

Buccal oscillation and lung ventilation in a semi-aquatic turtle, *Platysternon megacephalum*

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Summary

Movements of the hyobranchial apparatus in reptiles and amphibians contribute to many behaviors including feeding, lung ventilation, buccopharyngeal respiration, thermoregulation, olfaction, defense and display. In a semi-aquatic turtle, *Platysternon megacephalum*, x-ray video and airflow measurements from blowhole pneumotachography show no evidence that above water hyobranchial movements contribute to lung inflation, as in the buccal or gular pump of amphibians and some lizards. Instead, hyobranchial movements produce symmetrical oscillations of air into and out of the buccal cavity. The mean tidal volume of these buccal oscillations is 7.8 times smaller than the mean tidal volume of lung ventilation (combined mean for four individuals). Airflow associated with buccal oscillation occurs in the sequence of inhalation followed by exhalation, distinguishing it from lung ventilation which occurs as exhalation followed by inhalation. No fixed temporal relationship between buccal oscillation and lung ventilation was observed. Periods of ventilation often occur without buccal oscillation and buccal oscillation sometimes occurs without lung ventilation. When the two behaviors occur together, the onset of lung ventilation often interrupts buccal oscillation. The initiation of lung ventilation was found to occur in all phases of the buccal oscillation cycle, suggesting that the neural control mechanisms of the two behaviors are not coupled. The pattern of occurrence of both buccal oscillation and lung ventilation was found to vary over time with no obvious effect of activity levels.

Key words: buccal oscillation, lung ventilation, respiration, buccal pumping, tidal volume, Chelonia, Testudines

Introduction

The buccal cavity and hyobranchial apparatus are involved in a wide variety of behaviors in tetrapods including feeding, lung ventilation, buccopharyngeal respiration, thermoregulation, olfaction, defense and display. In reptiles, three distinct types of buccal movement have been described but are often confused (Cragg, 1978). The first type contributes to lung ventilation and is referred to as a buccal pump or gular pump. Early physiological studies of reptiles at rest found no evidence that buccal movements contribute to lung ventilation (McCutcheon, 1943; Cragg, 1978; Naifeh et al., 1970; Gans and Clark, 1976). However, recent studies

have found that some lizards do use a gular pump to supplement aspiration breathing during exercise and at increased temperatures (Owerkowicz et al., 1999, 2001; Al-Ghamdi et al., 2001). In contrast, recent studies show no evidence of buccal pumping in crocodylians during locomotion (Farmer and Carrier, 2000).

The second type of buccal movement described in reptiles is buccal oscillation, also referred to as buccal pulsation (Cragg, 1978). Buccal oscillation is the movement of air in and out of the buccal cavity without the air passing to the lungs. Buccal oscillation does not play a role in lung ventilation, which distinguishes it

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from buccal pumping (de Jongh and Gans, 1969; Gans, 1970). Cragg (1978) describes a third type of buccal movement occurring in sequence with lung ventilation. This movement involves a small buccal compression during exhalation of air from the lungs and a small expansion during inhalation. The compression during exhalation has been proposed to help reduce dead air space in the buccal cavity during lung ventilation.

Upon observing buccal movements in turtles resembling the throat movements of frogs and salamanders, it was once believed that turtles used a buccal pump for lung ventilation (e.g., Agassiz, 1857). However, Mitchell and Morehouse (1863) suggested that most turtles are unable to seal the mouth and nares sufficiently to pump air from the buccal cavity into the lungs. Their conclusion was later supported by McCutcheon's (1943) work on *Malaclemys centrata*. McCutcheon demonstrated that the glottis is closed and the tracheal pressure does not fluctuate during observed throat movements, indicating that they do not contribute to lung ventilation.

Buccal oscillation in turtles involves expansion of the buccal cavity during which air or water is drawn into the buccal cavity through the nares and then compression of the buccal cavity during which air or water is expelled back out through the nares. Some aquatic turtles have been found to extract oxygen from the water through well-vascularized buccopharyngeal mucosa (Dunson, 1966). In these turtles, aquatic buccal oscillation may contribute to buccopharyngeal gas exchange by increasing the flow of oxygenated water across the buccopharyngeal mucosa. However, studies of other aquatic turtle species suggest a minimal role for aquatic buccal oscillation in buccopharyngeal respiration and instead suggest that buccal oscillation increases the flow of water over the nasal epithelia with olfaction as the primary function (Belkin, 1968).

The function of aerial buccal oscillation in turtles on land is not known for certain but has been proposed to contribute to olfaction (McCutcheon, 1943). McCutcheon observed an increase in the occurrence of buccal oscillation when *Malaclemys centrata* was exposed to the smell of crushed fiddler crab, suggesting that the behavior has an olfactory role. Aerial buccal oscillation may also play a role in thermoregulation, as has been suggested for lizards at high temperatures (Heatwole et al., 1973).

In addition to performing aquatic buccal oscillations, turtles submerged in water have also been observed to poke their nares above water and perform aerial buccal oscillations (Brainerd, 1999; Belkin, 1968; Bagatto and Henry, 1999). Above water oscillation is the least studied of the buccal oscillation behaviors, and the relationship, if any, of this behavior to lung ventilation is unknown.

The primary goal of this study is to characterize the airflow associated with above water buccal oscillation and lung ventilation in a semi-aquatic turtle, *Platysternon megacephalum*. Although previous studies have found no evidence for the use of a buccal pump for lung ventilation in turtles, recent discoveries of gular pumping in some lizards suggest that it may occur in turtles but has simply not been documented. Therefore, a secondary goal is to examine the airflow patterns to determine whether any of the buccal movements observed contribute to lung ventilation.

Platysternon megacephalum (big-headed turtle) is a semi-aquatic turtle whose preferred habitat is fast-moving, cold-water mountain streams of Southeast Asia. These turtles are well equipped with strong claws and a long tail which aid in climbing over boulders and grasping rocks in the fast-moving water. They have relatively large heads which are covered in horny armor for protection, as they cannot withdraw their head into their shell. They are not well equipped for swimming and spend the day burrowed in the rocks. They emerge at night for feeding (Kirkpatrick, 1997). In captivity, they spend most of the time in the water, coming out occasionally if a basking place is provided. For lung ventilation while submerged in shallow water, they simply extend their heads until their nostrils reach the surface. Their large head and buccal region allow easy observation of hyobranchial movement and their lack of active swimming behavior makes *P. megacephalum* a good species for this study.

Materials and Methods

Animals

Two subadult *Platysternon megacephalum* were obtained from a commercial animal importer and two additional subadult specimens, kept as pets in the local area, were borrowed from their owners and returned at the end of this non-invasive study. The turtles ranged in mass from 127–208 g and in carapace length from 9.3–10.5 cm. All the specimens were kept in separate 10-gallon aquaria, with a water depth of approximately 8 cm and a 12 hour light/dark cycle. The water temperature ranged from 21–23 °C and the turtles were maintained on a diet of earthworms and feeder fish. All experiments were conducted with each turtle remaining in its home aquarium to reduce stress. Three additional species, *Staurotypus triporcatus*, *Chrysemys picta* and *Terrapene carolina*, were also observed for comparison with *P. megacephalum* (one individual each). The use of live animals in this project was approved by the Institutional Animal Care and Use Committee of the University of Massachusetts Amherst.

Blowhole pneumotachography

The water surface of each tank was covered with a plastic grid containing a blowhole (8.5 cm in diameter) at one corner at which the turtles could surface. The turtles were allowed to acclimate to the grid for a minimum of a week before data collection was started. The blowhole in the grid was covered by a pneumotach chamber, constructed from the top portion of a 16 oz polystyrene water bottle with a pneumotachograph (53 μ m nylon mesh screen) attached to the bottle cap. The pressure changes across the screen were measured using a differential pressure transducer (Validyne DP103-06) attached to a carrier demodulator (Validyne CD15). The signal was amplified $\times 10$ using a differential amplifier (Tektronix, model TM 502). A constant airflow of 700 ml/min was maintained through the blowhole and was regulated by a flow meter (Cole-Parmer). The pneumotach was calibrated using known volumes of air and known airflow rates. Both airflow and volume were linear over the ranges produced by the animals ($R^2 > 0.99$), and airflow rate had no effect on volumes measured.

Each turtle's behavior was recorded for about three hours between 12:00 and 19:00 hours. Airflow (pneumotach) traces were recorded and displayed in real time on an Apple Macintosh computer with a G.W. Instruments A/D conversion board and SuperScope II 2.0 software. Real time airflow traces were superimposed on live video of the animal, and the resulting split screen video was recorded on a VCR. The volumes of exhalation and inhalation for both ventilation and oscillation were calculated by obtaining the area under the curve for each event and converting it into volume using the calibration equations. To determine the level of activity of the turtle, the flow trace and video were examined. If a majority of the flow trace fluctuated (due to the water disturbance) above 250 mV over the 5 minute time period, the turtle was considered active during that period.

A paired t-test (Excel 98) was used to compare inspiratory and expiratory volumes for both lung ventilation and buccal oscillation.

X-ray videography

X-ray videography was used to observe the airflow patterns during buccal oscillation and lung ventilation. Lateral and dorsoventral views were obtained using a Siemens cineradiographic unit with a Sirecon image intensifier. X-ray videos were recorded for two individuals using a built-in tube camera as well as a Sony VX1000 digital camcorder (shutter speed 1/250 s). A small metal marker was attached with cyanoacrylate adhesive to the ventral region of the neck to make buccal movements more clear.

Hyobranchial movement

Hyobranchial depression was measured by digitizing video sequences at 15 fps (Adobe Premiere 5.1 and NIH Image 1.62). The perpendicular distance between the top of the head and the most depressed portion of the buccal cavity was measured for each frame and then graphed over time (KaleidaGraph 3.0.4). This graph was then superimposed over the airflow trace to correlate hyobranchial movement with airflow.

Results

In the laboratory, *Platysternon megacephalum* spends most of the time submerged under water, resting. Periodically, they lift their heads and extend their necks to reach the surface for lung ventilation. After several cycles of lung ventilation, the turtles either resubmerge or remain with their nares at the surface. When they remain at the surface they often perform aerial buccal oscillations interspersed with further bouts of lung ventilation.

After arrival in the lab, the two specimens obtained from an importer showed no buccal oscillations for approximately four months. After this period of adjustment, oscillations could be seen regularly during surfacing events in these two individuals as well as in the other two specimens which had been in captivity for at least one year. Two aquatic turtle species, *Staurotypus triporcatus* and *Chrysemys picta*, and a semi-aquatic species, *Terrapene carolina*, were also observed to perform aerial buccal oscillations (observed under similar conditions as *P. megacephalum*). These three additional turtles had also been in captivity for at least one year.

Aquatic buccal oscillations were also observed under water in both *P. megacephalum* and *S. triporcatus*. In *P. megacephalum*, these aquatic buccal movements are much smaller in amplitude than aerial buccal movements and occur as a compression-expansion cycle in contrast to the expansion-compression cycle of aerial buccal oscillation.

Kinematics

The pattern of airflow during above water buccal oscillation and lung ventilation can be seen in still frames from a lateral view, x-ray video of *P. megacephalum* (Figs. 1 and 2). Lung ventilation begins with the lungs expanded and the hyobranchium in its resting state (Fig. 1A). The lungs compress and exhalation occurs (Fig. 1B). The lungs then expand, drawing air in and completing the ventilatory cycle (Fig. 1C). As indicated by the metal marker glued to the outer surface of the buccal cavity, there is little to no movement of the buccal cavity during lung ventilation.

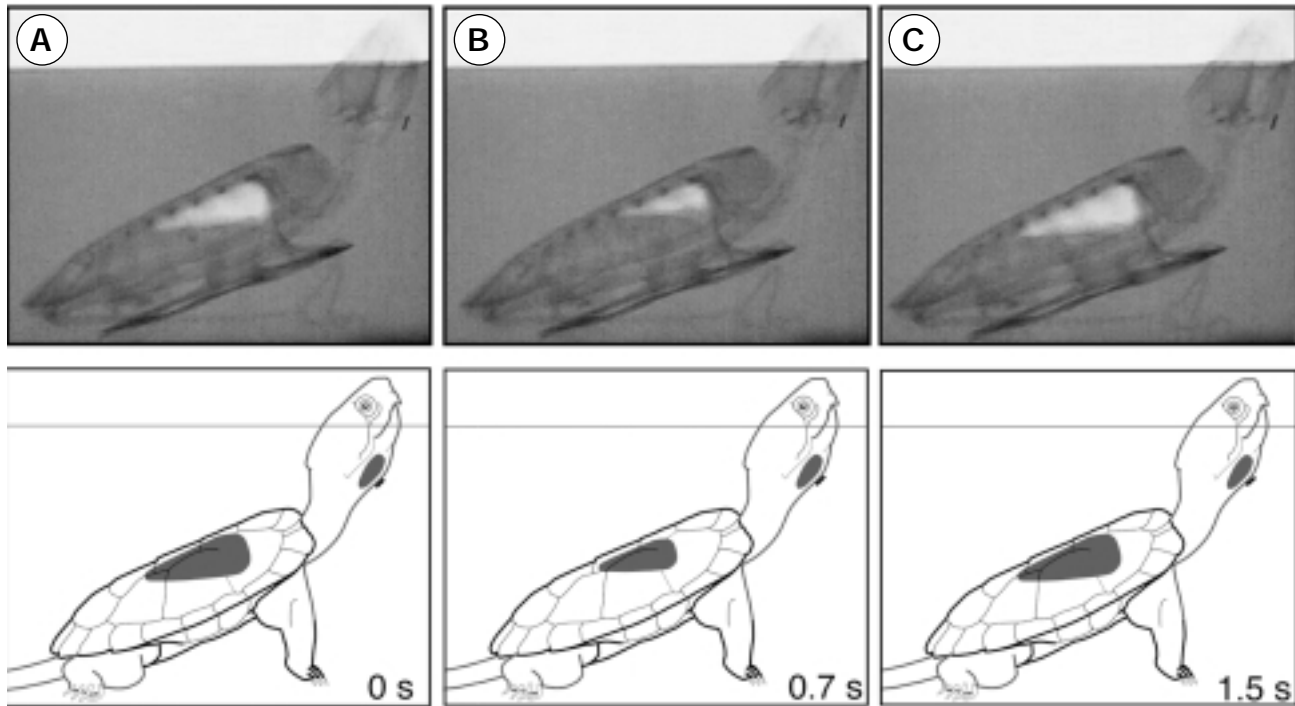


Fig. 1. X-ray positive video images of lung ventilation in *Platysternon megacephalum* with corresponding outlines of body, lungs and buccal cavity. The sequence shows three stages of the ventilatory cycle: (A) immediately prior to exhalation; (B) maximum exhalation; and (C) maximum inhalation and completion of breath. A small metal marker glued to the outer surface of the buccal cavity shows that there is little to no movement of the buccal cavity during lung ventilation.

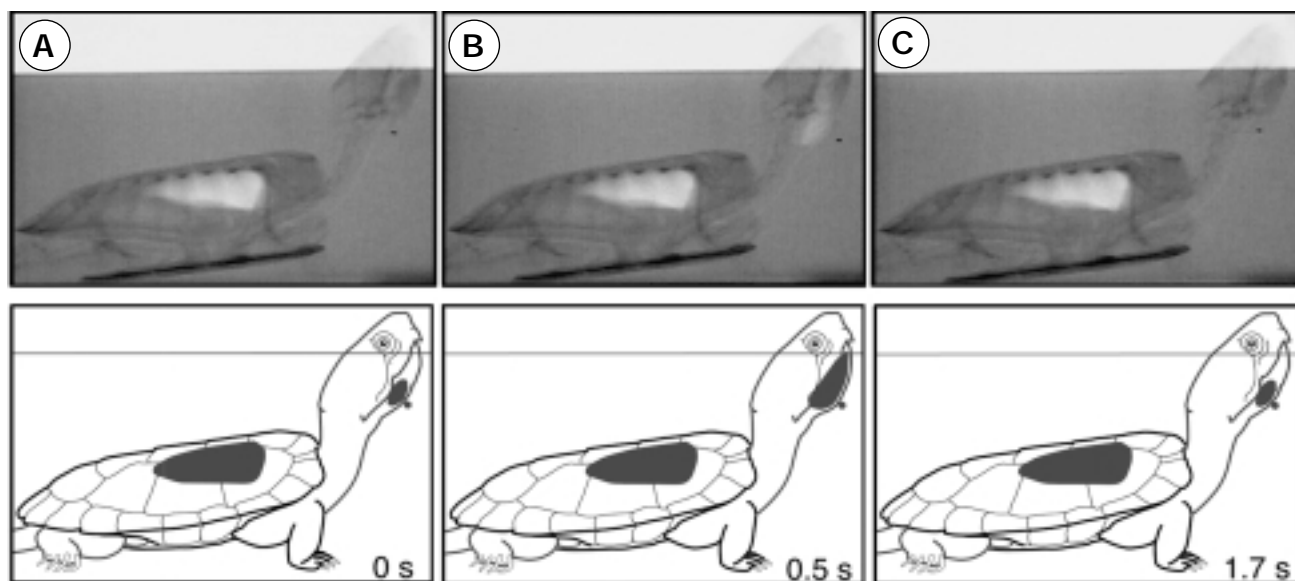


Fig. 2. X-ray positive video images of aerial buccal oscillation in *Platysternon megacephalum* with corresponding outlines of body, lungs and buccal cavity. The sequence shows three stages of the oscillatory cycle: (A) immediately prior to start of buccal expansion; (B) maximum buccal expansion; and (C) end of buccal compression. A small metal marker glued to the outer surface of the buccal cavity makes buccal movements more clear.

Buccal oscillation begins with the lungs expanded and the buccal cavity compressed as in lung ventilation (Fig. 2A). The buccal cavity expands, drawing air into the buccal cavity through the nares with no expansion of the lungs (Fig. 2B). After peak expansion, the buccal cavity then compresses, expelling the air back out through the nares completing the oscillatory cycle (Fig. 2C).

Airflow and volumes

In airflow traces, buccal oscillation and lung ventilation can be distinguished by the sequence of exhalation and inhalation and by the volume of air moved. Following a period of apnea, buccal oscillation begins with the inhalation of air followed by exhalation (Fig. 3A) whereas lung ventilation begins with exhalation followed by inhalation (Fig. 3A,C). Mean tidal volumes were measured for each turtle for both lung ventilation and buccal oscillation to allow a comparison of the relative volumes (Table 1). Mean tidal volumes for lung ventilation were 4.8–12.5 times larger than mean tidal volumes for buccal oscillations (based on comparison of mean expired volumes in Table 1), with an overall mean of 7.8 times larger for the four individuals studied. Tidal volumes associated with buccal oscillation ranged from 0.031 to 2.274 ml of air and ventilatory volumes ranged from 2.513 to 10.482 ml air. The number of breaths recorded for each turtle and used for this analysis ranged from 65 to 90, and the number of oscillations recorded ranged from 48 to 232 (Table 2).

During buccal oscillation and lung ventilation, mean inspiratory and mean expiratory volumes are roughly equal (Table 1). Statistically significant differences between buccal inhalation and exhalation were detected in two turtles, but in one case buccal inhalation was larger than buccal exhalation and in the other case buccal exhalation was larger than buccal inhalation (Table 3).

Hyobranchial movement

A strong correlation exists between hyobranchial movement and airflow during buccal oscillation (Fig. 4). Peak hyobranchial depression occurs slightly after peak inhalation and the hyobranchium returns to its resting state between peak exhalation and the end of the oscillatory cycle. In addition to the hyobranchial movement during buccal oscillation, a small depression of the buccal cavity is observed during some, but not all lung ventilation cycles (Fig. 4, indicated by *). This expansion begins at the start of exhalation, with the buccal cavity returning to its resting state before the start of inhalation.

Table 1. Mean tidal volumes (ml) of lung ventilation and aerial buccal oscillation in four individuals of *Platysternon megacephalum* (mean \pm s.d.). Sample sizes in Table 2.

Individual	Ventilation (out ¹)	Ventilation (in ²)	Oscillation (in)	Oscillation (out)
2	7.30 \pm 0.682	7.19 \pm 0.756	1.02 \pm 0.517	1.00 \pm 0.570
3	4.25 \pm 0.838	4.36 \pm 1.008	0.92 \pm 0.376	0.88 \pm 0.415
4	6.52 \pm 0.829	6.60 \pm 0.914	0.97 \pm 0.509	0.95 \pm 0.569
5	6.73 \pm 1.630	6.54 \pm 1.680	0.48 \pm 0.326	0.54 \pm 0.416

¹out indicates expiratory phase

²in indicates inspiratory phase

Table 2. Number of events recorded for four *Platysternon megacephalum*.

Individual	Body mass (g)	Ventilations	Combinations*	Oscillations
2	127	65	24	148
3	134	68	46	232
4	166	90	40	126
5	208	47	14	48

*combinations are events in which buccal oscillation is interrupted by lung ventilation.

Table 3. *P* values from paired *t* tests comparing exhaled and inhaled volumes of lung ventilation and above water buccal oscillation. Sample sizes in Table 2.

Individual	Ventilation	Oscillation
2	<i>p</i> = 0.16	<i>p</i> = 0.15
3	<i>p</i> = 0.22	<i>p</i> = 0.0005 ¹
4	<i>p</i> = 0.22	<i>p</i> = 0.2800
5	<i>p</i> = 0.37	<i>p</i> = 0.05 ²

¹inspiratory oscillations larger than expiratory oscillations

²expiratory oscillations larger than inspiratory oscillation

Patterns and variation

The relationship between lung ventilation and buccal oscillation during surfacing events is highly variable, ranging from no oscillation (Fig. 3C) to a few buccal oscillations interspersed between lung ventilation (Fig. 3A) to a continuous pattern of oscillation and ventilation (Fig. 3B).

In examining the temporal relationship between buccal oscillation and lung ventilation, we found that buccal oscillations were often interrupted by the start of lung ventilation (Fig. 3A, B). Lung ventilation may begin at any time during a buccal oscillation, indicating that there is no fixed phase relationship between buccal

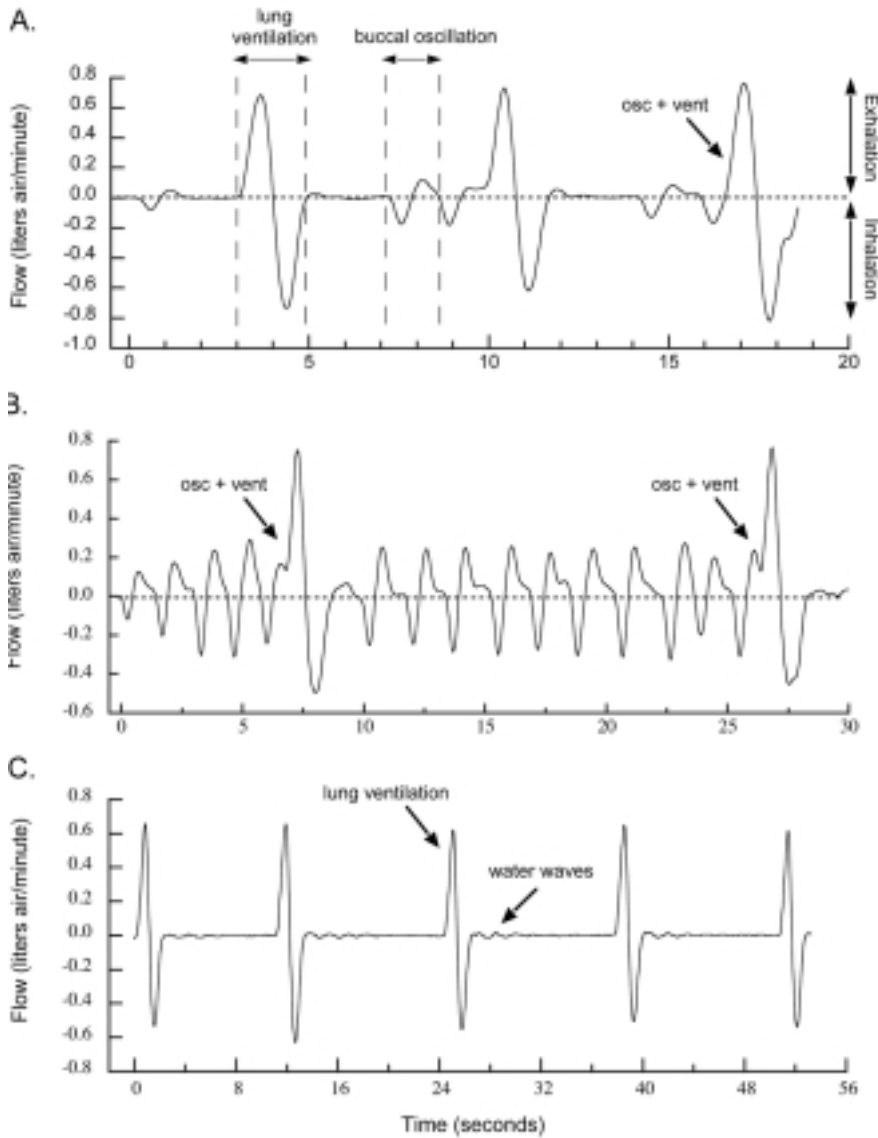


Fig. 3. Representative airflow traces of lung ventilation and buccal oscillation. (A) Intermittent buccal oscillation interrupted by lung ventilations. Note that lung ventilation begins with exhalation followed by inhalation whereas buccal oscillation begins with inhalation followed by exhalation. (B) Continuous buccal oscillation interrupted by two lung ventilation cycles. (C) Lung ventilation without buccal oscillation. Small movements of the animal during each breath produce water waves which are recorded as small flow

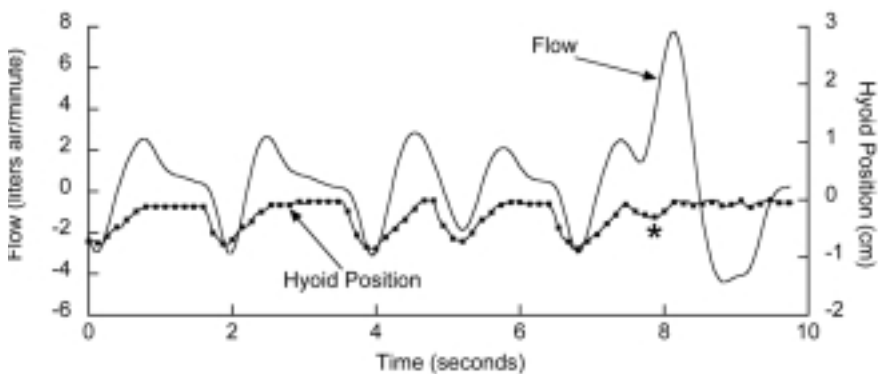


Fig. 4. Airflow trace synchronized with hyobranchial (hyoid) position showing large hyoid depressions during buccal oscillation and a small hyoid depression (*) during the expiratory stage of lung ventilation. Hyoid position was measured from standard light video at 15 images per second (shown with square symbols; half of the points have been omitted from the plot for clarity).

oscillation and lung ventilation. For example, in figure 3B, two ventilations begin toward the end of the expiratory phase of buccal oscillations (osc + vent). The resulting airflow trace is a sum of the airflow due to exhalation of air from the lungs and the airflow due to compression of the buccal cavity. In figure 3A, a ventilation interrupts an oscillation at the beginning of the expiratory phase of buccal oscillation (at 9.5 s) and another ventilation interrupts an oscillation toward the end of the inspiratory phase (at 16.5 s; osc + vent).

The percentage of buccal oscillations that were interrupted by lung ventilation ranged from 14 to 24 percent of the total number of oscillations recorded (Table 2). Overlapping oscillations and ventilations were not included in the analysis of tidal volumes because the flow associated with lung ventilation and buccal oscillation could not be differentiated.

The occurrence of buccal oscillations and lung ventilations within 5-minute time intervals was highly variable with no evidence of a regular pattern (Fig. 5). The ratio of buccal oscillations to lung ventilations varied as well. There does not seem to be an obvious effect of activity levels on the ratio of oscillation to lung ventilation or on the interval between surfacing events (Fig. 5).

Discussion

The above water buccal oscillations observed in *Platysternon megacephalum* are similar to those observed in aquatic turtle species including *Chelydra serpentina* (Bagatto and Henry, 1999), *Sternotherus minor* (Belkin, 1968), *Trachemys scripta* (Belkin,

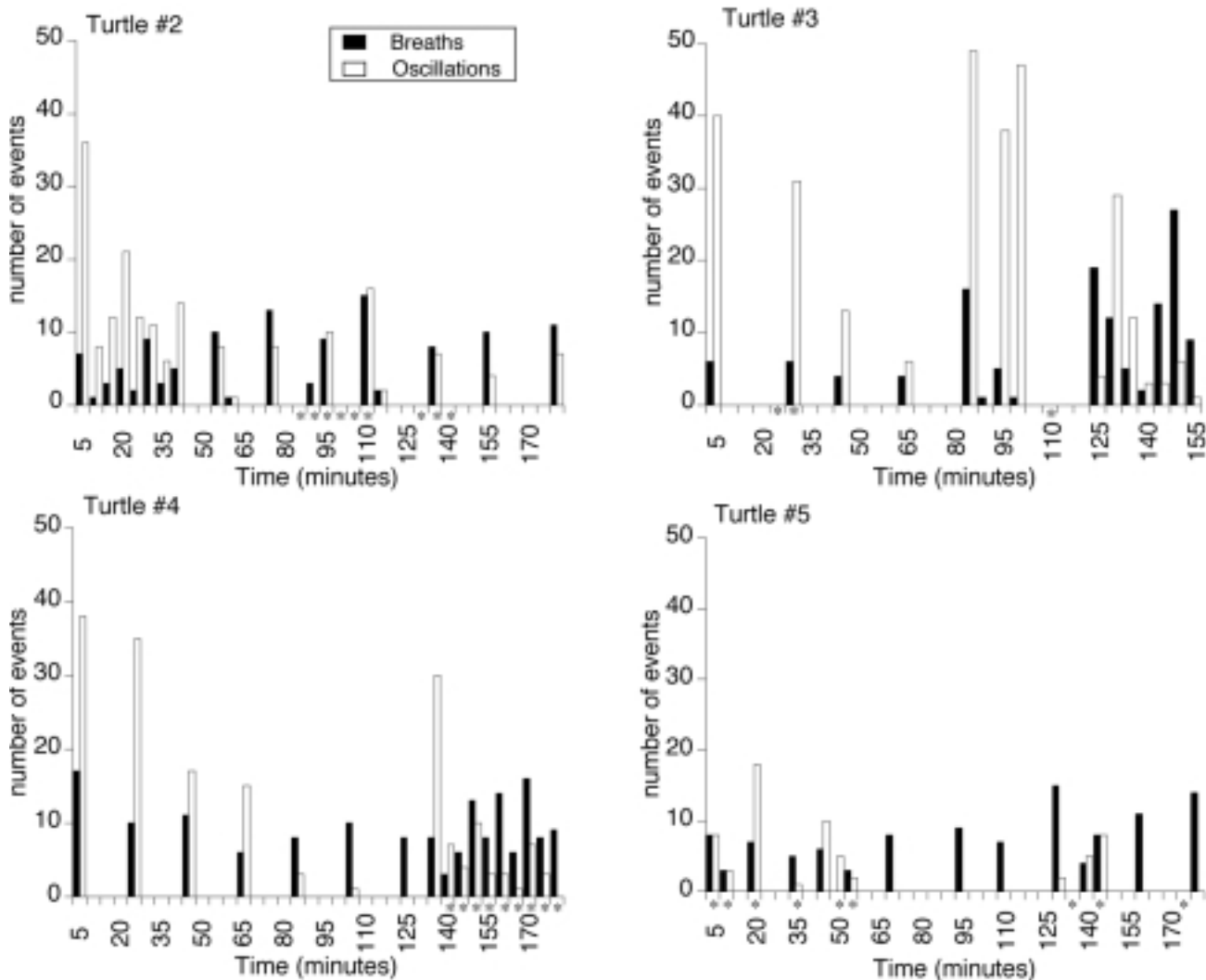


Fig. 5. Number of breaths and buccal oscillations per five minute period. The four graphs represent recordings from four individual turtles. * indicates activity during the time period.

1968), and *Chrysemys picta* and *Staurotypus triporcatus* (pers. obs., K.A.D.). Many turtles, including *P. megacephalum*, also exhibit aquatic buccal oscillations in which water is drawn into the buccal cavity. Previous studies have concentrated on this underwater behavior and its role in buccopharyngeal respiration. However, it is important to note that in *P. megacephalum*, aquatic and aerial buccal oscillations differ. Under water, the buccal movements are noticeably smaller and occur as compression-expansion cycles compared to the expansion-compression cycles above water. The same pattern of compression and expansion under water, in contrast to the expansion-compression cycle above water, occurs in *Staurotypus triporcatus* (pers. obs., K.A.D.). This reversal suggests that buccal oscillations may have different functions in these two environments.

Kinematics and airflow

X-ray video recordings confirm that the above water buccal movements observed in *P. megacephalum* are buccal oscillations and are not involved in lung ventilation (no buccal or gular pump present). During aerial buccal oscillation, the buccal cavity is first expanded, drawing air in through the nares. As the buccal cavity compresses and returns to its resting state, the air is expelled back out through the nares without the air moving to the lungs (Fig. 2). The expansion of the buccal cavity is due to the retraction and depression of the hyobranchial apparatus. Then, as the hyobranchium is protracted and elevated, the buccal cavity is compressed and the air is expelled.

In contrast to buccal oscillation, lung ventilation occurs as an exhalation-inhalation sequence, as shown by both x-ray images and airflow traces (Figs. 1 and 3). Analysis of hyobranchial movement and airflow also confirm an inhalation-exhalation pattern during buccal oscillation with a strong correlation of hyobranchial movement and airflow (Fig. 4). In addition to the normal hyobranchial movement during buccal oscillation, a small buccal expansion is sometimes seen during the expiratory phase of lung ventilation. This may be a passive expansion due to the flow of air out of the lungs (Fig. 4). A similar expansion has also been observed during exhalation in a South American crocodylian, *Caiman sclerops* (Naifeh et al., 1970; Huggins et al., 1968). The small hyobranchial expansion in *P. megacephalum* only occurs during exhalation with the buccal cavity compressing back to its resting state by the end of exhalation. This buccal compression during exhalation may be similar to the buccal movement reported by Cragg (1978) in which buccal compression was seen during exhalation and was thought to aid in reducing dead air space.

Tidal volumes and patterns

Mean tidal volumes for above water buccal oscillation were an average of 7.8 times smaller than the mean volumes associated with lung ventilation (Table 1). Airflow traces indicate that the observed buccal movements do not contribute to pumping air into the lungs (buccal or gular pumping). If gular pumping were occurring similar to the gular pumping that has been found in a monitor lizard, a large exhalation would be followed by a number of small gular inhalations as air is taken into the gular cavity (Owerkowicz et al., 1999, 2001). Each gular inhalation is followed either by a period of no flow or a small expiration due to a small leakage of air out the mouth or nares while most of the air is pumped into the lungs. Thus gular pumping may be recognized by asymmetrical gular inhalations and exhalations. No evidence of this pattern was seen and all buccal movements recorded had roughly equal volumes for the inspiratory and expiratory phases. Exhaled and inhaled volumes were not always completely symmetrical, but oscillations with a larger expiratory phase were just as common as oscillations with a larger inspiratory phase (Tables 1 and 3).

The relationship between lung ventilation and buccal oscillation varied greatly (Fig. 3). Surfacing bouts of buccal oscillation without lung ventilation were rarely recorded. However, bouts with only lung ventilation were common. Also, in all but one instance, all bouts began with lung ventilation. This would suggest that the primary purpose of surfacing is lung ventilation and not buccal oscillation. The pattern of buccal oscillation varied from continuous movements to sporadic, infrequent occurrences. The number of breaths and buccal oscillations varied per surfacing bout over time, and the rate of occurrence of buccal oscillation and lung ventilation does not appear to be correlated with activity levels (Fig. 5).

Functions of buccal oscillation

Three functions for buccal oscillation in reptiles have previously been proposed: buccopharyngeal respiration (gas exchange), thermoregulation and olfaction. Aquatic buccal oscillation has been found to play a role in both buccopharyngeal respiration and olfaction in trionychids (Dunson, 1966), but is thought to primarily be concerned with olfaction in musk turtles (Root, 1949). Thermoregulation is a possible function of aerial buccal oscillation and has been thought to help in heat dissipation in some lizards (Heatwole et al., 1973) as well as birds (gular flutter).

Previous studies have suggested that the primary role for buccal oscillation in turtles on land is olfaction (McCutcheon, 1943). Olfaction has also been proposed

as the primary function for geckos (Dial and Schwenk, 1996) and crocodylians (Naifeh et al., 1970). Buccal oscillation for olfaction is analogous to mammalian "sniffing" with the expansion of the buccal cavity drawing fresh air over the nasal epithelium and buccal compression expelling the air back out through the nares. An observed increase in buccal oscillation during stimulation and disturbance in geckos supports this hypothesis (Dial and Schwenk, 1996).

These proposed functions, however, do not seem plausible for above water buccal oscillation in *P. megacephalum*. The buccopharyngeal mucosa of *P. megacephalum* is not highly vascularized, suggesting no morphological specialization for buccopharyngeal gas exchange (Winokur, 1988). Furthermore, even with highly vascularized mucosa, there is no plausible reason for turtles to exchange gases across buccopharyngeal mucosa while they are able to ventilate the lungs. Buccal oscillation is likely to promote evaporation from the buccopharyngeal mucosa which would tend to cool the animal down. However, it is unlikely that a turtle submerged in water would be concerned with heat loss due to the high heat of conduction of water.

Olfaction seems the most likely function for above water oscillation, but it is unclear what airborne chemical signals turtles in water would benefit from detecting. Most aquatic turtles feed primarily on aquatic prey, and it seems unlikely that sniffing for aerial or terrestrial predators would be an effective strategy. However, the possible effects of observing captive rather than wild turtles must be considered. It is possible that the prevalence of aerial buccal oscillation in captive turtles is exaggerated by the fact that captive turtles are fed from the surface (J. Wyneken, pers. comm.). This possibility is supported by our finding that specimens of *P. megacephalum* recently brought into captivity did not perform a lot of buccal oscillations until they had been captive for about four months. Furthermore, turtles seemed to perform buccal oscillations most readily when people were moving around their aquaria, indicating that they may associate humans with food coming from above the surface. Observations of aquatic and semi-aquatic turtles in the field will be necessary to determine the natural prevalence of this behavior.

Implications for neural control of oscillation and ventilation

Previous researchers have questioned whether buccal oscillation and lung ventilation are controlled by the same or different central pattern generators (CPGs) (Shelton, et al. 1986; Smatresk, 1990). The observed temporal relationship between oscillation and ventilation in *P. megacephalum* suggests that they may be con-

trolled by different CPGs. Buccal oscillations and lung ventilations overlap as buccal oscillations are often interrupted by the initiation of lung ventilation (Figs. 3A, B; Fig. 4; Table 2). On average, about 19% of the total number of buccal oscillations recorded were interrupted by the initiation of lung ventilation. Interruption occurs during continuous rhythmic buccal oscillation as well as during isolated buccal oscillations, and may occur during either the expiratory or inspiratory phase of buccal oscillation. The finding that the two behaviors overlap and that there is no fixed phase relationship between the two suggests that the neural control systems of oscillation and ventilation are not tightly coupled.

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