

The kinematics of feeding and drinking in palaeognathous birds in relation to cranial morphology

Sander W. S. Gussekloo* and Ron G. Bout

Institute of Biology Leiden, Evolutionary Morphology, Leiden University, Kaiserstraat 63, NL-2311 GP Leiden, The Netherlands

*Author for correspondence at present address: Division of Anatomy and Physiology, Department of Pathobiology, Faculty of Veterinary Medicine, Utrecht University, Yalelaan 1, 3584 CL Utrecht, The Netherlands (e-mail: s.w.s. gussekloo@vet.uu.nl)

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Summary

Cranial kinesis is an important feature in avian feeding behaviour and involves the transmission of quadrate movement to the upper bill by the Pterygoid–Palatinum Complex (PPC). The PPC in Palaeognathae is remarkably different from that found in Neognathae. In this study we analyse whether the special morphology of the PPC is an adaptation to the feeding behaviour of the Palaeognathae. Behavioural analyses of the rhea *Rhea americana* showed that the feeding behaviour of the rhea is typical ‘Catch and Throw’ behaviour, independent of the size of the food item. Drinking is achieved by a scooping movement followed by a low-amplitude tip-up phase. During feeding

rhynchokinetic movements of the upper bill were observed. However, cranial kinesis was limited and may differ from rhynchokinesis in neognathes as a clear bending zone seemed absent. Since the movement patterns are considered very similar to the basic feeding behaviour in neognathous birds it is concluded that the specific morphology of the PPC is not the result of specific functional demands from palaeognathous feeding behaviour.

Key words: feeding behaviour, palaeognathae, cranial morphology, adaptation, *Rhea americana*.

Introduction

Since Merrem (1813) separated the Palaeognathae from all other birds, the taxon Palaeognathae has caused many disputes among ornithologists. One of the most important characters that separates the Palaeognathae from all other modern birds (Neognathae) is the dromaeognathous (= palaeognathous) palate, first described by Huxley (1867). It is not only the ‘palate’ that is different from that found in Neognathae, but a whole complex of morphological characters, which includes structures such as the pterygoid, quadrate and vomer (see McDowell, 1948; Bock, 1963; Gussekloo and Zweers, 1999). The character set of the jaw mechanism that discriminates the Palaeognathae from the Neognathae will be referred to as the palaeognathous Pterygoid–Palate Complex (palaeognathous PPC; Gussekloo and Zweers, 1999). The mechanical function of this PPC in neognathous birds is well known. The PPC participates in the movement of the upper bill (Bock, 1964). Upper bill movement is induced by rostral rotation of the quadrate, which pushes both the lateral jugal bars and the medial pterygoid–palate bar forward. Each bar transfers its forces and movement onto the premaxilla. The forward movement of the premaxilla results in an upward rotation of the upper bill around a hinge, either in the nasal–frontal area (prokinesis) or in the rostral part of the bill (rhynchokinesis), depending on the position of a flexible zone. In the palaeognathous birds it is assumed that a large flexible zone is

present in the centre of the upper bill (Fig. 1, Zusi, 1984). The pterygoid–palate bar and the quadrate are of great importance for cranial kinesis since these bars transfer the forces, and the muscles for the movement of the upper bill attach to these elements.

Although many authors have used the palaeognathous PPC for systematic purposes (Fürbringer, 1888; Gadow, 1892; Beddard, 1898; McDowell, 1948; de Beer, 1956; Bock, 1963), studies on the function of the system are very limited. Most previous analyses assumed that the special morphology of the PPC in Palaeognathae is related to rhynchokinesis (Hofer, 1954; Simonetta, 1960; Bock, 1963), mainly because of the osteology of the PPC, the flexibility of the dorsal and ventral bars of the upper bill, and the incomplete ossification of the lateral bar (Zusi, 1984). The movement pattern of the PPC during bill opening has been measured, and showed very little difference between Palaeognathae and Neognathae (Gussekloo et al., 2001). These studies, however, were done on either osteological specimens or head preparations and it is currently unknown if movement of the PPC and rhynchokinesis actually occurs in living palaeognathous birds.

In the present study we did a functional analysis of the feeding behaviour of the greater rhea *Rhea americana* (L.) in order to elucidate the function and origin of the palaeognathous PPC. Several hypotheses can be postulated about the evolution

of the special PPC morphology in the Palaeognathae. Our main hypothesis is that the specific palaeognathous morphology of the PPC is an adaptation to selective forces that act on the PPC in palaeognathous birds, but not in neognathous birds. Since the function of the PPC is the transfer of forces and movements during upper bill movement, it is assumed that these selective forces must be related to bill movement. Feeding behaviour is considered the strongest selection force acting on bill movement, and therefore on the PPC. Other behaviours such as vocalisation, preening and social behaviour are considered to have little effect on the osteology of the bills. To investigate whether differences in selection forces on bill movement are present, bill movement of a typical palaeognathous bird during feeding will be described and compared with a previously described general neognathous-feeding pattern (Zweers et al., 1994). If differences are found in the feeding behaviour it may be possible to infer which selective forces resulted in the differences in PPC morphology. If no differences in feeding pattern can be found between Neognathae and Palaeognathae it must be concluded that no different selective forces act on the PPC during feeding and an alternative hypothesis about the

origin of the difference in morphology between Neognathae and Palaeognathae must be postulated.

Materials and methods

The greater rhea *Rhea americana* (L.), a middle-sized palaeognathous bird from South-America, was chosen as representative for the Palaeognathae. This species has a general palaeognathous PPC configuration (McDowell, 1948) and its natural history and behaviour are well known (Raikow, 1968, 1969; Bruning, 1974; Martella et al., 1995, 1996; Rebores and Fernandez, 1997). For the analysis two animals, one male and one female, were trained to feed on several food types within the experimental set-up. For this analysis, feeding will include only the behavioural elements from picking-up the food item until swallowing. All phases prior to the picking-up for intra-oral transport are considered a part of food-acquisition.

The feeding behaviour of the birds was recorded using video imaging (25 frames s^{-1}). The recordings were made in an experimental set-up in which a lateral view and a frontal view of the bird were obtained in the same frame using a mirror situated in front of the bird at an angle of 45° . The birds had to approach the feeding arena through a small corridor, ensuring a good lateral position of the bird with respect to the camera. Behind the bird, from the camera's viewpoint, a grid ($2 \text{ cm} \times 2 \text{ cm}$ squares) was placed to make scaling possible.

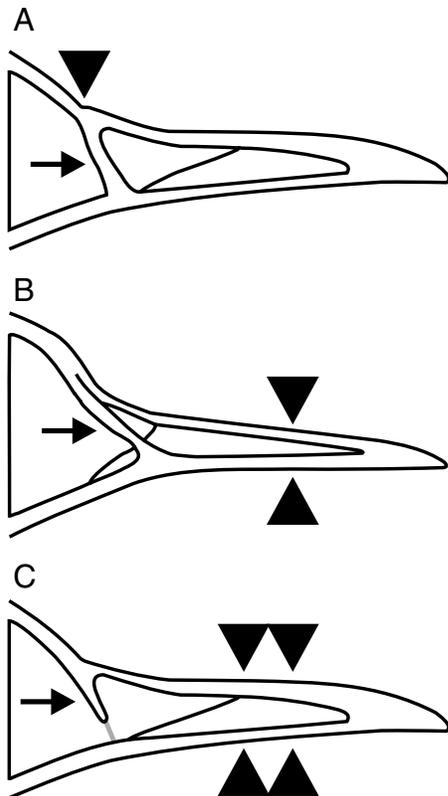


Fig. 1. Types of cranial kinesis in birds. (A) Prokinesis, (B) distal rynchokinesis, (C) central rynchokinesis. Skull outlines are given in lateral view. Black triangles indicate the main area of rotation, multiple triangles in a single element indicate the boundaries of an bending zone. The triangle in A indicates the nasal-frontal articulation. Arrows indicate the lateral (nasal) bar of the upper bill, which is incomplete in C. Ligament is shown in gray. (Adapted from Zusi, 1984.)

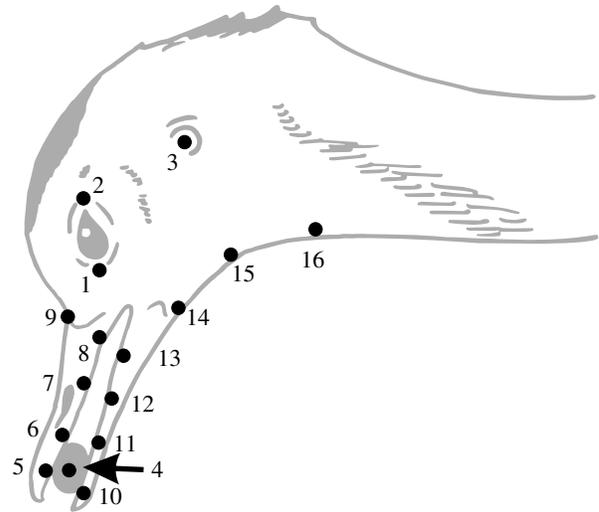


Fig. 2. Digitised points in each frame of the feeding scenes. (1) Rostral edge of the eye, (2) caudal edge of the eye, (3) centre of the ear, (4) centre of the food item, (5) upper bill, near the bill tip (ventral edge), (6) upper bill, rostral of the bending zone (ventral edge), (7) upper bill, caudal of the bending zone (ventral edge), (8) upper bill, caudal part (ventral edge), (9) upper bill, most rostral point with feathers, (10) lower bill, near the bill tip (dorsal edge), (11) lower bill, rostral of the bending zone (dorsal edge), (12) lower bill, caudal of the bending zone (dorsal edge), (13) lower bill, caudal part (dorsal edge), (14) throat, near end rhamphotheca, (15) throat, near end lower jaw, (16) throat, 2 cm below marker 15. In addition to the points shown, three standard points on the background grid were digitised to determine horizontal and vertical axes and to scale the images.

Table 1. Calculated parameters used in the kinematic analysis

No.	Parameter	Description
1	Standard measure	Measured on the reference grid (mm)
2	Gape	Distance between upper and lower bill tip (mm)
3	Distance food	Distance between the food item and the upper bill tip (mm)
4	X position head	Relative horizontal position of the head (ear) (mm)
5	Y position head	Elevation of the head (ear) above the ground (mm)
6	Flexion in nasal–frontal hinge	Angle between cranium and caudal part of the upper bill (deg.)
7	Flexion halfway the upper bill	Angle between the caudal and rostral part of the bill (deg.)
8	Opening lower bill	Angle between the cranium and lower bill (deg.)
9	Depression of the throat	Distance between the cranium (ear) and oropharynx floor near the larynx (mm)

The films were analysed, frame-by-frame, by digitising the position of several points on the upper and lower bill relative to the standard grid (Fig. 2). Prior to the feeding analysis the position of the bending zones was determined through manipulating osteological specimens. The positions found were compared to previous descriptions (Hofer, 1954; Simonetta, 1960; Bock, 1963; Zusi, 1984) and used to determine the position of points for digitising. In addition to these points on the bills, some reference points on the skull of the bird were also digitised (Fig. 2). From the complete set of digitised points a number of distances and angles was calculated (Table 1). The accuracy of the calculated distances and angles was determined on the basis of the variation in a standard measurement calculated as the distance between two digitised points of the reference grid. The standard error in this distance measurement was approximately 0.08 mm. The standard error in digitising a point was therefore approximately 0.04 mm in each direction. The errors for points were used to calculate the error for angles, which was dependent on the distance between the points and the angle between lines. The standard error of the mean angle of two parallel lines both of 4 cm (a typical length used in our analyses) is just under 0.5°. For each time point the mean value and 95% confidence intervals of the behavioural parameters were calculated and used to describe the mean behavioural pattern. The same data were also used to test if cranial kinesis is present in palaeognathous birds.

The data on head displacement were used to determine maximum velocities and accelerations of the head during feeding. The complete trajectory of the head was determined by interpolation to 250 points s⁻¹ using a cubic-spline interpolation technique. The spline interpolation technique was used under the assumption that head movements follow a gradual and symmetric path around the points of change of direction. Behavioural observations confirm these assumptions. The acceleration data, in combination with the mass of the head (estimated from the head mass in other individuals) were used to determine the forces acting on the head.

A range of food types was offered (Table 2), varying in size between 4 mm and 35 mm in length. At least five items of each food type were analysed for each bird. Large apples were only eaten by the male and only on three occasions. Drinking cycles

Table 2. Approximate dimensions of offered food types

No.	Food type	Dimensions (mm)
1	Apple large	35×35×35
2	Apple small	25×25×25
3	Pellets	10×10×25
4	Seeds	4×3×8
5	Water (drinking)	–

were observed in both individuals, but only seven cycles could be analysed.

To investigate the diversity and variability of the feeding behaviour, a Principal Component Analysis (PCA) was used to describe the variation in feeding behaviour due to different food-types. The PCA, with Varimax rotation, was based on the correlation matrix of characters. The characters were obtained from the movement patterns of the different head elements involved in feeding (Table 3; see also Figs 5, 6). Differences in principal component scores were determined using an analysis of variance (ANOVA).

In addition to an analysis of the structure of the general feeding and drinking pattern, emphasis was laid on the presence of cranial kinesis, since many authors have coupled the morphology of the palaeognathous PPC directly to it. During all the observed feeding cycles both movement near the nasal–frontal area and movement in the upper bill were monitored to determine if cranial kinesis is present during normal feeding behaviour. Changes in angles were compared statistically using ANOVA to determine if bending actually occurs.

Results

General feeding behaviour

When describing the feeding behaviour of the rhea, the same elements are used as in the general description for neognathous feeding used by Zweers et al. (1994). The first elements of the neognathous feeding behaviour are preliminary head fixation, preliminary head approach and final head fixation. None of these elements are observed in the rhea. After final fixation neognathous feeding behaviour continues with the following elements: (1) final head approach, (2) catch at jaw tips, (3) stationing and repositioning, (4) catch at jaw tips, (5) intra-oral transport ('Catch and Throw'), (6) intra-pharyngeal transport.

Table 3. *Measured parameters*

Group	No.	Parameter	Description
Gape	1	Gape 1	Maximum gape during the approach
	2	Gape 2	Maximum gape during 'Catch and Throw'
	3	Gape level	Mean gape between Gape 1 and 2
	4	Gape level s.d.	Standard deviation of no. 3 (indicator for repositioning)
	5	Gape period	Time between Gape 1 and 2
	6	Gape 2 Moment	Time from start to Gape 2
Lower bill	7	Lower bill 1	Maximum depression of the lower bill during the approach
	8	Lower bill 2	Maximum depression of the lower bill during the 'Catch and Throw'
	9	Lower bill level	Mean depression of the lower bill between Lower bill 1 and 2
	10	Lower bill s.d.	Standard deviation of no. 9 (indicator for repositioning)
	11	Lower bill period	Time between lower bill 1 and 2
	12	Lower bill 2 moment	Time from start to lower bill 2
Prokinesis	13	Prokinesis at Gape 1	Angle around nasal-frontal hinge at Gape 1
	14	Prokinesis at Gape 2	Angle around nasal-frontal hinge at Gape 2
	15	Prokinesis level	Mean angle around nasal-frontal hinge between Gape 1 and Gape 2
	16	Prokinesis level s.d.	Standard deviation of no. 15 (indicator for constancy of kinesis)
Rhynchokinesis	17	Rhynchokinesis at Gape 1	Angle around bending zone in the upper bill at Gape 1
	18	Rhynchokinesis at Gape 2	Angle around bending zone in the upper bill at Gape 2
	19	Rhynchokinesis level	Mean angle around bending zone in the upper bill between the moment of Gape 1 and Gape 2
	20	Rhynchokinesis level s.d.	Standard deviation of no. 19 (indicator for constancy of kinesis)
Food	21	Food level	Mean distance between the cranium and the food-item between the moment of grasping and swallowing
	22	Food level s.d.	Standard deviation of no. 21 (indicator for inter-oral transport other than 'Catch and Throw')
	23	Food period	Duration of holding the food item
	24	Food min moment	Moment of release of the food item in the 'Catch and Throw'
Head Y	25	Head elevation period	Time between minimum and maximum elevation of the head
	26	Difference head elevation	Maximum distance of head elevation
	27	Max head elevation moment	Moment of maximal head elevation
Head X	28	Head X period	Time between minimum and maximum horizontal displacement of the head
	29	Difference head X	Maximum distance of horizontal head displacement
	30	Min head X moment	Moment of minimal horizontal extension of the neck (head closest to the body)
Neck	31	Neck neck period	Time between maximal and minimal flexion of the neck
	32	Difference neck neck	Difference in angle between maximal and minimal flexion
	33	Neck neck moment	Moment of minimum neck flexion
Throat	34	Throat period	Period between minimum and maximum throat depression
	35	Difference throat	Distance between minimum and maximum throat depression
	36	Throat moment	Moment of maximum throat depression

The general feeding sequence of the rhea (Figs 3A, 4) resembles this pattern: the bird approaches the food item while opening the bills and the food item is picked up. When the head hits the ground the acceleration of the head is approximately 11.30 m s^{-2} ($\mathbf{a}=11.30\pm 6.57 \text{ m s}^{-2}$, $N=41$). With an estimated head mass of 0.25 kg, the mean calculated impact force was 2.83 N and the maximum did not exceed 7.54 N ($\mathbf{a}_{\text{max}}=30.17 \text{ m s}^{-2}$).

Grasping the food is sometimes followed by repositioning behaviour. Repositioning occurs in the rhea more often when large rather than small food items were eaten.

When the food item was correctly positioned, a single

'Catch and Throw' movement is used to transport the food particle into, or near to, the entrance of the oesophagus. A 'Catch and Throw' movement starts when the food is fixed between the bills, the head is accelerated upward and slightly backward. Then the bills open and the head is suddenly moved forward. The accelerated food item continues to move upward while the head of the bird moves downward, which results in the transport of the food item. The palaeognathous single 'Catch and Throw' movement is accompanied by a large gape and a large depression of the tongue. This depression results in an enlargement of the buccal cavity, which facilitates transport of the food item into the caudal part of the

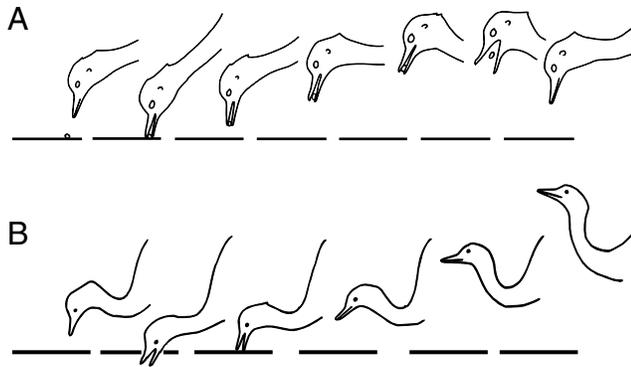


Fig. 3. Outline drawings of feeding behaviour (A) and scoop drinking behaviour (B) of the greater rhea *Rhea americana*. Horizontal lines represent ground level in A or water level in B.

oropharynx. No tongue movement was observed other than the one resulting in the depression of the mouth floor. The limited functions of the tongue in feeding are reflected in the morphology of the tongue, which is relatively small with no remarkable features (Fig. 5). The oropharynx itself also shows very little remarkable characters that might indicate feeding patterns other than 'Catch and Throw' behaviour.

General drinking behaviour

The rhea uses two different types of drinking behaviour, depending on the area of water available to drink from. The

preferred method of drinking can be described as scoop drinking followed by a low-amplitude tip-up phase (Fig. 3B). During drinking the bird opens the bill, inserts it into the water, and with a forward scooping motion of the head the lower bill is filled with water. The bill is then closed and the head is elevated until the neck is almost completely stretched, while the head itself is in a horizontal position. Finally, the water is transported into the oesophagus by a slight elevation of the bill tips and a retraction of the tongue. In some cases small horizontal 'Catch and Throw' movements are used to transport the water more caudally in the oropharynx just prior to swallowing.

When the size of the water surface limits the scooping movement, the rhea uses a drinking technique that is very similar to pecking behaviour. The bill is opened and inserted almost vertically into the water, the bill is then closed and in a single head jerk the water is accelerated vertically, the bill is opened and the water is transported to the back of the oropharynx. Since this behaviour strongly resembles pecking, and is not the basic drinking behaviour, it was not included in this analysis.

Quantitative differences between food types

To characterise the movement patterns quantitatively 36 parameters were chosen (Table 3, Figs 4, 6) and analysed using a Principal Component Analysis (PCA). The first three principal components of the PCA (PC1–3), based on the characters of the feeding and drinking behaviours described 63% of the total variance. An analysis of variance (ANOVA) over the principal component scores was used to determine the main differences between individuals/sexes and food types. None of the first three principal components showed a difference between individuals/sexes (d.f.=47, PC1: $F=0.264$, $P=NS$; PC2: $F=0.198$, $P=NS$; PC3: $F=0.240$, $P=NS$, where NS=not significant) and therefore the data from both individuals were combined. It is clear from the plot of the first principal component (PC1) against the second principal component (PC2) that drinking behaviour is remarkably different from feeding behaviour (Fig. 7, Table 4). The first principal component describes the absence

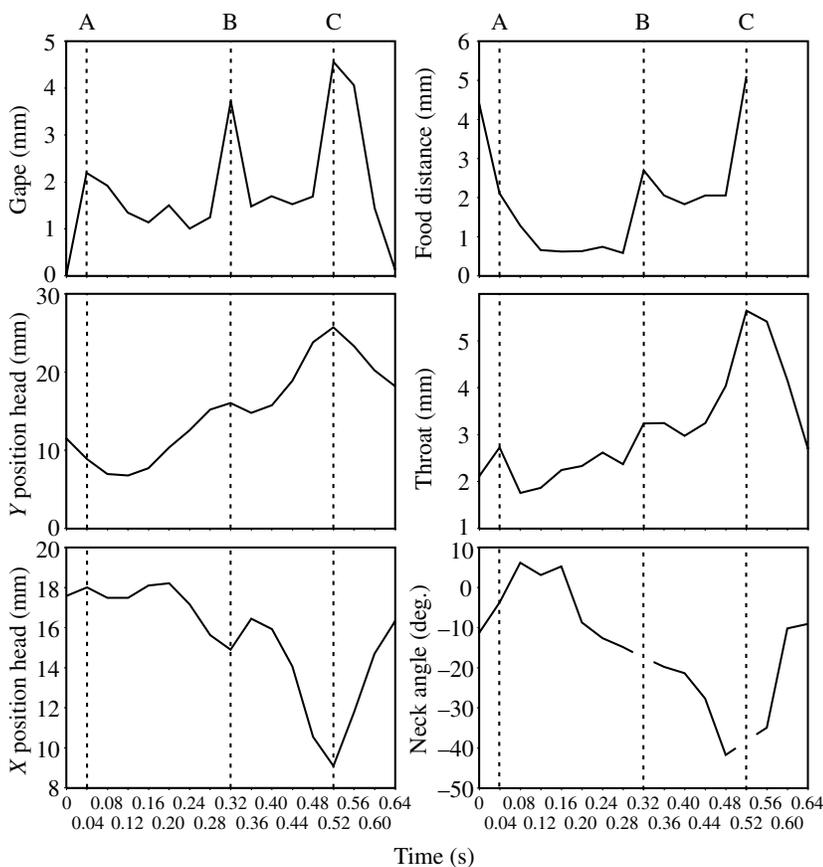


Fig. 4. A characteristic feeding cycle of the greater rhea *Rhea americana*. The vertical broken lines indicate characteristic moments in the feeding cycle. In chronological order: (A) picking up the food item (grasp), (B) maximum gape during a repositioning cycle and (C) maximum gape during the transport phase. The graphs show the gape, the vertical (Y) and horizontal (X) positions of the head, the distance between the food item and the bill tips, the depression of the throat and the flexion of the most rostral part of the neck.

of the second gape movement ('Catch and Throw' movement), differences in neck movement (duration of the

neck cycle) and the duration of the total feeding cycle (Table 5). The second principal component describes differences in food manipulation by the bills, such as position of the food item between the bills, depression of the lower bill and upper bill kinesis. To investigate the differences between food types without the large distorting effect of drinking, the PCA was repeated using the four types of feeding behaviour only. In this analysis 65% of the variance was explained by the first three principal components. To test whether there are significant differences between food types, a one-way ANOVA over the first three principal components scores was used. Differences between the food types were tested using a *t*-test with Bonferroni correction. There are significant differences between food types on both the first and third principal component (d.f.=40, PC1: $F=28.678$, $P<0.001$; PC2: $F=0.365$, $P=NS$; PC3: $F=3.628$, $P<0.05$). It is clear that PC1 describes the effect of food size (Fig. 8). The differences on the first principal component represent mainly the effect of the duration of the movement for each food type (e.g. gape period, head elevation period, food period, lower bill period), the size of the first gape (Gape 1) and the elevation of the head (difference head *Y*; Table 6). All these parameters increase with an increase of the size of the food type, which indicates that the movement pattern of food uptake is relatively constant and that only the duration, mainly the effect of repositioning,

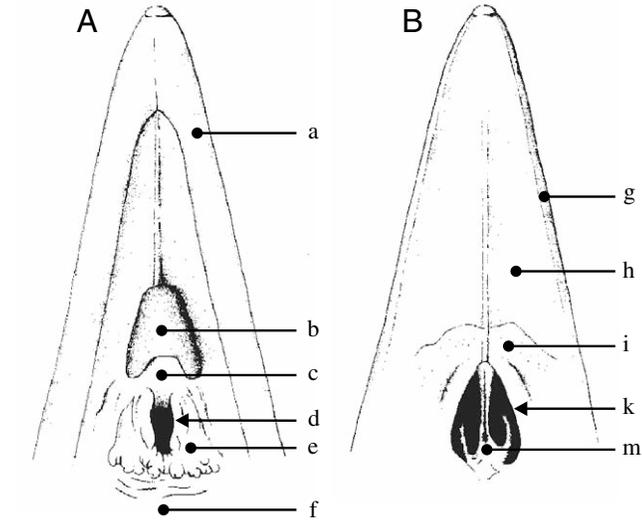
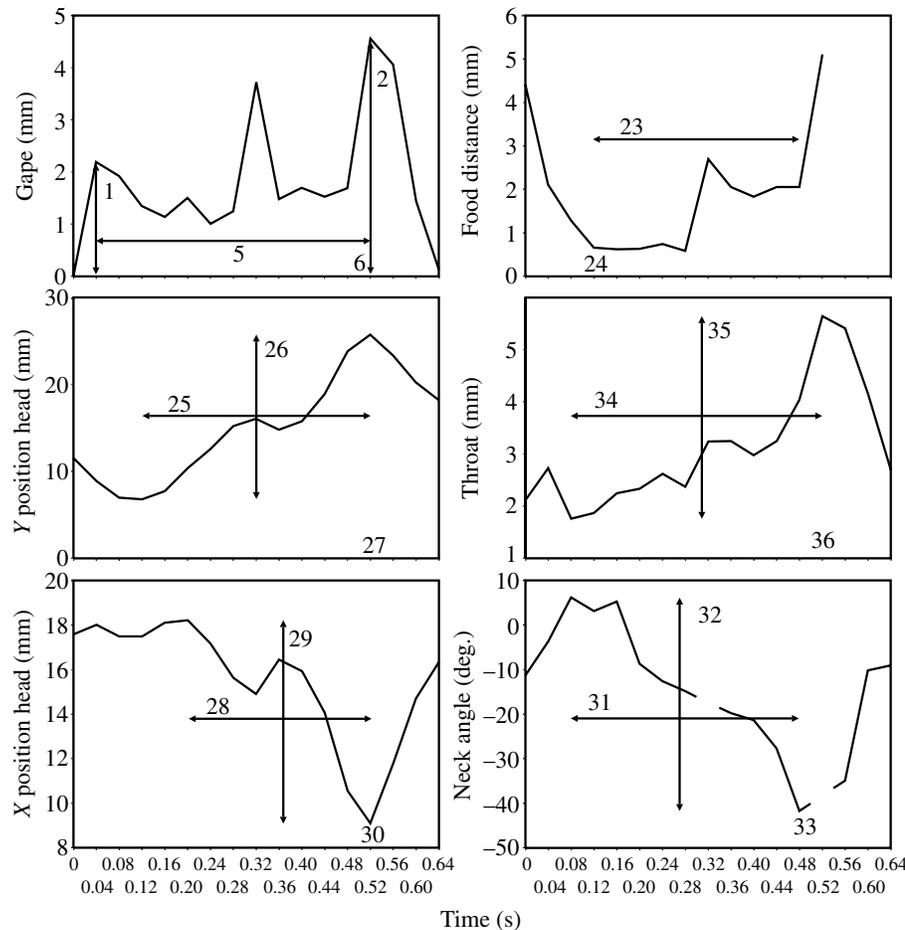


Fig. 5. Oropharynx of the greater rhea *Rhea americana*. (A) Dorsal view of oropharynx floor. (B) Ventral view of oropharynx roof. a, rhamphotheca; b, tongue cushion; c, tongue base; d, opening of the trachea; e, larynx; f, esophagus; g, rhamphotheca; h, bony palate; i, soft palate; k, choana; m, vomer.



and amplitude of the movement differ between different food sizes. The change in movement described by PC1 becomes smaller when the size of the food items increases. A difference on PC1 is only found between seeds and all other food types (food type 1 vs 2, 3 and 4, *t*-test, Bonferroni correction, $P<0.001$).

The third principal component mainly describes the handling of the food item, which affects the amount of depression of the lower bill (lower bill at Gape 1), position of the food item between the bills during the upward movement of the head (food level, food level s.d.), and

Fig. 6. Measurements selected to describe the feeding behaviour of the greater rhea *Rhea americana* and used in the principal component analysis. Numbers in the graphs refer to parameters listed in Table 3. Measurements from the groups 'gape', 'lower bill', 'prokinesis' and 'rynchokinesis' are correlated to the maximum gape during food pecking (gape 1; no. 1) and the maximum gape in the transport phase (gape 2; no. 2). Graphs of prokinesis, rynchokinesis and lower bill depression are not given but they strongly resemble the pattern shown in the gape graph.

amplitude of cranial kinesis (e.g. prokinesis at Gape 1 and 2, rhynchokinesis at Gape 2; Table 6). Differences between food types on PC3 are only found between large apples and seeds (food type 1 vs 4, *t*-test, Bonferroni correction, $P < 0.05$). However, no clear trends can be determined with a change in size of the food types.

Cranial kinesis

To test the presence of kinesis in the skull of the rhea, several measurements were taken. The movement between the

cranium and the upper bill around the point where the nasal–frontal hinge would be in prokinetic birds was measured, and will be further referred to as prokinetic movement (Fig. 1A). A second measure of kinesis was the movement between the rostral and caudal part of the upper bill with the border of the two parts in the bending region of the upper bill. Movement of the rostral part relative to the caudal part of the upper bill will be referred to as the rhynchokinetic movement (Fig. 1B). Since food types are different in size, the kinesis of the upper bill was determined for each food type separately.

Table 4. Mean values per food type for all characters used in the principal component analysis

Group	No.	Parameter	Food				
			1 Apple large	2 Apple small	3 Pellets	4 Seeds	5 Water
Gape	1	Gape 1 (cm)	2.80	2.31	2.09	1.49	4.66
	2	Gape 2 (cm)	7.53	5.47	5.24	2.43	0
	3	Gape level (cm)	3.46	1.88	1.67	0.52	0.37
	4	Gape level s.d. (cm)	0.74	0.86	0.72	0.55	0.90
	5	Gape period (frames)	18.33	14.73	17.18	7.86	21.43
	6	Gape 2 moment (frames)	17.67	13.82	15.73	6.36	19.71
Lower bill	7	Lower bill 1 (deg.)	32.37	42.94	41.23	41.16	40.20
	8	Lower bill 2 (deg.)	58.70	55.60	55.46	45.98	0
	9	Lower bill level (deg.)	39.06	38.50	39.74	32.74	25.56
	10	Lower bill s.d. (deg.)	8.60	5.87	5.48	3.82	6.50
	11	Lower bill period (frames)	18.67	14.27	17.27	7.79	21.14
	12	Lower bill 2 moment (frames)	18.00	13.45	16.00	6.29	19.71
Prokinesis	13	Prokinesis at Gape 1 (deg.)	20.58	21.94	21.83	23.42	13.53
	14	Prokinesis at Gape 2 (deg.)	18.60	21.49	23.44	22.68	22.36
	15	Prokinesis level (deg.)	21.00	22.29	22.50	25.37	17.19
	16	Prokinesis level s.d. (deg.)	4.11	3.98	3.28	3.66	5.04
Rhynchokinesis	17	Rhynchokinesis at Gape 1 (deg.)	6.12	6.19	8.92	4.29	-4.48
	18	Rhynchokinesis at Gape 2 (deg.)	2.29	2.39	3.65	4.56	3.52
	19	Rhynchokinesis level (deg.)	3.50	3.29	5.15	2.29	0.99
	20	Rhynchokinesis level s.d. (deg.)	5.53	4.78	4.63	4.75	7.17
Food	21	Food level (cm)	1.91	1.43	1.46	1.33	3.37
	22	Food level s.d. (cm)	0.62	0.60	0.66	1.47	1.88
	23	Food period (frames)	15.33	12.45	15.36	6.64	23.71
	24	Food min moment (frames)	-1.00	-0.27	-0.58	-1.14	-0.29
Head Y	25	Head elevation period (frames)	17.67	12.90	15.45	6.64	20.43
	26	Difference head elevation (cm)	25.03	21.71	21.24	15.23	84.92
	27	Max head elevation moment (frames)	18.00	12.70	15.09	5.93	20.00
Head X	28	Head X period (frames)	12.33	12.73	10.45	6.64	8.43
	29	Difference head X (cm)	3.92	9.37	8.27	5.86	6.13
	30	Min head X moment (frames)	16.00	11.18	15.09	5.36	7.86
Neck	31	Neck neck period (frames)	16.00	12.45	15.55	5.69	5.43
	32	Difference neck neck (deg.)	46.81	57.11	50.99	32.82	36.26
	33	Neck neck moment (frames)	16.00	12.27	15.18	5.08	4.86
Throat	34	Throat period (frames)	17.33	14.91	17.54	5.79	12.00
	35	Difference throat (cm)	5.09	3.09	3.41	2.51	2.36
	36	Throat moment (frames)	17.67	14.09	15.91	6.64	6.86

Values are measurements relative to either the cranium or the reference grid; $N=3$ (large apple), 11 (small apple), 12 (pellets), 14 (seeds), 7 (water).

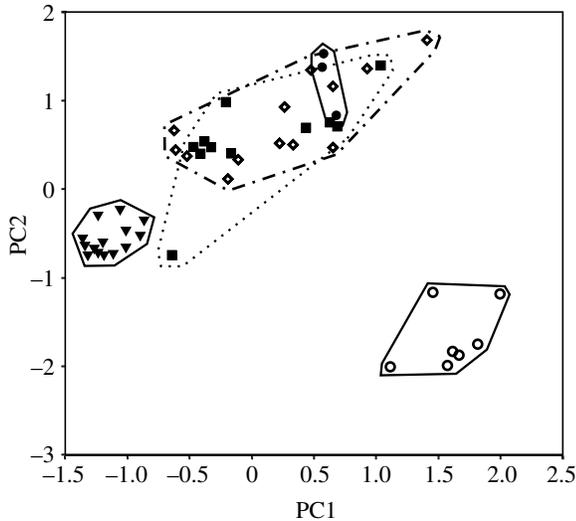


Fig. 7. Plot of PC1 against PC2 of the analysis, including drinking behaviour. Different food types are represented by different markers, and groups of a single food type are outlined. Circles, large apple; closed squares, small apple; open squares, pellets; triangles, seeds; open circles, drinking behaviour.

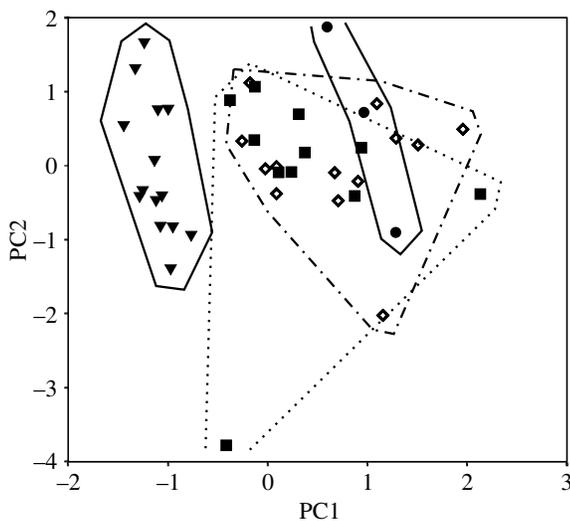


Fig. 8. Plot of PC1 against PC2 of the analysis of food types only. Different food types are represented by different markers, and groups of a single food type are outlined. Circles, large apple; closed squares, small apple; open squares, pellets; triangles, seeds.

The large apple was not used for this analysis due to the small number of repeated measurements.

It is assumed that maximal kinesis is observed during the large amplitude gapes when the food item is picked up or swallowed. Velocities of the head are very large during the second phase of the 'Catch and Throw' movement, which makes it very difficult to determine points accurately. Because of this low accuracy and the relatively small movements in the upper bill, cranial kinesis could only be analysed accurately in the grasping phase. From repeated experiments the average

Table 5. Main parameters contributing to the first three principal components of the total analysis

Character	PC1 (45%)	PC2 (10%)	PC3 (9%)
PC1			
Throat moment	0.983	0.063	0.037
Gape 2 moment	0.981	0.081	0.054
Lower bill 2 moment	0.977	0.038	0.087
Food 2 moment	0.975	0.054	-0.012
Gape period	0.974	0.082	0.043
Head elevation moment	0.966	0.091	0.093
Head elevation period	0.965	0.068	0.077
Lower bill period	0.956	0.119	0.103
Food period	0.951	0.029	-0.029
Throat period	0.946	0.008	-0.069
Neck neck moment	0.911	0.196	0.178
Neck neck period	0.907	0.183	0.191
Min head X moment	0.881	0.200	0.090
PC2			
Food level	0.091	0.428	0.055
Gape level s.d.	0.274	0.422	0.592
Food level s.d.	-0.247	0.404	-0.047
Lower bill level	0.634	-0.435	-0.002
Lower bill at Gape 1	0.103	-0.565	-0.385
Prokinesis level	-0.381	-0.628	-0.162
Prokinesis at Gape 2	0.023	-0.683	0.173
Prokinesis at Gape 1	-0.175	-0.714	0.102
PC3			
Throat displacement	0.362	0.123	0.672
Difference neck neck	0.417	-0.263	0.504
Lower bill level s.d.	0.416	0.397	0.486
Lower bill at Gape 2	0.571	-0.089	0.451
Difference head elevation	0.729	-0.064	0.443
Rhynchokinesis level s.d.	-0.043	-0.075	0.438
Rhynchokinesis at Gape 1	0.348	0.026	-0.410
Rhynchokinesis at Gape 2	-0.038	0.332	-0.679

For PC1, only parameters with loadings higher than 0.8 are selected; for PC2 and PC3, parameters with loadings higher than 0.4 are selected. Percentages indicate the explained variance on each PC.

pick-up cycle was calculated and plotted with the standard error. The plot of gape vs time shows a clear pattern (Fig. 9A) similar to a single food uptake cycle, and differences between the time segments are significant (ANOVA, small apple: d.f.=85, $P<0.001$; pellets: d.f.=90, $P<0.001$; seeds: d.f.=168, $P<0.001$; water: $P<0.001$).

A similar analysis was made for the lower bill movement, expressed as the depression angle (Fig. 9D). For all food types the same pattern was found, and only for the largest food type analysed (small apple) were the differences between successive time segments not significant, due to large variation (ANOVA, small apple: d.f.=86, $P=NS$; pellets: d.f.=89, $P<0.05$; seeds: d.f.=168, $P<0.05$; water: d.f.=100, $P<0.05$).

Angular measurements were also used to test the response of prokinetic and rhynchokinetic movement during the feeding cycle. Prokinetic movement showed a pattern similar to the

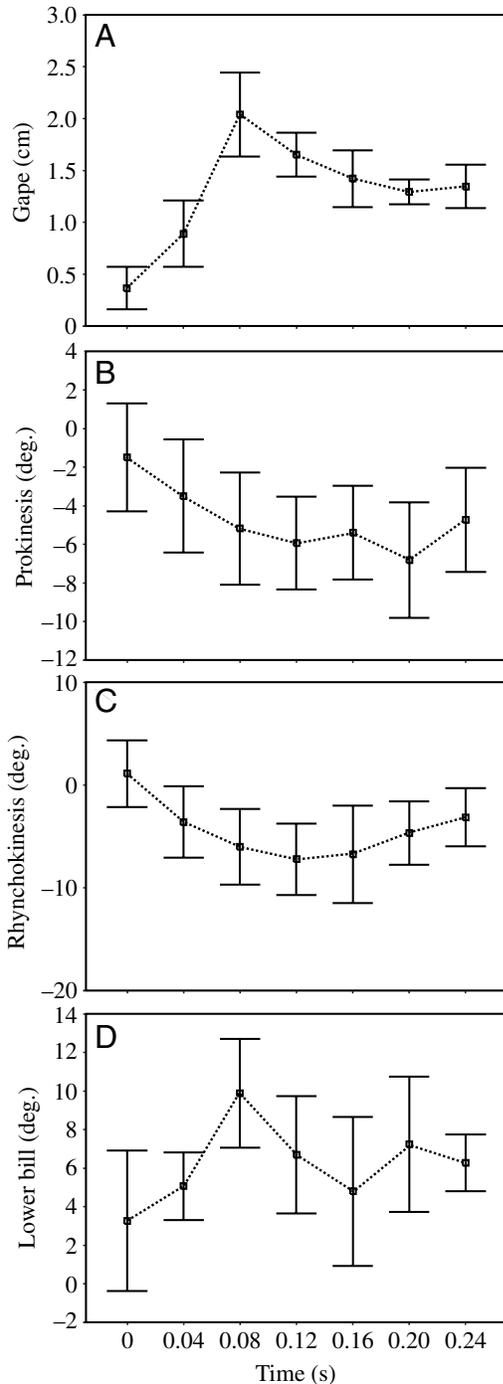


Fig. 9. Kinesis in the upper bill of the greater rhea *Rhea americana*. Squares indicate mean values ($N=13$, except at 0.24 s, where $N=12$) for each parameter at a certain time for the peck up phase with a medium sized food type (3: pellets). Vertical lines indicate 95% confidence intervals. The gape (A) is represented as the distance between the bill tips. Prokinesis (B), rhynchokinesis (C) and lower bill depression (D) are represented by change in angles (no absolute values). Negative angles for prokinesis and rhynchokinesis indicate elevation of the upper bill. Lower bill depression is represented by positive values.

lower bill movement but with a much smaller amplitude (Fig. 9B). However, the prokinetic movement pattern is not

Table 6. Main parameters contributing to the first three principal components of the food type analysis

Parameter	Principal component		
	PC1 (33%)	PC2 (25%)	PC3 (8%)
PC1			
Gape period	0.970	0.168	0.017
Head elevation period	0.970	0.135	0.012
Head elevation moment	0.968	0.166	0.002
Food period	0.968	-0.062	0.019
Food 2 moment	0.965	0.136	0.027
Gape 2 moment	0.963	0.219	0.025
Lower bill 2 moment	0.963	0.209	0.059
Lower bill period	0.959	0.164	-0.023
Difference head elevation	0.741	-0.617	-0.145
Gape 1	0.734	-0.462	-0.088
PC2			
Gape 2	-0.052	0.914	0.051
Neck neck moment	0.361	0.885	0.072
Neck neck period	0.364	0.877	0.085
Throat moment	0.421	0.860	0.168
Gape level	0.200	0.829	-0.073
Lower bill at Gape 2	-0.482	0.804	0.203
Head X moment	0.514	0.748	0.017
Lower bill level	-0.142	0.721	0.410
PC3			
Prokinesis at Gape 2	0.034	-0.154	0.744
Prokinesis at Gape 1	-0.429	0.143	0.639
Lower bill at Gape 1	-0.041	-0.004	0.513
Rhynchokinesis at Gape 2	-0.107	0	-0.474
Prokinesis level	-0.635	0.089	0.469
Difference neck neck	0.230	0.390	0.437
Food level s.d.	0.028	-0.298	-0.427
Food level	0.457	-0.317	-0.419

For PC1 and PC2, only parameters with loadings higher than 0.7 are selected; for PC3, parameters with loadings higher than 0.4 are selected. Percentages indicate the explained variance on each PC.

significant for any food type or drinking (ANOVA; small apple, d.f.=87, $P=NS$; pellets: d.f.=89, $P=NS$, seeds: d.f.=167, $P=NS$; water: d.f.=102, $P=NS$). The rhynchokinetic movement patterns can be clearly recognised except in the drinking behaviour (Fig. 9C), but are only significant for the two largest food types, small apple and pellets (ANOVA, small apple: d.f.=84, $P<0.05$; pellets: d.f.=88, $P<0.05$; seeds: d.f.=166, $P=NS$; water: d.f.=98, $P=NS$). In Table 7 the maximal changes in the mean angles of the different types of kinesis are given, showing an increase in cranial kinesis with an increase in food size.

Discussion

Kinematic analysis

Our study showed clearly that the feeding behaviour of the palaeognathous birds strongly resembles the feeding patterns of neognathous birds. Some differences are found in the

Table 7. Maximal change in mean of all feeding cycles of kinesis parameters

Food	N	Gape (cm)	Lower bill (deg.)	Prokinesis (deg.)	Rhynchokinesis (deg.)
Small apple	11	1.8	(5.4)	(1.1)	10.1
Pellets	13	1.7	6.6	(3.7)	7.1
Seeds	12	0.9	4.2	(1.1)	(2.9)
Water	7	3.7	24.5	(6.6)	(4.3)

Values within parentheses indicate non-significant changes.

approach phase, the intra-oral transport and intra-pharyngeal transport. In general the tongue plays a more important role in neognathous feeding behaviour than in palaeognathous feeding behaviour. The complete intra-oropharyngeal transport phase in palaeognathous birds is achieved by a single 'Catch and Throw' movement, which is in large contrast with the complicated 'Slide and Glue' mechanism and complex transport of food through the oropharynx often used by neognathous birds. However, for large food items neognathous birds may also use a single 'Catch and Throw' movement, but still show complex intra-pharyngeal transport (Zweers et al., 1994). The difference between the single 'Catch and Throw' movement of neognathous and palaeognathous birds is that the former use this movement to transport the food item onto the lingual base, while the latter use it to transport the food item to the area caudal to the lingual base. Tomlinson (2000) showed that in palaeognathous feeding behaviour the final transport of the food item into the oesophagus is achieved by a single retraction of the tongue and larynx. The protraction/depression of the tongue during the 'Catch and Throw' movement and the retraction during swallowing are the main functions of the tongue during feeding.

Similarly, the drinking behaviour of the rhea lacks the tongue movement present in neognathous drinking. The general drinking pattern of neognathous birds (Zweers, 1992) consists of (1) a fixation phase, in which the bird orientates its head, (2) the downstroke, in which the head is lowered towards the water, (3) the immersion phase, during which the actual water intake takes place, and (4) the upstroke, in which the head is positioned in such a way that gravitational forces facilitate transport of the water from the oropharynx into the oesophagus (swallowing). All these phases are also represented in palaeognathous drinking behaviour and similar to neognathous phases. Large differences, however, are found in the immersion phase. In the rhea there is no stationary immersion phase but a scooping motion, the bill remains widely opened, and no tongue movement is observed during this phase. Intra-oral transport during immersion in Neognathes always includes pro- and retraction of the tongue. Only during the head upstroke does a single protraction of the tongue in rhea facilitate the movement of the water into the oesophagus.

Although feeding and drinking behaviours were analysed under controlled conditions, field data show that the observed feeding behaviours are present in the natural behaviour of the

rhea as well. The natural feeding and food-acquisition behaviour of all Palaeognathae, except the kiwi (*Apteryx* sp.), can be described as browsing, which means eating a wide variety of plant material with some occasional carnivorous food. The food preferences of the greater rhea in the wild (Martella et al., 1996) suggest that no fundamentally different feeding behaviours are required, other than the ones analysed in our study. The diet consists of a wide variety of food items, but is mainly vegetarian (Mosa, 1993; Martella et al., 1996; Quin, 1996). The assumption that the feeding behaviour is characteristic for all Palaeognathae is confirmed by a number of observations. The single 'Catch and Throw' feeding behaviour and both the scooping and 'Catch and Throw' drinking behaviour have been observed in the greater rhea in the wild. We also observed the single 'Catch and Throw' feeding behaviour in wild and captive ostriches *Struthio camelus* L., captive emus *Dromaius novaehollandiae* Latham and captive cassowaries *Casuaris casuaris* (L.). Although there are some differences between the diets of the various palaeognathous species, these seem due to local food availability, and not to preference or performance.

In order to determine the importance of cranial kinesis in the feeding behaviour of the palaeognathous species, we determined bending both in the area of the nasal-frontal articulation and in the upper bill itself. Our study showed that during feeding behaviour kinesis is found between the rostral and caudal part of the upper bill in rhea. No, or only very limited, bending occurs in the area of the nasal-frontal articulation, the position where in many neognathous species the naso-frontal hinge is situated. The elevation amplitude of the bill tip relative to the cranium in the rhea is similar to the elevation of the upper bill found in prokinetic neognathous birds (approximately 5–10°; Kooloos and Zweers, 1989; Heidweiller and Zweers, 1990; van den Heuvel, 1992).

One hypothesis about the role of rhynchokinesis states that it reinforces the grip on food items by simultaneously depressing the upper bill tip and elevating the lower bill tip, as found in certain Charadriiformes (Zusi, 1984). No upper bill depression is observed in the rhea, which indicates that rhynchokinesis is not used in this way in Palaeognathae.

Our video recordings of beak movement suggested that there may be a difference between neognathous rhynchokinesis and palaeognathous rhynchokinesis. While a clear bending point is present in Neognathae, the upper beak in rhea seems flexible over its full length. The elevation angle of the upper bill

gradually declines more caudally in the upper bill. This strongly suggests that a single hinge or narrow bending zone is not present in Palaeognathae. This conforms with the description of Zusi (1984), who named this flexibility over the full-length 'central' rynchokinesis. The relation between rynchokinesis and the detailed anatomy of the beak is explored in an accompanying paper (Gussekkloo and Bout, 2005).

Phylogenetic analysis of feeding behaviour

To determine whether the feeding behaviour of the Palaeognathae is derived or primitive within modern birds, a comparison can be made with the general feeding patterns found in other tetrapods. The method of feeding in tetrapods depends on the presence of a well-developed lingual apparatus. If a well-developed lingual apparatus is absent two main types of non-lingual feeding are present within the tetrapods: inertial feeding and the feeding pattern observed in snakes (de Vree and Gans, 1994). Comparison of the feeding behaviour of the rhea with the nearest living sister group of birds, the crocodylians, shows that the feeding behaviour of the rhea is more similar to reptilian inertial feeding than the general feeding pattern of neognathous birds (Zweers et al., 1994; Cleuren and de Vree, 1992). In crocodylian intra-oral transport the tongue elevates the food item until it presses against the palate. Then gape is rapidly increased and the cranium moved forward (the avian 'Catch and Throw'), while the tongue is depressed to enlarge the buccal cavity and to facilitate the transport of the food item. In the rhea the final transport of a food item into the oesophagus is achieved by a retraction of the hyolingual apparatus (Tomlinson, 2000), similar to transport in crocodylians. The fact that feeding behaviour of the rhea resembles feeding behaviour of crocodylians, and lacks certain elements found in the general feeding pattern of neognathous birds, seems to suggest that inertial feeding behaviour is basal within birds. This would agree with the widely accepted hypothesis that the Palaeognathae are the oldest offshoot in the phylogeny of modern birds (Bock, 1963; Meise, 1963; Parkes and Clark, 1966; Cracraft, 1974; de Boer, 1980; Prager and Wilson, 1980; Sibley and Ahlquist, 1981; McGowan, 1984; Feduccia, 1985; Handford and Mares, 1985; Elzanowski, 1986; Houde, 1986; Bledsoe, 1988; Caspers et al., 1994; Lee et al., 1997; van Tuinen et al., 1998; Simon et al., 2004). However, lingual feeding is found in the more primitive amphibians (de Vree and Gans, 1994), and present in many reptilians (Bramble and Wake, 1985; Reilly and Lauder, 1990; Herrel et al., 1996). As crocodiles are a very distant sister group of birds the possibility remains that crocodiles and Palaeognathae are specialized inertial feeders and that lingual feeding is the most primitive avian feeding mechanism. Tetrapod inertial feeding is believed to have evolved many times independently within vertebrates (de Vree and Gans, 1994). The simple movement patterns of the tongue in rhea may be the consequence of a reduction in size related to efficient 'Catch and Throw' feeding behaviour. Since it cannot unambiguously be determined whether the feeding pattern of the palaeognathous birds is primitive or a specific adaptation,

these data cannot be used to determine the phylogenetic position of the Palaeognathae.

General discussion

From the comparison of feeding patterns we conclude that the feeding and drinking behaviours of the rhea resemble those of neognaths, but lack certain elements found in the general feeding pattern of neognathous birds, especially with respect to tongue movements. We found no elements in the feeding behaviour that might impose additional functional demands on the PPC, nor are any of the behavioural elements investigated more demanding than in neognathous feeding. This indicates that the specific morphology of the PPC is not the result of specific functional demands from palaeognathous feeding behaviour. Also the hypothesised role of rynchokinesis in relation to the cranial morphology could not be confirmed. Central rynchokinesis is present in the upper bill, but does not play an important role in improving grip on the food item or in increasing the gape. It must therefore be concluded that the kinetic feature of the bill is not the factor that determined the morphology of the PPC.

Alternative explanations for the presence of the characteristic PPC complex have been suggested. Bock (1963) proposed that the special morphology of the PPC might be an adaptation to the high impact forces on the bill during pecking. Our movement analysis showed that the rhea is capable of controlling the impact force of pecking. The head hits the ground at approximately 11.30 m s^{-2} . The mean calculated impact force was 2.83 N and the maximum did not exceed 7.54 N. Using a compressive strength of $170 \times 10^6 \text{ Pa}$ for bone we can calculate that a cross-sectional area of the bones of just 0.05 mm^2 is sufficient to withstand these forces. It seems clear that this area is many times smaller than the actual cross-sectional area in the skull of the rhea.

Another explanation is that the morphology of the palaeognathous PPC is the result of selection forces that are not directly related to feeding, but do affect the morphology of the PPC indirectly. While Palaeognathae are often believed to be basal to Neognathae, an alternative hypothesis states that Palaeognathae have actually a derived phylogenetic position and have evolved through neoteny from a flying ancestor (de Beer, 1956). The hypothesis on the neoteny origin of the Palaeognathae was recently revived by physiological/ontogenetic data (Dawson et al., 1994) and molecular systematics (Mindell et al., 1997; Härlid and Arnason, 1999). The physiological/ontogenetic experiments showed that induced neoteny in neognathous birds results in a morphology of the PPC that was similar to that of the Palaeognathae, while the molecular systematic data show a derived position of the Palaeognathae within the Neognathae and not a basal position of the group. A comparison of the cranial morphology of the Palaeognathae with different developmental stages of neognathous birds showed, however, that not a single developmental stage resembles the palaeognathous configuration (Gussekkloo and Bout, 2002). This is a clear indication that the palaeognathous PPC is not the result of neoteny.

A third hypothesis on the origin of the special morphology of the palaeognathous PPC proposes that the morphology of the extant palaeognathous PPC is the result of the continuous reduction of bony and ligamentous elements in the lateral aspect of the skull (Gussekloo and Zweers, 1999). Although birds in general have less bony and ligamentous elements in the lateral aspect of the skull than closely related groups such as dinosaurs and other reptiles, Palaeognathae have even less than most birds. Compared to Neognathae, Palaeognathae lack a clear *Ligamentum postorbitale* and the lateral bar of the upper bill (Bock, 1964; Zusi, 1984). The reduction of these elements might have resulted in a relatively unstable configuration of the upper bill, especially under conditions of external loading. The only type of food acquisition that is not covered by our study is pulling leaves off plants. It is possible that this way of feeding imposes special functional demands on the construction of the upper beak. The removal of leaves is mainly achieved by neck motion, and generates external forces on the upper bill. While preliminary observations showed that the transport of the food items used in the present study is very similar to the transport of grass or leaves that are removed from the plant, it is possible that the morphology of the upper bill of the Palaeognathae is adapted to oppose the reaction forces during pulling (see also Gussekloo and Bout, 2005). Although it seems that such a force regime is not unique for Paleognathae (e.g. grazing geese, pulling off berries by passerines), it is unique when combined with the absence of lateral bars in the skull. Since the Palaeognathae could not counteract the external forces by reinforcing these lateral elements, it may have been necessary to reinforce the unstable upper bill configuration in the ventral elements, resulting in a more rigid PPC. As a consequence of this reinforcement of the ventral plane of the upper bill, active kinesis of the upper bill may also become limited. Additional experiments to test this hypothesis are described in the accompanying paper (Gussekloo and Bout, 2005).

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