olfactory). Abbreviations as in Fig. 1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4.2. Conchae as baffles

The atrial and rostral conchae in birds are comprised of stratified squamous epithelium (Bang, 1971), a common epithelial type for structures within the nasal vestibule (e.g., Parsons, 1970; Harkema, 1992). This contrasts with the ciliated or respiratory epithelium that tends to cover the rest of the nasal passage (Parsons, 1970; Bang, 1971; Harkema, 1992). This alternate epithelial coating for the atrial and rostral conchae led Bang (1971) to hypothesize that these conchae offered an alternative function to warming inspired air, and instead these conchae acted as airway baffles that redirected air to specific parts of the nasal passage. We found support for this hypothesis upon removal of the atrial concha. This concha provided a strong directional force for inspired air and maintained a distinctive lateral channel of air across the rostral concha (Fig. 4). This channel of air traversed more of the nasal vestibule than it would have otherwise, banking off the crista nasalis prior to entering the CNP. A similarly strong baffling function was observed in the rostral concha, as its presence produced a distinct medial channel of air. This channel of air ultimately made its way into the olfactory recess. Maintenance of airflow separation during inspiration may be advantageous for odor discrimination. Interestingly, the rostral concha appears necessary for air to move around the base of the crista nasalis (Fig. 12A). The base of the crista nasalis receives the products of the nasal gland and acts as a reservoir (vestibular cis-

terna Bang and Wenzel, 1985). Dry air passing over this reservoir vaporizes the fluid, partially humidifying the air prior to entering the CNP. When the rostral concha was removed no moving air passed over this reservoir (Fig. 12A). These results indicate that the baffle function of the rostral concha is necessary for proper humidification of incoming air streams and that rostral concha removal may significantly alter the moisture content of inspired air within the nasal passage. Recently, physical concha ablation treatments in emus (Owerkowicz et al., 2015) revealed that the trachea in birds is capable of compensating for ablated conchae where heat transfer is considered. Although not measured, these benefits likely extended to airway humidification as well given that tracheal mucosa is very similar to respiratory conchae in its histology (Owerkowicz et al., 2015). These results suggest that the elongate tracheae of birds may provide a complementary air conditioning function for respired air, reducing the need for highly efficient nasal conchae. That the nasal passage of birds still appears to function as the initial stop for inspired air humidification is not unexpected. Nasal gland products are also known to drain into the nasal vestibules of mammals (Bojsen-Møller, 1964) and reptiles (Parsons, 1970), suggesting that the air conditioning properties of the nasal passage are a plesiomorphic trait for Amniota.

Within the CNP, airflow separation was produced solely by the middle and caudal conchae regardless of the flow patterns imparted by the more rostral conchae. This indicated that airflow baffling is



Fig. 11. Results of a sensitivity analysis performed on the original airway of a wild turkey (*Meleagris gallopavo*, OUVC 10599). Inset boxes highlight the portions of the air field around the nasal vestibule (A) and olfactory recess (B), where air patterns began to break down between flow rates. Flow rate numbers represent flow rate through one side of the nasal passage only (i.e., flow through one nostril).



Fig. 12. (A) Comparison of airflow around the base of the crista nasalis of a wild turkey (*Meleagris gallopavo*, OUVC 10599) in the relevant airway models during resting inspiration. (B) Diagram showing two different means of transferring heat and odorant molecules in a nasal passage. Parallel segmentation of the air field (red arrow) may be advantageous over serial air flow when the cost in anatomical space is great. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

a more localized process than we had previously suspected. The only observed effect of the rostral conchae on CNP airflow was on the speed and strength of the incoming air jet. The smaller calibers of the airway in the original airway nasal vestibule imparted a higher airway velocity, which translated into an overall greater jetting effect for the air field entering the CNP. When the middle concha was present, this jetting effect was delayed until the air field reached the nasopharyngeal duct. When the middle concha was removed, the air field jetted immediately from the nasal vestibule into the CNP. With only the crista nasalis present in the M and MC models (Figs. 7 and 9), this air jet traveled quickly along the surface of the crista nasalis. However, the relatively sharp corners of this nasal structure compared to the more canal-like conchae, created a deceleration zone immediately caudal to the crista nasalis, followed by flow separation and vortex formation. This vortex-shedding zone acted as a barrier for air passing through the CNP, resulting in the majority of inspired air traveling through the mid-portion of the middle meatus, with the ventral portion containing relatively slowly recirculating flow (Figs. 7 and 9). This fluid dynamic pattern was reminiscent of airflow over non-aerodynamic trucks (e.g., Wang et al., 2009; Ha et al., 2010).

Ablation of the crista nasalis removed this vortex-shedding zone and produced nearly completely homogenous flow throughout the nasal passage during inspiration, with resulting low olfactory flow (Fig. 10). These results suggest that, along with aiding air humidification during inspiration, the crista nasalis can function as a ramp to launch air from the nasal vestibule into the vaulted olfactory recess.

Although turkeys are hardly renowned for their olfactory prowess (Pelham and Dickson, 1992), the relatively simple caudal concha of turkeys still produced noticeable-and physiologically important-differences in the air field when it was present. Unlike some other birds (e.g., Turkey vultures; Bang, 1971) and many other macrosmatic animals such as dogs and crocodylians (Weldon and Ferguson, 1993; Craven et al., 2010), turkeys do not have a blind olfactory recess. The caudoventral end of the olfactory recess is confluent with the nasopharyngeal duct, allowing the full draw of pressure from the lungs to affect airflow within the olfactory region along with producing olfactory washout during expiration. Nonetheless, the presence of the caudal concha did provide a buffer to this pressure drop. The dorsolateral portion of the caudal concha formed a pocket of relatively higher-pressure air that was buffered from the effects of the nasopharyngeal duct (Fig. 8). This shallower pressure gradient within the olfactory recess slowed down air streams passing through it. This would have provided more time for odorant molecules to bind to olfactory receptors. As with the crista nasalis, we found it impressive that these rather simplistic geometries were sufficient to produce noticeable differences in pressure and concomitant olfactory flow within the nasal capsule.

The nasal anatomy of turkeys is characteristic of Galliformes and many other avian orders (Bang, 1971). Thus, the results obtained from our experimental simulations may broadly be applied to other bird groups. Our analyses support the hypothesis that avian conchae do have a baffle-like function, minimally in turkeys but probably in other birds, as well. This ability to partition and redirect air to certain regions of the nose is beneficial for the various physiological functions of the nasal capsule. In turkeys, medial air channels have the capacity to move air at slower speeds through to the olfactory recess where pressure buffering from the caudal concha can further slow down air around some of the olfactory epithelium. Lateral air channels can move at a higher speed, decreasing transit time through the nose and into the lungs for oxygenation of the body. These results agree well with previous analyses that have observed a baffle-like function for some of the conchae in mammals (Elad et al., 1993; Churchill et al., 2004; Craven et al., 2010). Whether conchae evolved as baffles or were exapted for this

function is beyond the scope of this analysis. Regardless, the benefits of this function are readily observable.

4.3. Laminarity and airway partitioning

The presence of largely laminar flow both predicted (see Section 2.6) and observed in the turkey nasal passage agreed well with other resting respiration studies that showed laminar airflow to dominate the nasal passage during restful respiration (Schmidt-Nielsen et al., 1970; Hahn et al., 1993; Craven et al., 2009; Jiang and Zhao, 2010; Bourke et al., 2014). Similar to previous authors (Churchill et al., 2004), we found that respiratory conchae/turbinates-counter to their name-seem to reduce turbulence rather than promote it. The presence of conchae in the nasal capsule greatly decreases airway caliber which steepens the local pressure gradient, imparting an increased velocity magnitude to the local air field. Despite higher velocities, these small airway calibers promote stability of the flow field via increased nasal wall surface area. In contrast, removal of conchae produced large spaces within the nasal passage that did promote vortex formation in some regions (see Sections 3.8 and 3.9). That conchae appear to promote laminar flow seems counterproductive for thermoregulation. Laminar flow is less efficient at heat transfer than turbulent flow due to the development of a non-motile boundary layer at the nasal-wall-air interface. This boundary layer creates an obstacle to energy transfer from the air to the mucosa (Vogel, 1994). In contrast, turbulent flow breaks up this boundary layer, promoting greater heat transfer at the air-wall boundary. However, the chaotic nature of turbulent flow is more costly in terms of nasal resistance. Under laminar flow, resistance increases linearly with velocity (Vogel, 1994). With turbulent flow, the localized pressure drops that occur during vortex formation cause resistance to increase by the square of velocity in narrow passageways such as the nasal capsule. Higher resistance can greatly increases the energetic cost of moving air through the nose (Swift, 1982; Vogel, 1994). It appears that the costs of moving turbulent air through the nasal passage outweigh any potential thermoregulatory benefits. Birds have incorporated other less energetically demanding means of reducing boundary layer thickness, such as increasing air field velocity. Higher velocity air flow has an inverse effect on boundary layer thickness (Vogel, 1994). Similarly, the small transverse distance of the air field between these conchae, coupled with their increased surface area partially caused by the curving of the conchae, further promotes bulk heat transfer in laminar flowing air (Schmidt-Nielsen et al., 1970), ultimately producing an efficient heat exchange mechanism with only a minimal cost in respiratory energetics. Although we did not test heat exchange in the nose of our turkey models, our observations of the anatomy of their nasal passages agree well with the criteria for effective heat transfer in the nose (Schmidt-Nielsen et al., 1970; Collins et al., 1971).

Another potential benefit of conchae is that they partition the air field into multiple parallel channels. Once again, this partitioning of the air field into multiple, smaller caliber airways appears to be detrimental to airflow as resistance of the airway is known to increase in a manner described by part of the Hagen-Poiseuille equation (Vogel, 1994):

$$R = \frac{8\mu l}{\pi r^4},\tag{1}$$

where R=resistance, μ =dynamic viscosity, l=the length of the "pipe" and r=the radius of the "pipe." Resistance is highly sensitive to the radius of the structure through which a fluid flows. As indicated by the exponent associated with the radius, decreasing airway caliber by half would increase resistance of fluid flow by 16 fold (Vogel, 1994). This highly sensitive aspect of fluid resistance is offset, in conchae, by the breaking of the air field into multiple,

parallel streams. Parallel fluid streams act similar to parallel electrical current in a circuit:

$$R_{total} = \Sigma \frac{1}{\frac{1}{R_1} + \frac{1}{R_2} + \frac{1}{R_3} \dots},$$
(2)

where subscripts indicate each individual airway segment. In a parallel arrangement, decreasing airway caliber by half and spreading those half-caliber airways across four parallel segments only increases airway resistance by 4x. Splitting the half caliber airways across six parallel segments increases resistance by 2.6x and so on. This phenomenon of fluid flow allows conchae to partition the air field in a way that provides extensive physiological surface area with only a modest increase in nasal resistance (Fig. 12B).

In contrast, a long convoluted airway whether it is localized to the nasal passage or extended to include an elongated trachea (Owerkowicz et al., 2015), should offer the same potential heat transfer benefits as a concha-partitioned airways but at a reduced cost in nasal resistance. However, the cost in anatomical real estate is greater, and the serial arrangement of the air field limits the amount of air that can be processed at any one time (Fig. 12B). Using the air field partitioning ability of conchae to redirect air to different regions of the nasal capsule allows for aerodynamic segregation of the nasal passage without the need for hard-tissue excavations such as a dedicated olfactory recess. This could be beneficial for birds, which may pay a high cost, aerodynamically, for increases in cranial mass (Gussekloo and Cubo, 2013). Baffle-like conchae may have evolved as a means to compensate for the increasingly larger eyes of birds, many of which "squeeze" out the more typical olfactory recesses seen in extant amniotes (Witmer, 1995). Though conchae have been largely associated with the evolution of a high resting metabolism (Hillenius, 1992, 1994; Geist, 2000; Hillenius and Ruben, 2004) the results of our analyses indicate that conchae do provide other functions that may be equally as important. These alternate functions should be considered when investigating the evolution of these structures in amniotes.

Competing interests

The authors have no competing interests.

Author contributions

JMB ran analysis, interpreted results, wrote initial draft of manuscript. LMW aided analysis, worked with interpretations of results, and edited manuscript.

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