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Authors: Clark, Christopher J., and Brennan, Patricia L. R.

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Observations on the bill-drumming display of Ruddy Duck (*Oxyura jamaicensis*)

Christopher J. Clark[1]* and Patricia L. R. Brennan[2]

ABSTRACT—Male ducks in the genus *Oxyura* produce bill-drumming displays, sometimes called “bubbling display.” We recorded high-speed video and sound of the bill-drumming display in ≥4 captive Ruddy Ducks (*Oxyura jamaicensis*) to ask: how is the sound produced? Our videos showed that, while floating in the water adjacent to a conspecific, the male struck his bill against his upper breast approximately 8.6 times over the course of 1 s. The breast, which had been inflated with air via both tracheal and interclavicular air sacs, visibly recoiled from each impact, producing motion in the water, including bubbles. These bill-to-breast collisions produced an atonal thumping sound; the display then ended with a vocalization as the tracheal air sac deflated. We recorded males performing this display on land and producing the normal sound, thus, the bubbling of the water is not integral to the acoustic qualities of the display. Histology on 4 birds showed that the tracheal air sac became more developed in breeding males, allowing males to inflate it, creating a stretched membrane that is struck with the bill (i.e., a drum). The entire structure in the neck of the Ruddy Duck male during the breeding season may develop to enhance sound production and/or protect the male against this constant beating created by the display. *Received 30 August 2023. Accepted 9 July 2024.*

Key words: high speed video, locomotion-induced sound, percussion, sonation.

[1] Evolution, Ecology, and Organismal Biology, University of California–Riverside, CA USA

[2] Department of Biological Sciences, Mount Holyoke College, South Hadley, MA USA

* Corresponding author: cclark@ucr.edu

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Observaciones sobre el tamborileo de *Oxyura jamaicensis*

RESUMEN (Spanish)—Los patos machos del género *Oxyura* hacen despliegues de tamborileo con el pico, a veces llamados "despliegue de burbujeo". Grabamos video de alta velocidad y sonido del tamborileo en $\geq$4 patos *Oxyura jamaicensis* en cautiverio, para preguntar: ¿cómo se produce el sonido? Nuestros videos mostraron que, mientras flotaba en el agua junto a un conespecífico, el machó golpeó su pico contra la parte superior del pecho aproximadamente 8,6 veces en el transcurso de 1 segundo. El pecho, que había sido inflado con aire a través de los sacos aéreos traqueales e intraclaviculares, retrocedió visiblemente con cada impacto, produciendo movimiento en el agua, incluidas burbujas. Estas colisiones entre el pico y el pecho produjeron un sonido de golpe atonal; luego, la exhibición terminó con una vocalización mientras se desinfló el saco aéreo traqueal. Grabamos a machos realizando este despliegue en tierra y produciendo el sonido normal, por lo tanto, el "burbujeo" del agua no es parte integral de las cualidades acústicas de la exhibición. La histología en cuatro aves mostró que el saco aéreo traqueal se desarrolló más en los machos reproductores, lo que les permitió inflarlo, creando una membrana estirada que se golpea con el pico: es decir, un tambor. Toda la estructura del cuello del macho de *Oxyura jamaicensis* durante la temporada de reproducción puede desarrollarse para mejorar la producción de sonido y/o proteger al macho contra los constantes golpes de su despliegue.

Palabras clave: sonación, sonido inducido por la locomoción, percusión, video de alta velocidad.

Oxyura is a genus of approximately 6 species of stiff-tailed ducks. During the spring, small groups of males gather in ponds or lakes to display to females and form short-term bonds. Males do not defend territories but engage in frequent fights with other displaying males, and are considered among the most combative ducks (Brua 2020). Males of some or possibly all 6 species have a display, performed during the breeding season, in which they produce a sonation (Bostwick and Prum 2003, Clark 2016) by striking their bill against their upper breast. In the Ruddy Duck (*Oxyura jamaicensis*) the display was described by Wetmore (1917) as males swimming with "swelling breast" and "neck drawn in" with an extension of the head with a series of short jerks as the male called *tick–tick–tickity quo–ack*. Others have described the display as a "bubble display," where males slap their bill rapidly against their chest, frothing the water (Pieplow 2017: p. 63). Johnsgard (1965: p. 323) described this "bubbling display" as:

> "The male begins by erecting his 'horns,' inflating his neck, and cocking his tail . . . He then suddenly begins to beat his bill against his inflated neck, forcing air out from under the feathers and causing bubbles to appear at the surface of the water, and at the same time producing a hollow tapping sound . . . The tapping speeds up toward the end of the display, and at the same time the tail is cocked even farther toward the head and the folded wings are slightly lifted for a moment just before the display terminates with a partial deflation of the air sac, accompanied by a forward movement of the head as the bill is opened and a low belching sound is uttered."

Wetmore (1917: p. 481) described the presence of a tracheal air sac below the loose skin of the neck in Ruddy Ducks that he speculated was inflated right before the male display:

> "The male ruddy duck about to display fills the air-sacs of the pulmonary series with air. The *rima glottidis* is then closed by the action of muscles controlling the arytenoid cartilages. This brings the points of connective tissue (pulvini laryngis) in the larynx together and these with the *ligula* close the larynx save behind. With the sterno-tracheal and cucullaris muscles relaxed, a slight contraction of the respiratory muscles would inflate the tracheal air-sac. Though no sphincter muscle is present, contraction at the anterior attachment of the sterno-tracheales may close the aperture of the air-sac by pressing the esophagus against it."

Upon further examination of live males with inflated sacs, Wetmore (1918) speculated that perhaps this tracheal air sac served as a reservoir of air that would allow males to stay submerged longer than usual. However, Wetmore also noted that the tracheal air sac is absent in females, and only weakly developed in younger males, so we speculated that the sac may be involved in the male display.

Here we investigated the kinematics of the male Ruddy Duck drumming display to ask: what role does the water play in the sound that is produced? To what degree might the acoustic qualities of the display have the potential to vary across species? We further describe the histology of the tracheal air sac and performed dissections of male and female ducks to determine if the tracheal air sac may function as a drum against which the male strikes his beak.

Methods

Captive Ruddy Ducks were filmed at the Ripley Waterfowl Conservancy (Lichfield, Connecticut, USA) on 4 May, 2 June, and 4 June 2010. Two mixed species flocks of $\sim$30 ducks and geese (each) were filmed. The flocks were housed outdoors and each enclosure had a large pond as well as dry land to stand on. Within each flock were 6 or 7 male Ruddy Ducks that would display, sometimes spontaneously, and sometimes to a variety of stimuli such as female Ruddy Ducks, or each other. The recordist sat approximately 2–5 m away from the ducks, which were not disturbed by the nearby human. It was not possible to follow individual birds as they swam around, so it is not clear how many males were filmed and recorded in total, out of 13 available.

The ducks were filmed from idiosyncratic angles with a color Miro EX4 high speed camera at 200 frames per second (fps), 800×600 pixel resolution, or with a handheld HD Sony Handycam, at 30 fps. Additionally, we made sound recordings of displays using a MHK 70 shotgun microphone attached to a Sound Devices 702 recorder (24-bit, 96 kHz sampling rate). We report means ± 1 SD.

We also examined the neck and breast tissue of 4 recently euthanized Ruddy Ducks (3 males and 1 female) from a different study (Brennan et al. 2017; Yale University IACUC 2008–10906) to compare with the observations made by Wetmore and add histological data pertinent to the tracheal air sac. We removed the skin from the neck above the breastbone and cut it open at the back of the neck as it felt like the reproductive male had extra skin in this region. We measured the length (anterior to posterior) and width (circumferential) of 3 individuals: a female (#2595), a nonreproductive male (#91), and a reproductive male (#97). We preserved the trachea, tracheal air sac, and sterno-trachealis muscle of one reproductive male (#97) and used paraffin histology to examine the tissue of the tracheal air sac in transverse sections. Slides were stained with Masson's trichrome and photographed at 40$\times$ magnification.

Results

We obtained 37 high-speed videos of displays, from an absolute minimum of 4 ducks (likely, about 10 males were filmed). The display was stereotyped, with no obvious differences between the males, except possibly for the acoustic quality of the vocalization that completed the display. Some displays were spontaneous (not clearly directed at another duck), while others were performed when the focal duck approached another individual. We recorded displays in the water and one bout on land. We selected the 16 best recordings for quantitative analysis; the discarded recordings were out of focus, occluded, cut off (spatially or temporally), etc., but showed kinematic sequences consistent with the videos we chose for analysis.

Kinematics

To perform the display, the male adjusted his posture and his breast and neck swelled slightly. We interpret that he filled the tracheal air sac with air, between the upper breast and lower neck. During their displays, males hit their bill against their upper breast 8.62 ± 0.88 times (range: 7–11, $n = 16$) at an accelerating pace (Fig. 1a). Example recordings have been uploaded to the Macaulay Library (https://www.macaulaylibrary.org/), including high speed videos: (ML 618729479, ML 618729262), regular video (ML 618729464), a high-speed video of a bird displaying on land (ML 618729409), and a sound recording (ML 608274322). With each bill-to-breast collision, a short atonal sound was produced (Fig. 1b), and the breast visibly recoiled, with a wave of motion that spread out from the point of contact to encompass the entire front of the duck. When the duck was in the water, the action of the breast recoiling from the impact of the bill caused the water around the duck to slosh back and forth in response. The initial collisions and sloshing did not produce bubbles. Later collisions were faster tempo, which caused the water at the breast to froth, with some bubbles. At the end of the display, the males invariably vocalized once, evidenced by the bill opening slightly (labeled "croak" in Fig. 1). The total time taken for the display, including the croak, was 1.03 ± 0.12 s ($n = 14$).

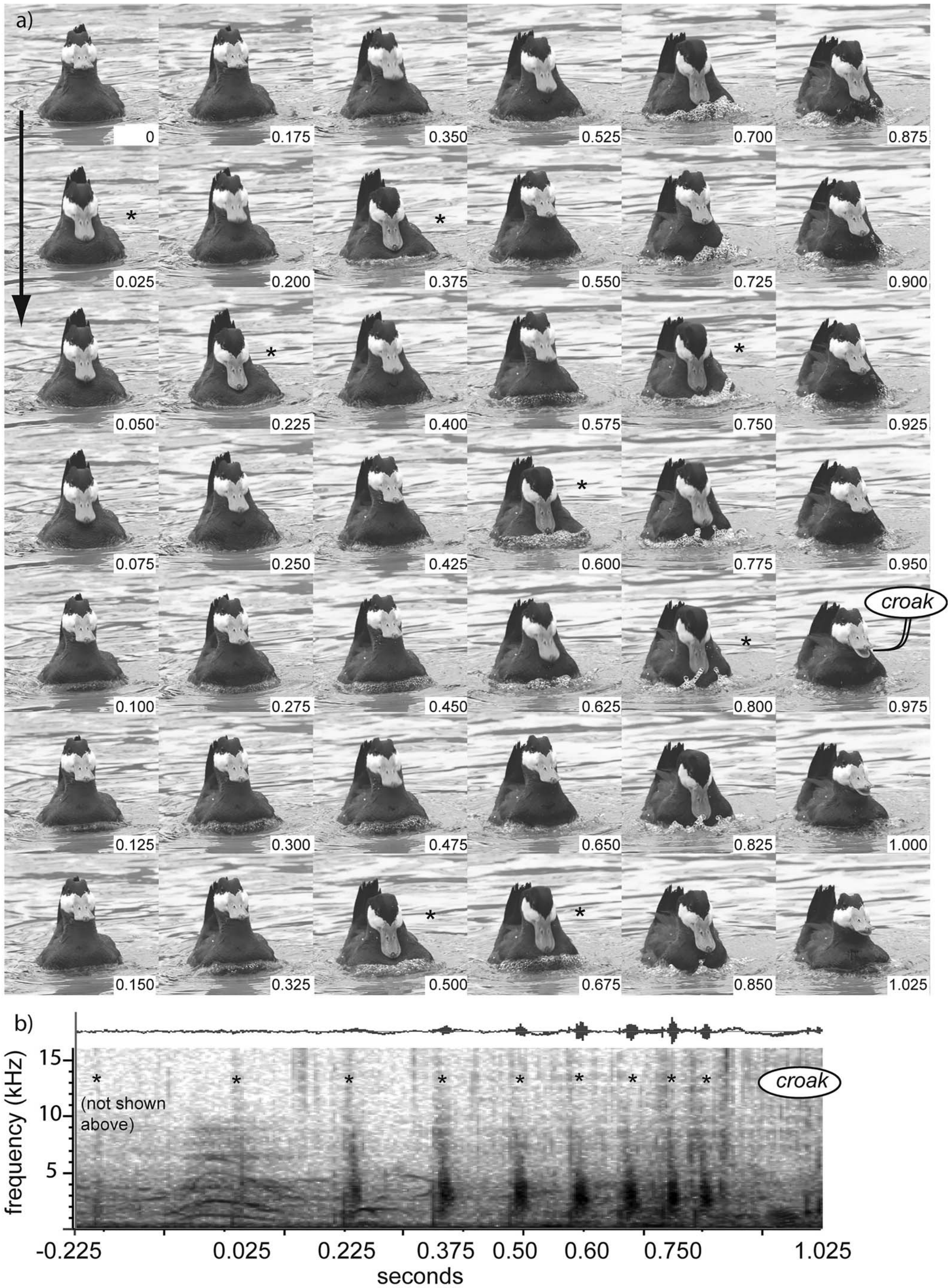

Figure 1. Kinematics and sound of the Ruddy Duck (*Oxyura jamaicensis*) drumming display. (a) The duck drummed his bill against the upper breast 9 times (8 shown *), at an accelerating pace, culminating in a vocalization (*croak*). (b) Sound recording of the same display. Considerable background sound is present below 2 kHz, including vocalizations of other duck species, and moving water. Sound pressure spikes are visible in the waveform (top panel) for the later bill–breast collisions.

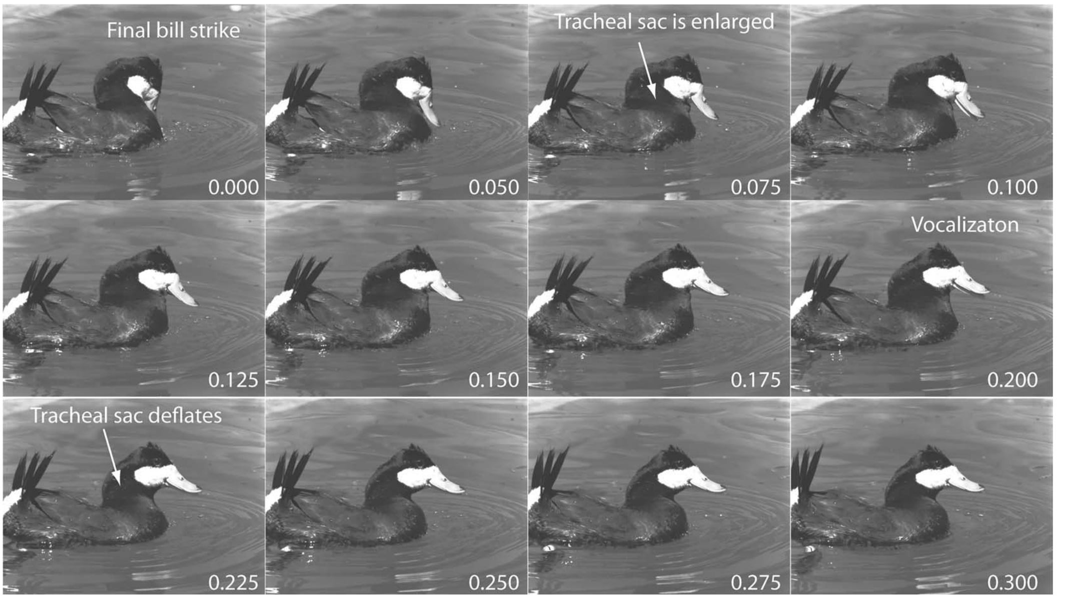

Figure 2. Lateral view of end of display (from end of ML 608274400). After the final bill-strike, the throat and breast are visibly enlarged; when the duck vocalizes, the throat (tracheal air sac) visibly deflates. Time in seconds after the final bill strike in lower right.

The sound overall was a *thpt…. thpt… thpt… thpt. thpt. thpt. thpt. thpt. croak*. In all of the high-speed videos, after the last collision, the upper breast of the duck suddenly moved, suggesting that the air trapped inside the breast in the vicinity of the tracheal sac was released, just as the vocalization was produced (Fig. 2).

Although this display was usually given by males that were swimming in the water, we obtained some recordings of displays by a duck standing out of the water (e.g., ML 618729409). These out-of-water displays seemed to have the same acoustic qualities as the swimming version of the display. The "bubbling" of the water thus seems to be a byproduct that does not contribute to airborne transmission of sound.

Dissections

The area of the skin of the neck above the breastbone was larger in the reproductive male (8.5×13.5 cm after being removed from the duck, $n = 1$) compared with the nonreproductive male (7×7 cm, $n = 1$) or the female (8×10 cm, $n = 1$) (Fig. 3). This may account for our impression that the skin of the neck seemed loose in reproductive Ruddy Duck males. The subcutaneous muscle, which Wetmore believed to be a deep layer of the *cucullaris*, was well developed and bulky in the reproductive male ($n = 1$), but much less so in the female and nonreproductive male. The subcutaneous muscles on the inner surface of skin were covered with a sheet of connective tissue that adheres tightly to the skin on one side, and to the connective tissue of neck and trachea on the other side. There was a medial gap between these muscles, so they do not meet in the middle of the skin of the neck. These muscles, on both sides, insert on the junction of the interclavicular air sac and the furcula. Notably, a thick pad of connective tissue and fat underlay the skin of the neck in the reproductive male ($n = 1$), but was absent in the female ($n = 1$) and nonreproductive male ($n = 1$). The tracheal air sac was extensive in the reproductive male, about 3.5 cm long, and 1.2 cm at its widest point, and its opening was dorsal. However, the air sac inflated ventrally and had 2 lateral structures. The tracheal air sac can be struck by the proximal end of the beak during the display. However, upon dissection we also noticed that, in addition, the interclavicular

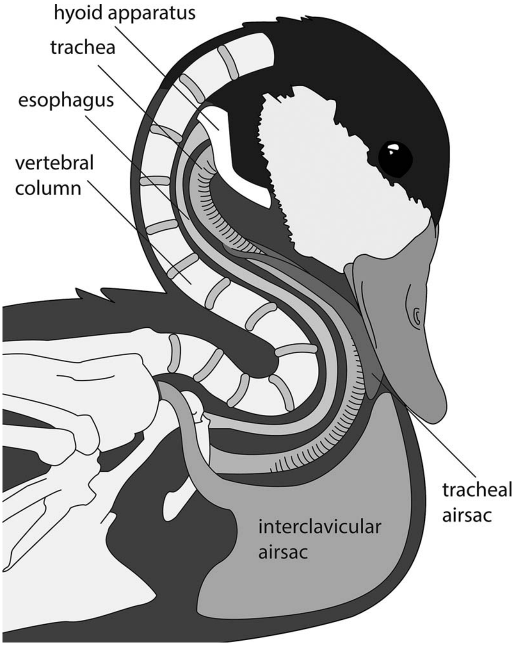

Figure 3. Anatomy of the breast drumming display. The male hits both the tracheal air sac and the interclavicular air sac when hitting his bill against his chest during display. Illustration by Rachel Keeffe.

air sac was quite extensive in the reproductive male duck and remained filled with air even postmortem. Manipulation of a freshly euthanized male allowed us to see that the distal end of the beak would strike the interclavicular air sac, inflated below the skin of the breast and neck. This suggested that both the tracheal air sac and the interclavicular air sac may be involved in the display (Fig. 3). The nonreproductive male ($n = 1$) had a comparably very small tracheal air sac only 1 cm long. The female ($n = 1$) had no tracheal air sac.

Histology

Paraffin histology of the tissue of the tracheal air sac in transverse sections confirmed that, as suggested by Wetmore, there was no sphincter at the opening of the tracheal air sac, and that there were 2 lateral branches of the sac, each surrounded by one branch of the sterno brachialis muscle. The tracheal air sac was composed of pseudostratified ciliated columnar epithelium, similar in nature to the tracheal mucosal tissue, but thinner. The tracheal air sac was connected to the external surface of the trachea by disorganized connective tissue, primarily collagen, with a few blood vessels running on this layer (Fig. 4).

Discussion

Our high-speed videos and dissections suggest that the Ruddy Duck display is a genuine drumming display. Our findings are consistent with most of the earlier observations of this display (see Introduction). However, a few of the prior ideas are not supported. The name for this display given by some, the "bubbling display," may be a misnomer. Our videos (Fig. 1; ML 618729479, ML 618729262) did not show any signs that bubbles are forced out of the plumage. Moreover, at least one of the captive males we recorded would sometimes produce this display while sitting or standing on the ground (ML 618729409), and the sound generated was similar, perhaps identical, to that in the typical display. We do not know whether wild males ever produce this display while on land, but our observation that it sounded similar to the waterborne display suggests that the water itself or bubbles are not an integral part of the sound-production mechanism. That said, it is likely to be a visual display as well as auditory, and moreover, we only measured airborne sound. The sender often displayed at close range (∼20 cm) from a receiver. It is possible that, in addition to the visual and acoustic components of the display, receivers might also detect waterborne vibration.

Our results suggest that the tracheal and interclavicular air sacs are both sexually and seasonally dimorphic, being larger in reproductive males than in nonreproductive males or females (Wetmore 1917). Moreover, the high-speed videos revealed a sudden shift in the duck's breast at the end of the display, right when he vocalized (Fig. 2), suggestive of air under pressure being released (i.e., to vocalize). From these observations, we propose that the male inflates both air sacs, and then clenches them, increasing pressure inside the air sacs and thus increasing tension in the skin between the air sacs and the plumage. An open question is how the male regulates airflow into these air sacs. We did not identify a clear

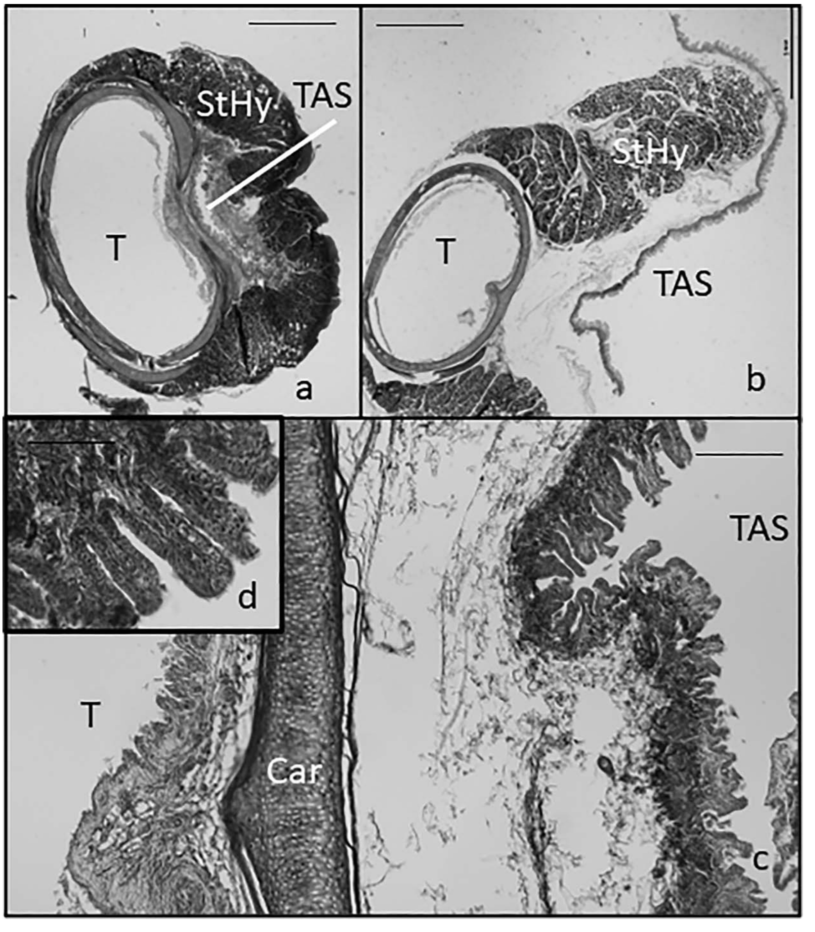

Figure 4. Transverse section of the tracheal air sac stained with Masson's trichrome. (a) Section just below the opening of the trachea (T) into the tracheal air sac (TAS). At this point the sac is flattened against the trachea and surrounded by sternohyoid (StHy) muscles. 1.75×. Scale bar: 2 mm. (b) At this lower section the TAS has opened laterally beyond the StHy muscles, and the thin layer of connective tissue connecting to the trachea is evident. 1.75×. Scale bar: 2 mm. (c) The tracheal epithelium is very similar to the epithelium of the TAS, as can be seen in 10× magnification. Scale bar 200 um. (d) Inset: 50× view of the pseudostratified ciliated epithelium of the tracheal air sac, which is deeply folded when not expanded.

sphincter that would close off the tracheal air sac, and in fact, birds seem to lack sphincters anywhere in their pulmonary system (Scheid et al. 1972, Schwarz-Wings and Frey 2008). Instead it seems that airflow into either sac must be regulated by other muscles adjacent to their connections.

Thus, according to our hypothesized mechanism, filling the tracheal and interclavicular air sacs creates a tensioned membrane overlying an air-filled cavity, similar to human-made drums (such as tambourine). According to our hypothesis, when the male strikes this "drum" with his bill, the acoustic qualities of the ensuing sound are set largely by the resonant properties (stiffness, mass) of the membrane, but possibly modified somewhat by the resonant frequencies of the underlying cavity, and/or by the air–water interface (Fletcher and Rossing 1998). The surface area of the membrane itself is fairly large, increasing the amount of sound that is radiated. Likely the sound is damped somewhat by the thick layer of plumage that overlies the air sacs, which would both adjust the acoustic frequencies at which the membrane vibrates and reduce the overall levels of sound. In total, we propose that the drumming sound of Ruddy Ducks is produced in a manner similar to human-made drums. There are not yet other known cases of this type of drumming in birds.

Although other birds are also said to "drum," this word is often used as a vague metaphor to describe a rapidly repeated, low-frequency, atonal sound. Ruffed Grouse (*Bonasa umbellus*) are said to "drum" by beating their wings against the air, but the actual source of sound seems to be aerodynamic (Archibald 1974, Garcia et al. 2012). Snipe are said to "drum" but this sound is actually made by aeroelastic flutter of their tail feathers (Reddig 1978, Clark and Prum 2015). Male Magnificent Frigatebirds (*Fregata magnificens*) perform "Gular Pouch Drumming" but this "drumming" sound has an unclear physical origin (bill-snapping?) that is subsequently filtered by the inflated gular pouch (Madsen et al. 2011). That is, in none of these examples is "drumming" percussive. Other taxa do drum with percussive physical acoustic mechanisms similar to what we have described here. Woodpeckers drum by striking their beak against external structures such as wood; when the structures contain a resonant cavity, the ensuing sound can be loud (Miles et al. 2018). Palm Cockatoos (*Probosciger aterrimus*) drum by holding a rigid substrate (e.g., piece of wood) and striking it against another external rigid surface (Heinsohn et al. 2017). *Manacus* manakins snap their wings together, such that their bones vibrate and radiate sound (Bostwick and Prum 2003, Bodony et al. 2016). In each of these cases, the vibratory surface is rigid rather than a membrane. If our hypothesis about how the drumming sound is produced by Ruddy Ducks is correct, this is the first example of an animal that produces sound via percussion against an elastic membrane, similar to a human drum. Many insects produce sounds with stiff membranes (made of cuticle), but not by striking them as Ruddy Duck does (Ewing 1989).

To what degree might other species of *Oxyura* produce different sounds? Sonations may evolve from changes in morphology and/or behavior (Clark 2018). Males seem to adjust the posture of their breast, and the tissue in the breast seems to become thicker during the breeding season (Wetmore 1917, 1918), which implies that the material of the breast affects the acoustic qualities of sound. The temporal components of the display (e.g., the accelerating nature of the bill collisions or the overall number of collisions within each display) are arbitrary and may easily evolve interspecific differences.

Acknowledgments

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