

## THE VENTILATORY MOVEMENTS OF THE AVIAN PELVIS AND TAIL: FUNCTION OF THE MUSCLES OF THE TAIL REGION OF THE PIGEON (*COLUMBA LIVIA*)

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### Summary

We have observed that birds of several different taxa move their tails in conjunction with sound production. These observations suggested to us that tail movements might also be associated with ventilation. Since we hypothesized that rhythmic movements of the tail and pelvis will ventilate the lungs, the activities of tail, epaxial and cloacal muscles of the pigeon were examined. Electromyograms (EMGs) were recorded from these muscles while ventilation was monitored. A muscle was considered to have ventilatory activity when the EMG activity had an obvious correlation to either inspiration or expiration. To obtain further information about the correlation between muscular activity and ventilation, we induced hyperpnea by administering 5% CO<sub>2</sub>. We report that the tail muscles that function as expiratory muscles are the *M. caudofemoralis*, the *M. pubocaudalis internus* and the *M. pubocaudalis externus*. We refer to these as the suprapubic abdominal muscles to distinguish them from the infrapubic (ventral) abdominal muscles. These muscles depress the pelvis and the uropygium and compress the thoracoabdominal cavity. *M. transversus cloacae* functions as an expiratory muscle by protracting the cloaca or by reducing its compliance. Of the suprapubic muscles we studied, the only inspiratory muscle is the axial muscle, *M. longissimus dorsi*. *M. longissimus dorsi* acts at the notarial–synsacral junction to elevate the pelvis. The rocking movements of the notarial–synsacral joint appear to be important for ventilation during conditions in which the sternum is ‘fixed’, such as when the bird is resting on its breast. We suggest that a division of labor may exist between the infra- and suprapubic abdominal muscles during ventilation such as panting or vocalization.

### Introduction

In a study of the functional anatomy of the tail apparatus of the pigeon, we observed that the tail moved during vocalization in some species of birds (Baumel, 1988). We observed that the crow, *Corvus brachyrhynchos*, depressed its tail each time it uttered a caw. In the warbling vireo, *Vireo gilvus*, and in a caged lovebird,

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*Agapornis* sp., the tail dipped in a stepwise manner which apparently corresponded with each note. In a nature film, we observed that each time a piping plover, *Charadrius melodus*, made a call it also depressed its tail.

Since our observations on vocalization indicated that the depressors of the tail were cooperating with the ventral abdominal expiratory muscles, driving air from the air sacs through the sound-producing syrinx, the obvious question arose: do the tail muscles also contribute to routine ventilatory movements? Our preliminary visual examination of several live pigeons indicated that depression of the uropygium coincides with the cyclic contraction of the ventral abdominal muscles and the elevation of the caudal border of the sternum. Electromyographic studies of avian breathing have been conducted using chickens and pigeons as the principal models (Fedde *et al.* 1969; Kadano *et al.* 1963; deWet *et al.* 1976; Burkart and Bucher, 1961; Wick and Bucher, 1963). These studies and others were reviewed by Fedde (1987), and he showed clearly that the ventral (infrapubic) abdominal muscles are all associated with expiratory breathing movements. Mention was not made of the possible function in breathing of the muscles which move the fleshy tail mass (uropygium) and pelvis. As movement of the uropygium would result in changes of the volume of the thoracoabdominal cavity, muscles which changed this volume were of interest to us (see Figs 1, 2 and 7).

We undertook the present electromyographic study to verify that tail muscles are concerned with ventilation and to determine which tail muscles participate in inspiration or expiration. We have also investigated the electrical activity of one of the cloacal and one of the epaxial muscles. We report here that certain suprapubic muscles are active in phase with inspiration or expiration, and that these muscles cause movement of the pelvis and uropygium which alters the volume of the thoracoabdominal cavity.

### Materials and methods

Twenty adult pigeons (*Columba livia*), white kings and other mixed breeds, weighing 350–700 g were used in this study. One or more days prior to the electromyographic (EMG) studies, the pigeons were anesthetized (Bree and Gross, 1969) (sodium pentobarbital, 32 mg kg<sup>-1</sup> intramuscularly followed by ketamine hydrochloride 20 mg kg<sup>-1</sup> intramuscularly). Most of the plumage was plucked from the dorsal and ventral surfaces of the uropygium, dorsum of pelvis and ventrolateral abdominal wall down to the caudal border of the sternum. During recovery, a topical anesthetic was applied to the follicles from which the feathers had been removed. After at least 1 day of recovery, the pigeons were re-anesthetized for EMG studies. Each bird resting on its sternum was secured in a restraining apparatus, which consisted of a canvas hammock slung between two parallel rods. This allowed us to avoid complications inherent in studies undertaken in the supine position (King and Molony, 1971). The rear of the bird was unsupported by the apparatus, allowing free access to the entire pelvic region.

After experiments that involved percutaneous implantation of the electrodes, the pigeons were allowed to recover. After experiments involving surgery to expose or incise the muscles, the pigeons received a lethal overdose of pentobarbital at the end of the experiment.

We recorded ventilatory movements of the thorax by means of an accordion bellows pneumograph. The bellows encircled the thorax, positioned near the middle of the length of the sternal carina, and were activated mainly by an increase in the dorsoventral dimension of the wall of the thoracoabdominal cavity, and to a lesser extent by an increase in its transverse dimension. The caudal ends of the sternum and pelvis undergo the largest excursions since they rotate around transverse axes located farther cranially. The pneumograph was connected to a differential transducer by polyethylene tubing. The signal from the transducer was relayed to a preamplifier and from there to an oscilloscope. This signal was also relayed to a digitizing oscilloscope and to a tape recorder (Racal 4DS).

Electromyographic (EMG) activity was recorded using a pair of steel insect pin electrodes. All but 1–2 mm of the tip of each of the electrodes was insulated with a plastic coating. The two electrodes were inserted into the muscle with their tips positioned within 2–5 mm of one another. The signals from the electrodes were relayed to a low-level, a.c. amplifier (Brumbley Electronics). The amplified signal was then relayed to the digitizing oscilloscope for visual observation and to the tape recorder. Permanent records of the EMG and the respiratory signal were obtained by tape replay through a rectilinear chart recorder or photographed directly from the oscilloscope. All the experimental procedures were carried out inside a shielded, grounded Faraday cage. To evoke a muscular contraction, the same pin electrodes were connected to a programmable stimulator in series with stimulus isolators. The parameters of the stimulus such as voltage, current, pulse duration and frequency were set to induce muscle contractions.

To determine accurately which muscles were active in respiration, we used the pin electrodes, which sample only a sub-population of fibers in each muscle. There was no noticeable 'cross-talk' between muscles, allowing us to determine whether the muscle into which the electrode was inserted was active; however, only a limited number of fibers was recorded at each electrode placement. The patterns of activity predicted by the 'size principle' (Henneman, 1957) in mammals (i.e. smaller units being recruited before larger units) were not always readily apparent in the EMGs of our birds. Averaged recordings of larger populations of fibers (Fedde *et al.* 1969) have shown that the muscles used by birds in respiration are also recruited in accordance with the size principle; our present findings in no way should be taken to contradict their observations.

#### *Functional classification of muscles*

First, we classified a muscle as inspiratory when its peak EMG activity consistently occurred during inspiration and as expiratory when its peak activity occurred during expiration in our population of pigeons. Second, to determine whether certain muscles not used for ventilation during eupnea would be recruited

to assist ventilation during dyspnea or hyperpnea, we challenged the pigeons with a gas mixture of air and 5% CO<sub>2</sub> administered from a funnel placed over the pigeon's beak. Carbon dioxide stimulates the central and peripheral chemoreceptors reflexly to increase minute volume, first by increasing tidal volume and then by increasing respiratory rate. The increase in tidal volume resulted in an increase in the excursion of the thoracoabdominal wall caused by enhanced activity of the muscles involved in ventilation. Third, in some specimens the pin electrodes were placed in bilateral pairs of muscles to observe whether muscles were activated simultaneously on both sides of the body.

#### *Placement of electrodes*

##### *M. caudofemoralis* (Figs 1, 7)

Electrodes were inserted into the muscle where it exits from the thigh musculature, i.e. where it angulates about its pulley (Fig. 1) and enters the lower surface of the uropygium.

##### *M. levator caudae* (Figs 1, 2)

Electrodes were inserted vertically into the muscle near the caudal border of the pelvis about 0.5 cm lateral to the vertebral spinous processes. Care was taken to avoid implanting the electrodes so deeply as to enter *M. depressor caudae* on the ventral side of the caudal vertebral column (see below, *M. depressor caudae*).

##### *M. lateralis caudae* (Figs 1, 2)

Electrodes were inserted into the cranial segment of the muscle adjacent to where it emerges from under the lateral edge of *M. levator caudae*.

##### *M. depressor caudae*

This muscle is the ventral counterpart of *M. levator caudae*. Located on the ventral side of the caudal vertebral column where it forms the visceral surface of the uropygium, it is the most inaccessible of the tail muscles. In order to implant electrodes into the depressor it was necessary to pass them ventrad through the *M. levator caudae* until they were stopped by striking one of the transverse processes of a caudal vertebra. The electrodes were then withdrawn to the surface, redirected and reinserted into the levator muscle until they penetrated an intertransverse space and entered the deeply situated *M. depressor caudae*.

##### *M. pubocaudalis externus* (Figs 1, 2, 7)

The ventral half of this sheet-like muscle is largely superimposed and adherent to the outer surface of the ventral (pelvic) part of *M. pubocaudalis internus*. Owing to the thinness of *M. pubocaudalis externus*, the electrodes of necessity were inserted parallel to its surface, near its origin from the rear of the pubis and adjacent ala of the ischium.

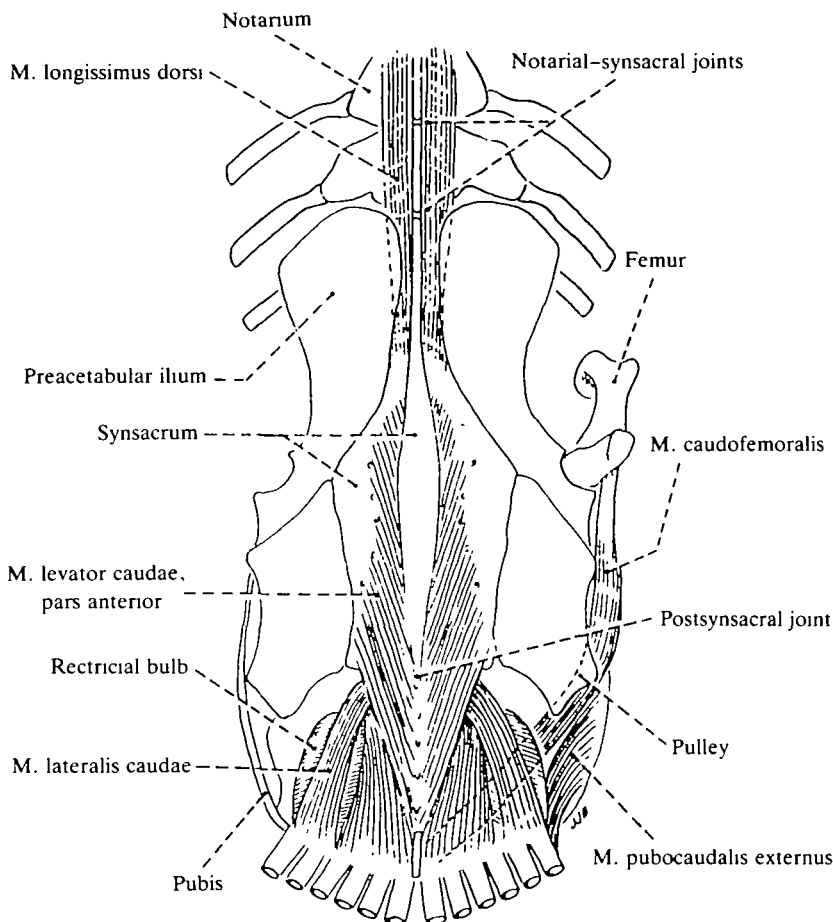


Fig. 1. Tail muscles and epaxial muscles of the trunk of the pigeon; dorsal view. Note that the parts of *M. levator caudae* and *M. longissimus dorsi* on the dorsum of the synsacrum are practically continuous with one another. Contraction of the paired *M. longissimus dorsi* causes dorsiflexion of the notarial-synsacral joints, bringing about dorsal movement of the pelvis with its appended uropygium. *M. caudofemoralis* (dashed lines) inserts on the ventral surface of the uropygium.

#### *M. pubocaudalis internus* (Figs 2, 7)

The pelvic and caudal bellies of this digastric muscle are separated by a tendinous intersection. The activity of only the pelvic segment was studied. Its caudal segment is attached to the ventral surface of the uropygium. In order to be certain of the placement of electrodes into its pelvic part, the origin of *M. pubocaudalis externus* was detached, exposing the underlying *M. pubocaudalis internus*. The electrodes were inserted parallel to the surface of the muscle about 0.5 cm dorsal to its origin from the extremity of the pubis and adjacent ischium.

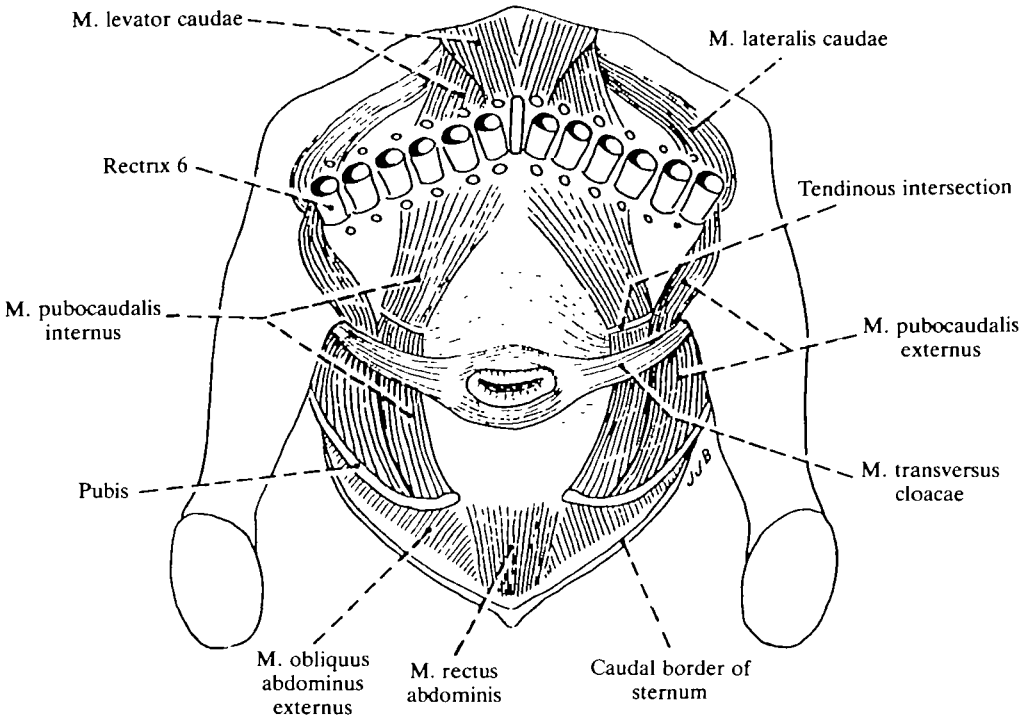


Fig. 2. Tail (suprapubic abdominal) muscles and infrapubic abdominal muscles of the pigeon; caudal view. The uropygium with the stumps of its implanted flight quills (rectrices) is elevated away from the opening (vent) of the cloaca, showing the ventral surface of the uropygium. Not shown are the caudofemoralis muscle and the deeper-lying internal oblique and transverse abdominis muscles.

#### *M. longissimus dorsi* (Figs 1, 7)

Electrodes were inserted into the part of the muscle slightly forward of the cranial ends of the preacetabular ilia in the region of the moveable joints between the two fused vertebral elements, the synsacrum and the notarium.

#### *M. transversus cloacae* (Fig. 2)

Electrodes were inserted parallel to the surface of the part of the muscle about 1 cm cranial to the lateral angle of the vent where *M. transversus cloacae* is attached to *M. sphincter cloacae*.

#### Terminology

Anatomical terminology is that of the *Nomina Anatomica Avium* (NAA) (Baumel *et al.* 1979). The uropygium is the fleshy mass organized about the short, free caudal vertebral column; the large tail quills (rectrices) are implanted into its paired rectricial bulbs on either side of the caudal vertebrae. The term 'uropygium' was reintroduced in the monograph of Baumel (1988), replacing 'pyga' of the NAA nomenclature.

### Results

We investigated the activity of eight suprapubic muscles. Only one muscle, the dorsal axial muscle, *M. longissimus dorsi*, was found to be active during inspiration. We recorded its activity in combination with that of four suprapubic muscles which proved to be expiratory (Figs 3–6).

#### *M. longissimus dorsi* (Figs 3–6)

The activity of this muscle occurred during inspiration, with spikes being seen at the same time as spikes in other inspiratory muscles, as described by Fedde *et al.* (1969). This relationship between inspiration and activity in *M. longissimus dorsi* occurred for respiratory rates ranging from less than the 35 breaths  $\text{min}^{-1}$  shown in Fig. 4 to the 60 breaths  $\text{min}^{-1}$  shown in Figs 3 and 5. Electrical stimulation of the muscle caused elevation of the pelvis, which increased the volume of the thoracoabdominal cavity, as indicated pneumographically, and is consistent with its apparent role as an inspiratory muscle.

During expiration, four of the eight muscles sampled demonstrated activity: *M. transversus cloacae*, *M. caudofemoralis*, *M. pubocaudalis externus* and *M. pubocaudalis internus*.

#### *M. transversus cloacae* (Fig. 3)

Contraction elicited by electrical stimulation of this muscle obviously compressed the abdominal cavity by pulling the region of the vent/cloaca cranially. *M. transversus cloacae* was, in general, activated early in expiration. Frequently, a large unit was activated no more than 100 ms after maximal inspiration. *M.*

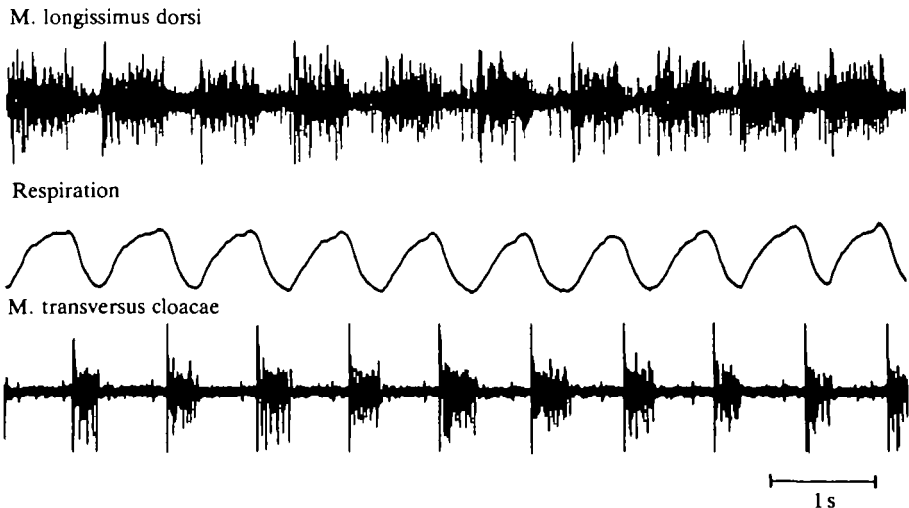


Fig. 3. Simultaneous recording from *M. transversus cloacae*, *M. longissimus dorsi* and a pneumograph. Inspiration is indicated by an upward deflection of the respiration trace, and expiration by a downward deflection. Activity in *M. transversus cloacae* is in phase with expiration, whereas that of *M. longissimus dorsi* is in phase with inspiration.

*M. longissimus dorsi*



Respiration



*M. caudofemoralis*



1 s

Fig. 4. Simultaneous recording from *M. caudofemoralis*, *M. longissimus dorsi* and a pneumograph. *M. caudofemoralis* was active in expiration. As in the previous figure, *M. longissimus dorsi* was active in phase with inspiration.

transversus cloacae was active during the expiratory phase in all the individuals studied. Its activity ceased near the end of expiration.

#### *M. caudofemoralis* (Fig. 4)

This muscle was found to be active during expiration. It usually became active near the beginning of expiration, with activity increasing until it suddenly stopped just prior to the next inspiration. Fig. 4 also demonstrates the recruitment of units in agreement with the size principle. When unilaterally stimulated, *M. caudofemoralis* caused a brisk depression and lateral flexion of the tail.

#### *M. pubocaudalis externus* (Fig. 5) and *M. pubocaudalis internus* (Fig. 6)

Both muscles often became active during expiration; however, in certain specimens these two muscles were *inactive* during quiet respiration. Without apparent cause, these muscles often became active spontaneously, and this activity began and continued in phase with expiration. Also, when quiescent, these muscles could be activated using a challenge of 5% CO<sub>2</sub> in air. Once challenged, the muscles either returned to quiescence or remained active in phase with respiration. Both the pubocaudalis muscles appear to be recruited when more vigorous ventilation is required and uropygial depression is added to pelvic depression.

#### *Non-ventilating tail muscles*

*M. levator caudae*, *M. lateralis caudae* and *M. depressor caudae* were studied and found not to be active during eupneic or CO<sub>2</sub>-stressed ventilation. Electrical



stimulation confirmed our electrode placement by eliciting muscle contraction. Generalized EMG activity was seen during CO<sub>2</sub> challenge; however, we did not observe rhythmic activity that could be correlated with ventilatory movements.

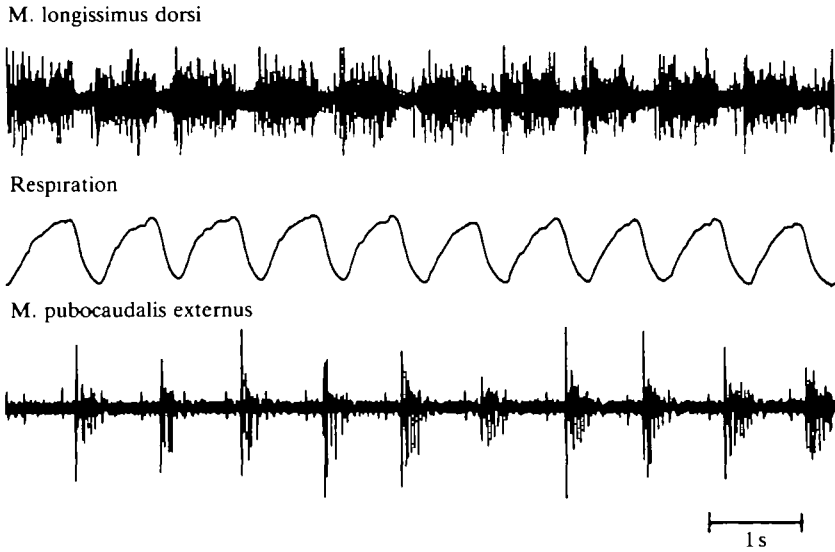


Fig. 5. Simultaneous recording from *M. pubocaudalis externus*, *M. longissimus dorsi* and a pneumograph. *M. pubocaudalis externus* was active during expiration. *M. longissimus dorsi* was active in phase with inspiration.

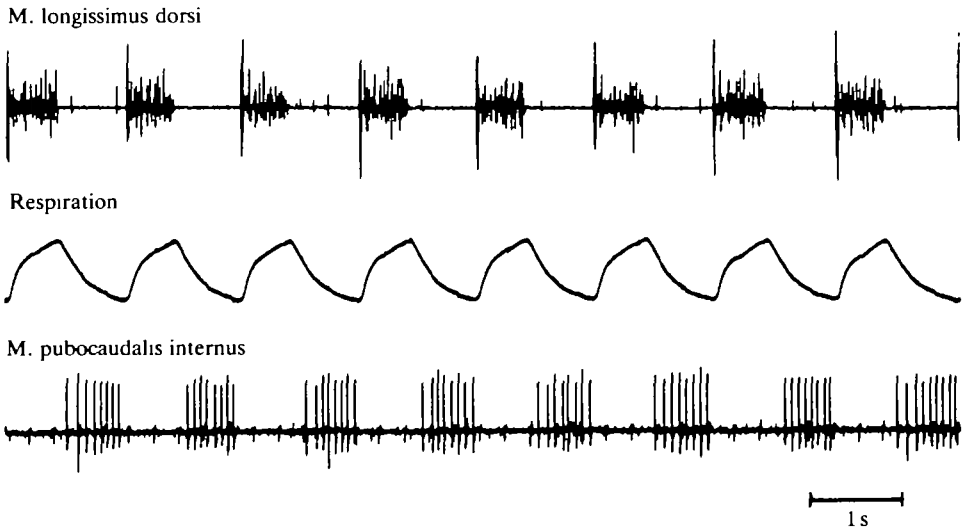


Fig. 6. Simultaneous recording from *M. pubocaudalis internus*, *M. longissimus dorsi* and a pneumograph. *M. pubocaudalis internus* was active in phase with expiration. *M. longissimus dorsi* was active during inspiration.

### Discussion

We initially noticed movement of the tail in phase with respiration and subsequently expanded our study to include pelvic movements. Of the six paired tail muscles studied electromyographically, the *M. caudofemoralis*, *M. pubocaudalis externus* and *M. pubocaudalis internus* participated in ventilation. Each was active during the expiratory phase of the ventilatory cycle. All three are extrinsic tail muscles, i.e. their origins are from structures other than the vertebral column. None of the intrinsic group of tail muscles studied, i.e. *M. levator caudae*, *M. lateralis caudae* or *M. depressor caudae*, had activity related to the ventilatory cycle; however, tonic contraction of these muscles may assist ventilation by stiffening the postsynsacral joint and therefore holding the uropygium in its neutral position. Thus, the dorsal wall of the caudal thoracoabdominal cavity could be converted, when needed, into a rigid consolidated unit consisting of the pelvis and the uropygium.

Two of the muscles that we investigated had ventilatory-related activity, but were not tail muscles *per se*. These are the *M. longissimus dorsi* (inspiratory) and the *M. transversus cloacae* (expiratory). *M. transversus cloacae* is a suprapubic abdominal muscle closely related topographically to the pubocaudalis muscles; according to Nishi (1938) it is derived embryologically from the same anlage. Salt and Zeuthen (1960) and Duncker (1971) regarded *M. transversus cloacae* (*M. transv. analis*) as a ventilatory muscle, listing it as one of the abdominal muscles that contributes to compression of the thoracoabdominal cavity. None of the tail muscles was listed as ventilatory by these authors.

#### *Inspiratory muscles*

Early in our studies we observed the repetitive movements of elevation/depression of the uropygium that corresponded with expansion/compression of the ventral abdominal wall. We assumed that most of this was tail movement, taking place mainly at the postsynsacral joint (Figs 1, 7) between the rear of the synsacrum and the first free caudal vertebra. In fact, much of the dorsal/ventral movement of the uropygium with its implanted quills was taking place at the junction in front of the pelvis, and the entire pelvis, with the uropygium appended to it, was rotating at that notarial-synsacral junction (Figs 1, 7). The paired *longissimus dorsi* produces dorsiflexion of the pelvis at the notarial-synsacral joint, thereby bringing about elevation of the caudal border of the pelvis. *M. longissimus dorsi* was consistently active during inspiration over a range of breathing rates (Figs 3-6).

Our observations on the EMG activity of *M. longissimus dorsi* do not agree with those of Salt and Zeuthen (1960) or Fedde (1987), who categorize this muscle as an expiratory muscle. Fedde states that in many cases it is '...electrically active during expiration', but the position of the bird was not mentioned.

The other main inspiratory muscles are the external intercostals, the *levator costarum* and the *costisternales* (Fedde, 1987). All these muscles act on the ribs,

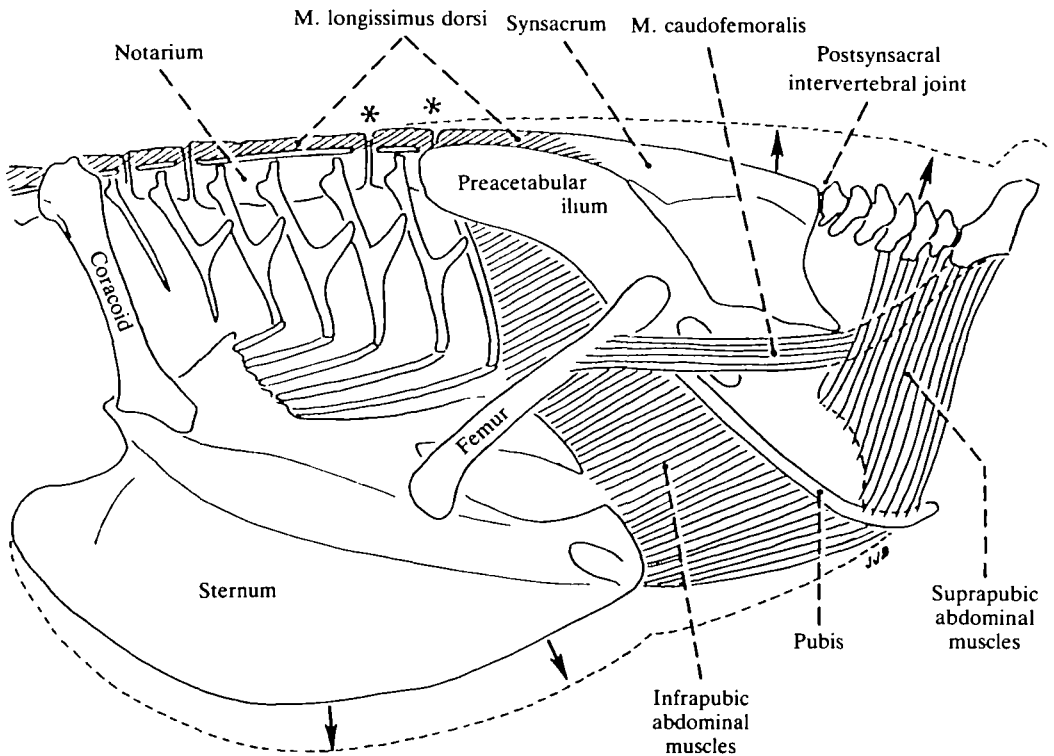


Fig. 7. Scheme of ventilatory movements of pelvis and sternum and muscle groups in the pigeon; lateral view of trunk and tail. Arrows pointing dorsally and ventrally and dashed lines at top and bottom of figure indicate excursions of the pelvis and sternum during *inspiration*. Note that these movements do not occur simultaneously. Asterisks indicate the intervertebral joints between the synsacrum and the notarium; dorsi- and ventriflexion at these joints raise and lower the pelvis with its appended uropygium. Depression of pelvis plus uropygium is associated with the expiratory phase of ventilation (see Figs 4–6). The suprapubic group of abdominal muscles includes Mm. pubocaudalis internus and externus; these are not attached directly to the caudal vertebrae, as shown, but are actually attached to the rectricial bulb (see Figs 1, 2). Contraction of the caudofemoralis and pubocaudalis muscles depresses the pelvis plus uropygium. When the bird is standing and the pelvis fixed, these depressor muscles act at the postsynsacral joint to lower *only the uropygium*.

expanding the volume of the thoracoabdominal cavity, *pushing* the sternum and vertebral column apart by increasing the angles between the vertebral and sternal ribs (Fig. 7). The longissimus dorsi, in contrast, contributes to inspiration by dorsiflexing the thoracic vertebral column, *pulling* the synsacral (pelvic) vertebrae upwards away from the sternum.

#### *Expiratory muscles*

Whether a bird is standing on its hind limbs or resting on its sternum, the elastic

recoil of the thorax provides part of the force to accomplish expiration (Duncker, 1971; Peek *et al.* 1975). This elastic recoil is supplemented by the contraction of the infrapubic abdominal muscles, such as the internal and external obliques and transversus abdominus that draw the caudal border of the sternum dorsally. Conversely, with the pigeon's weight resting on the sternum, the pelvis in its inspiratory (raised) position is returned to its expiratory position, compressing the thoracoabdominal cavity passively, by elastic recoil and gravity, and actively, by the four suprapubic tail/abdominal expiratory muscles (Fig. 7).

The expiratory activity of the *M. caudofemoralis* is shown in Fig. 4. We found it to be active in both eupneic and hyperpneic ventilation, making it the primary expiratory muscle acting on the tail. The line of action of the *M. caudofemoralis* from the upper shaft of the femur to the ventral surface of the uropygium is shown in Fig. 7. In the tailed amphibians, lizards and crocodiles, *M. caudofemoralis* is associated with locomotion. It contributes to lateral tail flexion as the rear limb of its side is advanced and planted during walking (Haines, 1935) or, if bilaterally activated, its attachments indicate that it also ventrally flexes the tail. In birds, *M. caudofemoralis* acts unilaterally as one of the principal lateral flexors of the uropygium (Baumel, 1988). However, EMG evidence of this present study (Fig. 4) indicates that when bilaterally activated, it also participates in ventralflexing the notarial-synsacral joints and depressing the pelvis; it is thus one of the antagonists of *M. longissimus dorsi*.

The consistent expiratory function of the *M. caudofemoralis* is in contrast to the function of the *pubocaudalis internus* and *pubocaudalis externus* muscles. These muscles were not always active during eupneic breathing, but expiratory activity could be induced by the administration of carbon dioxide and air. The ventilatory action of the *pubocaudalis* muscles effects movement of the uropygium but not the pelvis; the *caudofemoralis* can move both.

Apparently there is no antagonist of the *pubocaudalis* muscles during expiratory (depression) movements of the uropygium at the postsynsacral joint. Presumably the depressed uropygium returns to its neutral position by visco-elastic recoil of the muscles and ligaments of the tail.

#### *Relationship between inspiration and expiration*

One other aspect of quiet ventilation in pigeons may be seen by comparing the time spent during inspiration ( $T_I$ ) to time spent during expiration ( $T_E$ ). In mammals the  $T_I/T_E$  ratio is usually 1:2, meaning that twice as much time is spent in expiration than in inspiration. Brackenbury (1987) points out that the avian breathing pattern is similar to that observed in mammalian breathing. He notes that in birds expiration is the longer phase, and in normal breathing the expiratory air sac pressure and air flow waves show an exponential decay. In our pigeons, we found great variability in this ratio, with ratios ranging from less than 2:3 (Fig. 6) to more than 3:2 (Fig. 5). The functional significance of this finding is unclear to us, as these ratios changed during quiet breathing.

*Relationships between posture and ventilation*

The resting ventilatory needs of a bird are similar whether the bird is standing or is supported on its sternum. Elevation of the highly mobile uropygium alone is obviously capable of producing less increase in volume of the thoracoabdominal cavity than elevation of the pelvis plus the uropygium. Interestingly, in the pigeon the surface area of the visceral surface of the sternum is roughly equivalent to the combined areas of the visceral surfaces of the pelvis and the uropygium, making an upward displacement of the pelvis plus uropygium produce approximately as much increase in volume of the thoracoabdominal cavity as that produced by downward displacement of the sternum. Pelvic respiratory movements therefore can apparently substitute for sternal movements, but we have not made any volumetric determinations to establish whether the two mechanisms produce equivalent volume changes.

Birds ventilate while standing, supported on the sternum on a solid substratum or water, or suspended by their wings. The ventral depression of the caudal end of the sternum while a bird is standing is brought about by increasing the angles between the sternal and vertebral ribs. When the bird is standing, the weight of the viscera on the sternum and ventral abdominal wall assists in inspiratory depression of the sternum (Duncker, 1971). Although movements of the uropygium can occur, neither elevation of the pelvis nor dorsal displacement of the vertebral column of the trunk is likely to take place in the standing bird, since the pelvis is suspended upon the two planted hind limbs.

Birds commonly rest with the breast pressing against the ground or the perch when roosting, while sitting on the nest during incubation and brooding, as well as during swimming (Duncker, 1971). Under these conditions the ventral excursions of the sternum during inspiration are restricted, so that ventral enlargement of the rib cage may be replaced or assisted by elevation of the pelvis. According to Duncker (1971) with the sternum fixed the angular displacement of the more compliant vertebral column in a dorsal direction away from the sternum rotates about a transverse axis passing through the two shoulder joints.

Ventilation during flight may involve both sternal movement and elevation of the pelvis. Recently Jenkins *et al.* (1988) have studied cineradiographically the wind-tunnel flapping flight of the starling (*Sturnus vulgaris*) and have demonstrated sternal movements that are coupled with wingbeats. They suggest that the sternal excursions might represent a secondary respiratory cycling mechanism between air sacs and lungs which is capable of operating independently of inhalation and exhalation. Duncker (1971) noted that depression of the sternum is limited when the bird is hanging on its wings during flight. If the sternal excursions were restrained during soaring, for example, then the muscles acting on the vertebral–pelvic–uropygial complex we have described might substitute, assuming the ventilatory role of expansion and compression of the thoracoabdominal cavity in the manner of the bird resting on its breast. Whereas fixation of the sternum has not been shown in flapping flight of the starling (Jenkins *et al.* 1988), it does seem reasonable that sternal movement in soaring birds may have a restricted range.

*Division of labor of ventilatory muscles*

We have already distinguished two functional sets of respiratory muscles. Although not completely distinct from one another, the suprapubic abdominal set of respiratory muscles (including *M. transversus cloacae*) and the infrapubic set show to some extent a division of labor between them, depending on whether the bird's sternum is stabilized or freely mobile.

The works of several authors suggest that there might be other sorts of divisions of labor between the two sets of respiratory muscles. Gaunt and Gaunt (1983) state that the abdominal muscles are active not only in expiration but also affect amplitude modulation in generating warbles and trills during phonation. Ramirez and Bernstein (1976) described compound ventilation that occurs during panting in pigeons, and described how high rates of thermoregulatory panting are superimposed on normal expiratory rhythms. Brackenbury (1978) reported that bursts of pulsed sound in clucking chickens and honking geese (*Anser*) were attributable to a series of pant-like movements superimposed upon single expirations. Perhaps the infrapubic and suprapubic muscle groups (Fig. 7) have separate functions when high-frequency expiratory pulses are produced. One group of muscles might be providing the constant driving pressure for respiratory expiration, the other group providing the fine control of the expiratory pulsations of panting and complicated singing. It would be interesting to take simultaneous recordings from one each of the suprapubic and infrapubic expiratory abdominal muscles during complicated sound production to determine if the EMG activities of the two were out of phase.

Does the uropygium itself participate in ventilatory movements of the standing bird with its pelvis stabilized? One would expect so, but our study does not answer this directly since all our EMGs were of birds resting on their breasts. Our indirect observations of perched, vocalizing birds definitely indicate that some of the tail depressor muscles must be contracting in order to produce the characteristic lowering of the uropygium *independent of pelvic movements*, thereby assisting in compression of the thoracoabdominal cavity.

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