CHAPTER 7

EVOLUTIONARY IMPLICATIONS OF FEEDING BEHAVIOUR OF PALAEOGNATHOUS BIRDS

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 related to the feeding behaviour of the Rhea (Rhea americana). The feeding behaviour of the Rhea is typical 'Catch & 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. Neither the feeding nor the drinking behaviour require adaptations different from those found in Neognathous birds, which indicates that the specific morphology of the PPC is not the result of specific functional demands from palaeognathous feeding behaviour. Cranial kinesis is limited and observed during gaping only. The feeding behaviour of the Palaeognathae is either derived optimised 'Catch & Throw' behaviour or primitive within birds.

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). Not only the 'palate' 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 & Zweers, 1999). The set of characters of the jaw mechanism that discriminates the Palaeognathae from the Neognathae will be referred to as the Palaeognathous Pterygoid-Palate Complex (Palaeognathous PPC; Gussekloo & Zweers, 1999). The mechanical function of this Pterygoid-Palate Complex in neognathous birds is well known. In these birds the PPC participates in the movement of the upper bill (Bock, 1964). Upper bill movement is induced by rostrad 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 the flexible zone. The pterygoid-palate bar and the quadrate are of great importance, since 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), the number of authors that has studied the function of the system is very limited. In all functional analyses it was assumed that the special morphology of the PPC in Palaeognathae is related to rhynchokinesis (Hofer, 1954; Simonetta, 1960; Bock, 1963). This assumption was based on 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 occurrence of rhynchokinesis has, however, never been tested in alive birds.

Several hypotheses can be postulated about the evolution of the special PPC morphology in the Palaeognathae. First, different selective forces may have acted directly on the PPC and upper beak movement of the Neognathae and of the Palaeognathae, resulting in a difference in morphology. These selective forces might be the direct effect of differences in the role of the PPC. In this analysis the function of the PPC is considered to be the transfer of forces from the quadrate onto the upper bill, and its role the elevation or depression of the upper bill. To investigate whether differences in selection forces on bill elevation, and therefore on the PPC, are present, upper bill movement of the Palaeognathae during feeding will be described and compared with its function and role in a general neognathous-feeding pattern. If no differences can be found in the present function of the PPC between Neognathae and Palaeognathae it is plausible that no differences in selective forces are present.

Second, when differences in selective forces are not responsible for the difference in morphology other mechanisms must have played a role. Alternative explanations would be that the specific morphology of the palaeognathous PPC is an epi-phenomenon or is the result of evolution under the same selective forces but from a different starting design or within different developmental constraints. The historical explanation (different starting design) is complicated because it is not yet known whether the Palaeognathous configuration of the PPC represents a primitive or a derived condition within the phylogeny of modern birds.

In this study we investigated whether the morphology of the PPC in Palaeognathae is an adaptation to its present feeding behaviour. Feeding behaviour is considered the strongest selection force acting on the upper bill opening mechanism and the PPC is one of the key-elements within that mechanism. Other behaviours such as vocalisation, preening and social behaviour are considered to have little effect on the osteology of the bills. Once the feeding behaviour and especially the use of upper bill kinesis of the Palaeognathae is known, it is possible to compare it with the general neognathous feeding pattern. This comparison between the two feeding behaviours might indicate differences in selective forces acting on the PPC in Neognathae and Palaeognathae and explain the differences in the morphology of the PPC. 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.

For a functional-evolutionary analysis of feeding behaviour of an animal it is necessary to know the natural food-types of the animal, and to determine the general feeding behaviour and the flexibility of the general pattern. When these are known, functional demands for the morphology can be postulated, and it can be determined whether the morphology is an

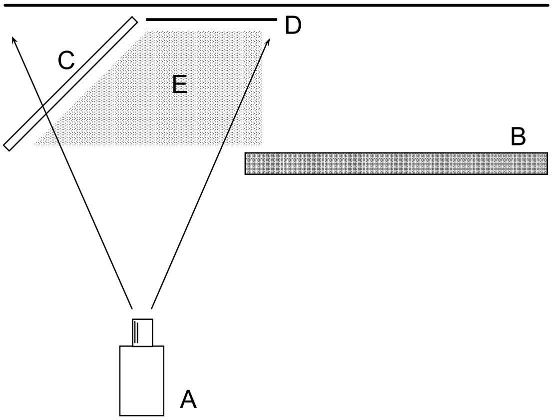

Figure 7.1. Experimental Set-up in top view. The Video camera (A) captures an image of the feeding arena (E), a reference grid (D, squares 2x2 cm), and an indirect frontal image of the animal via a mirror (C). A corridor (B) is used to force the birds into a lateral position relative to the camera at the feeding arena.

adaptation to the specific functional demands of palaeognathous feeding. In this study a comparison is made between the feeding behaviour of the Palaeognathae and the general neognathous feeding patterns as described by Zweers *et al.* (1994). Kinematic differences are identified that might indicate differences in selective forces on the PPC. Furthermore, both morphology and behaviour can be used for outgroup comparison to determine whether the palaeognathous PPC configuration represents a primitive or derived condition.

Table 7.1. Markers on the head of the Rhea, markers are also shown in figure 7.2.

No.	**Marker**
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, two centimetres below marker 15

Materials and Methods

The Greater Rhea (*Rhea americana*), a middle-sized palaeognathous bird from South-America, was chosen as representative for the Palaeognathae. This Rhea has a general palaeognathous PPC configuration (McDowell, 1948) and its natural history and behaviour are well known (Raikow, 1968; Raikow, 1969; Bruning, 1974; Martella *et al.*, 1995; Martella *et al.*, 1996; Reboreda & Fernandez, 1997). For the analysis two specimens, one male and one female, were trained to feed on several food-types within the experimental set-up. The feeding behaviour of the birds was recorded using video imaging (25 frames per second). 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 the bird at an angle of 45 degrees (Fig. 7.1). 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

Table 7.2. Calculated parameters used in the kinematic analysis.

No.	Description	Measure
1	Standard measure, measured on the reference grid	Millimetres
2	Gape, distance between upper and lower bill tip	Millimetres
3	Distance food, distance between the food item and the upper bill tip	Millimetres
4	X Position Head, relative horizontal position of the head (ear)	Millimetres
5	Y Position Head, elevation of the head (ear) above the ground	Millimetres
6	Flexion in nasal-frontal hinge, angle between cranium and caudal part of the upper bill	Degrees
7	Flexion halfway the upper bill, angle between the caudal and rostral part of the cranium	Degrees
8	Opening lower bill, angle between the cranium and lower bill	Degrees
9	Depression of the throat, distance between the cranium (ear) and oropharynx floor near the larynx.	Millimetres

camera's point of view, a grid (squares 2 x 2 cm) was placed to make scaling possible. 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. 7.2, Table 7.1). In addition to these points on the bills, some reference points on the skull of the bird were also digitised (Fig. 7.2, Table 7.1). From the complete set of digitised points a number of distances and angles was calculated, which are summarised in table 7.2. The accuracy of the calculated distances and angles were determined on the basis of the variation in a standard measurement calculated as the distance between two digitised points of the reference grid. The error in digitising a point was approximately 0.4 cm, the error in distance measures approximately 0.6 cm. The errors for points were used to calculate the error for angles. For angles the error is dependent on the distance between the points and the angle between lines. We estimated the error for the upper bill rotation to be 7 degrees for angles of 10 degrees. The markers used for the calculation of angles were approximately in the range of these errors.

The data on head displacement were used to determine maximum velocities and accelerations of the head during feeding. The complete movement of the head was determined by interpolation to 250 points per second 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 interpolated data were used to calculate both velocities and accelerations. The acceleration data in combination with the weight of the head (estimated from the weights of heads in other individuals) were used to determine the forces acting on the head.

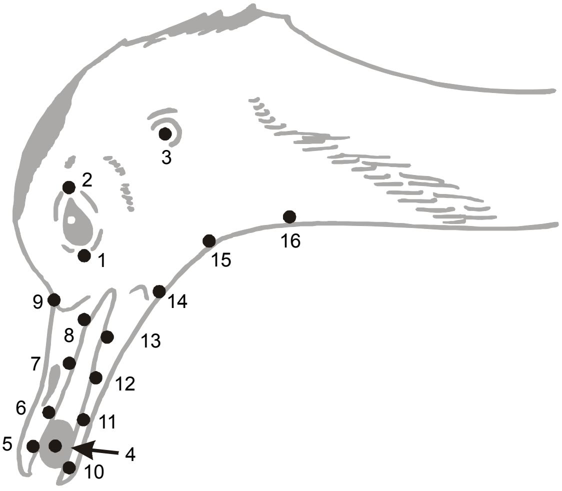

Figure 7.2. Digitised points in each frame of the feeding scenes. Numbers refer to table 7.1. In addition to the points shown three standard points on the background grid were digitised to determine horizontal and vertical axis and to scale the images.

A range of food-types was offered (Table 7.3). The size of the different food-types varied between 4 mm and 35 mm in length and all food-types were offered individually. For the analysis of each bird, at least five items of each food-type were analysed. Large apples were only eaten by the male and only three times. Drinking cycles were observed in both individuals, but only seven cycles could be analysed. Only separate food-items were offered since our preliminary observations showed that the transport of individual food-items is very similar to the transport during grazing, when leaves are removed from the plant by sudden head jerks and transported into the oesophagus. The effect of this type of food-acquisition will be discussed later.

To investigate the diversity and variability of the feeding behaviour, a Principle Component Analysis 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 important in feeding (Table 7.4, Figs. 7.5 & 7.6). Differences in Principal Component scores were determined with an Analysis of Variance (ANOVA).

The natural food preferences of the Greater Rhea were obtained from the work of Martella *et al.* (1996). Prior to the feeding analysis the position of the bending zones was determined through manipulating osteological specimens. The found positions were compared to previous descriptions (Hofer, 1954; Simonetta, 1960; Bock, 1963; Zusi, 1984) and used to determine the position of points for digitising.

Results

1. General feeding and drinking behaviour

A general feeding sequence of the Rhea (Fig. 7.4a & 7.5) consists of the following elements: the bird approaches the food-item while opening the bills. A fixation phase as in the general model for neognathous feeding described by Zweers (1994) could not be distinguished. The food-item was picked-up, sometimes followed by repositioning behaviour. Repositioning occurred more often when large food-items were eaten than when small food-items were eaten. Although it has been suggested that the special morphology of the PPC might be an adaptation to the high impact forces on the bill during pecking (Bock, 1963), the movement analysis showed that the Rhea is capable of limiting the impact force of pecking. When the head hit the ground the acceleration of the head was approximately 11.30 m/s^2 ($a = 11.30 \pm 6.57$ m/s^2, $n = 41$). With an estimated weight of the head of 0.25 kg, the maximum calculated impact force did not exceed 7.54 Newton ($a_{max} = 30.17$ m/s^2).

When the food-item was correctly positioned a single ‘Catch & Throw’ movement was used to transport the food-particle into, or near to, the entrance of the oesophagus. A ‘Catch & 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

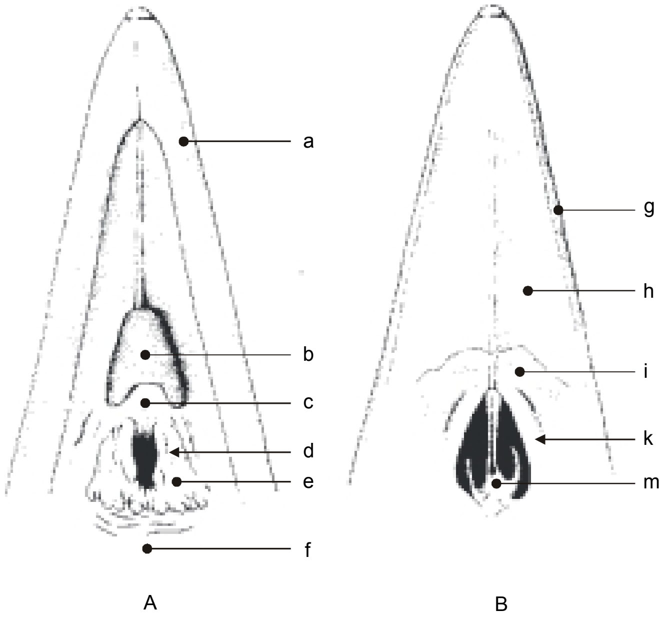

Figure 7.3. Oropharynx of the Greater Rhea (Rhea americana). A. dorsal view of oropharynx floor. B ventral view of oropharynx roof. a) rhamphotheca, b) tongue cushion, c) tongue base, d) opening of the trachea, e) larynx, f) esophagus, g) rhamphotheca, h) bony palate, i) soft palate, k) choana, m) vomer.

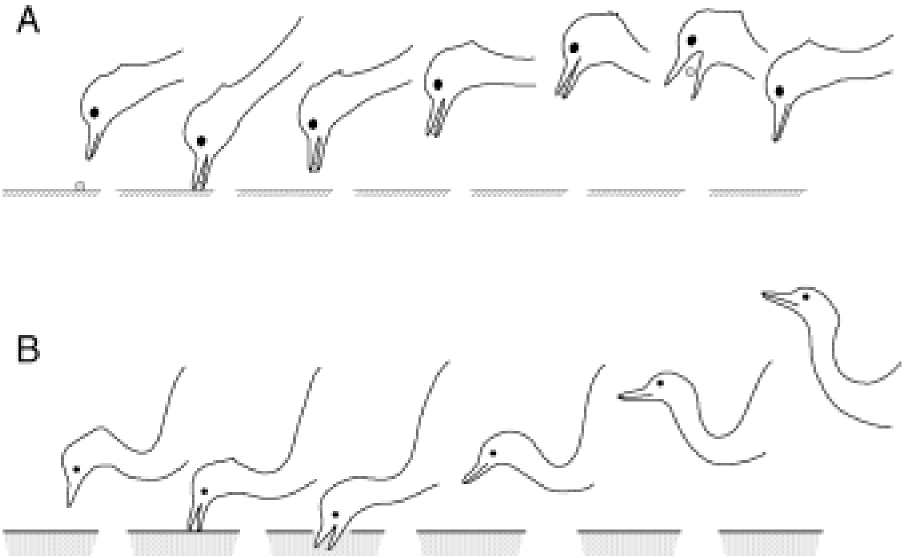

Figure 7.4. Outline drawings of feeding behaviour (A) and scoop drinking behaviour (B) of the Greater Rhea (Rhea americana). Horizontal lines represent ground level (A) or water level (B).

food-item. During the ‘Catch & Throw’ movement the floor of the mouth and pharynx were pulled downward which increases the total volume of the buccal cavity. No tongue movement was observed other than the one resulting in the depression of the mouth floor.

The Rhea used 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. 7.4b). In this behaviour the bird opens the bill, inserts it into the water, and with a forward scooping motion of the head the bill is filled. 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 a small horizontal ‘Catch & Throw’ movement may occur just prior to swallowing. When the size of the water surface limits the

Table 7.3. Approximate dimensions of offered food types

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

scooping movement, the Rhea used 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.

Although feeding behaviour was analysed under controlled conditions, field data show that the observed feeding behaviours are present in the natural behaviour of the Rhea as well. The

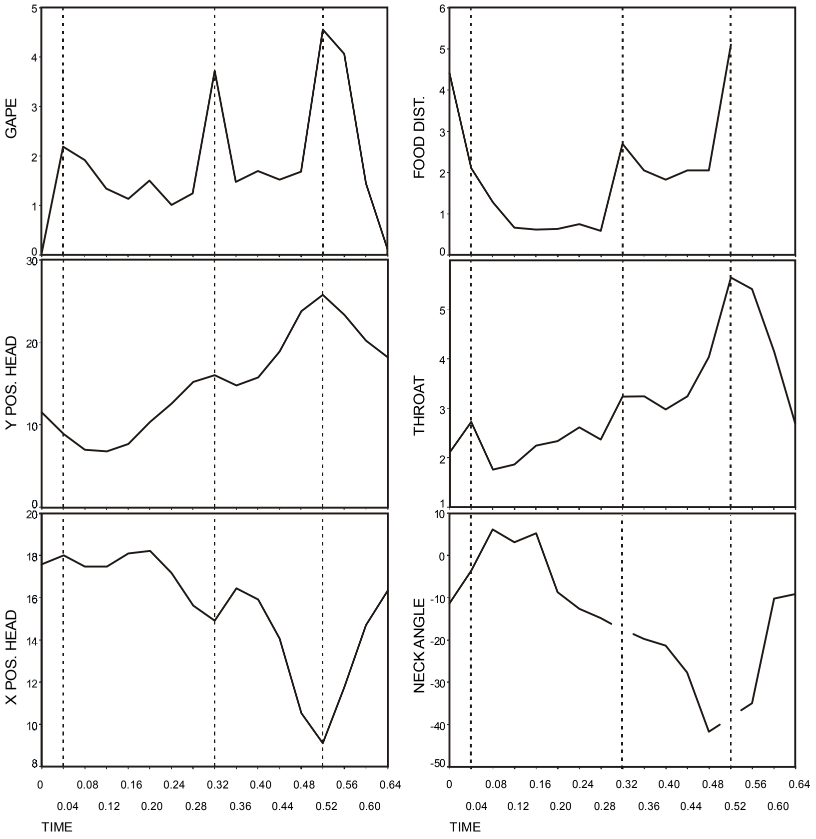

Figure 7.5. A characteristic feeding cycle of the greater rhea (Rhea americana). The vertical dashed lines indicate characteristic moments in the feeding cycle. In chronological order: picking up the food item (grasp), maximum gape during a repositioning cycle and maximum gape during the transport phase. The graphs show the gape, the vertical and horizontal position 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.

single 'Catch & Throw' feeding behaviour and both the scooping and 'Catch & Throw' drinking behaviour have been observed by Greater Rhea in the wild (Navarro, personal communication, 1998). We also observed the single 'Catch & Throw' feeding behaviour in wild and captive Ostriches (*Struthio camelus*) and captive Emus (*Dromaius novaehollandiae*) and cassowaries (*Casuarius casuarius*). These observations indicate that the drinking/feeding behaviour of the Rhea is characteristic for most Palaeognathae.

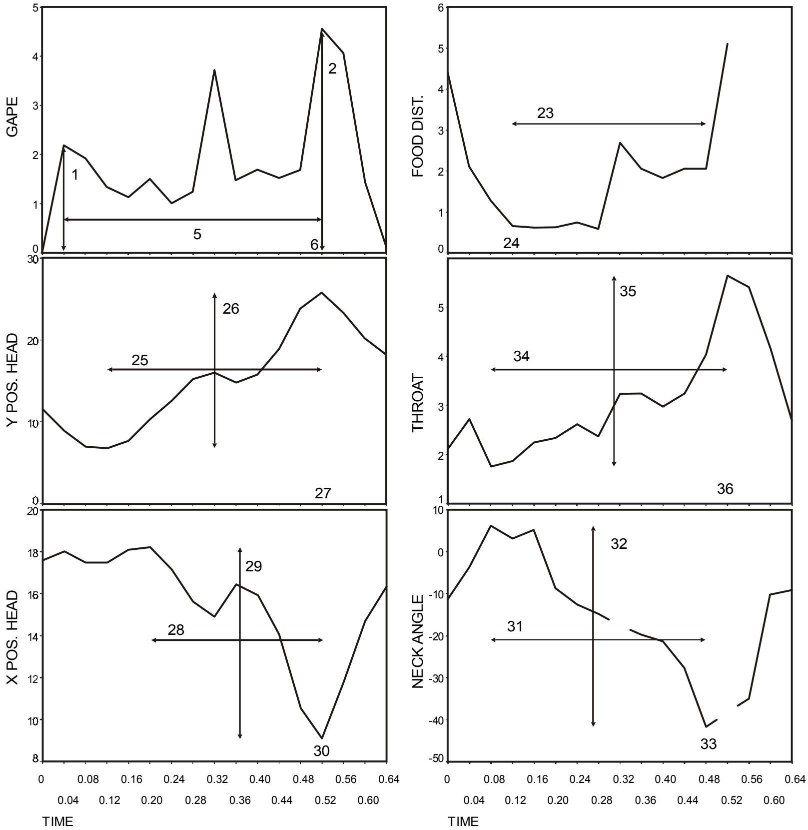

Figure 7.6. Measurements selected to describe the feeding behaviour of the greater rhea and used in the principal component analysis. Numbers in the graphs refer to table 3. Measurements from the groups 'gape', 'lower bill', 'prokinesis' and 'rhynchokinesis' are correlated to the maximum gape during food pecking (gape 1; no. 1) and the maximum gape in the transport phase (gape 2; no. 2). Graphs of prokinesis, rhynchokinesis and lower bill depression are not given but they strongly resemble the pattern shown in the gape graph.

Table 7.4. Measured Parameters

No.	Group	Parameter	Description
1	Gape	Gape 1	Maximum gape during the approach
2		Gape 2	Maximum gape during 'Catch & Throw'
3		Gape Level	Mean gape between Gape 1 and 2
4		Gape Level Std	Standard deviation of measure 4(Indicator for repositioning)
5		Gape Period	Time between Gape 1 and 2
6		Gape 2 Moment	Time from start to Gape 2
7	Lower Bill	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 & Throw'
9		Lower Bill Level	Mean depression of the lower bill between Lower bill 1 and 2
10		Lower Bill Std	Standard deviation of measure 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
13	Pro.	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 Std	Standard deviation of measure 15 (Indicator for constancy of kinesis)
17	Rhyncho.	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 Std	Standard deviation of measure 19 (Indicator for constancy of kinesis)
21	Food	Food Level	Mean distance between the cranium and the food-item between the moment of grasping and swallowing
22		Food Level Std	Standard deviation of measure 21(Indicator for inter-oral transport other than 'Catch & Throw')
23		Food Period	Duration of holding the food item
24		Food Min Moment	Moment of release of the food item in the 'Catch & Throw'
25	Head Y	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
28	Head X	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)
31	Neck	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
34	Throat	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

Table 7.5. Mean values per food type for all characters used in the Principle component analysis. Values are measurements relative to either the cranium or the reference grid.

No.	**Group**	**Parameter**		**Food 1 Apple large (n=3)**	**Food 2 Apple small (n=11)**	**Food 3 Pellets (n=12)**	**Food 4 Seeds (n=14)**	**Food 5 Water (n=7)**
1	Gape	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	0.00
3		Gape Level	cm	3.46	1.88	1.67	0.52	0.37
4		Gape Level Std	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
7	Lower Bill	Lower Bill 1	degrees	32.37	42.94	41.23	41.16	40.20
8		Lower Bill 2	degrees	58.70	55.60	55.46	45.98	0.00
9		Lower Bill Level	degrees	39.06	38.50	39.74	32.74	25.56
10		Lower Bill Std	degrees	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
13	Prokinesis	Prokinesis at Gape 1	degrees	20.58	21.94	21.83	23.42	13.53
14		Prokinesis at Gape 2	degrees	18.60	21.49	23.44	22.68	22.36
15		Prokinesis Level	degrees	21.00	22.29	22.50	25.37	17.19
16		Prokinesis Level Std	degrees	4.11	3.98	3.28	3.66	5.04
17	Rhyncho.	Rhynchokinesis at Gape 1	degrees	6.12	6.19	8.92	4.29	-4.48
18		Rhynchokinesis at Gape 2	degrees	2.29	2.39	3.65	4.56	3.52
19		Rhynchokinesis Level	degrees	3.50	3.29	5.15	2.29	0.99
20		Rhynchokinesis Level Std	degrees	5.53	4.78	4.63	4.75	7.17
21	Food	Food Level	cm	1.91	1.43	1.46	1.33	3.37
22		Food Level Std	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
25	Head Y	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
28	Head X	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
31	Neck	Neck Neck Period	frames	16.00	12.45	15.55	5.69	5.43
32		Difference Neck Neck	degrees	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
34	Throat	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

2. Quantitative differences between food-types

To characterise the movement patterns quantitatively thirty-six parameters were chosen (Table 7.4 & 7.5, Fig. 7.5 & 7.6) and analysed using a Principal Component Analysis. The first three principal components of the PCA based on the characters of the feeding and drinking behaviours described 63% of the total variance. An analysis of variance (ANOVA) over the principle component scores was used to determine the main differences between individuals/sexes and food-types. None of the first three principle components showed a difference between individuals/sexes (df=47, PC1: F=0.264, p=N.S.; PC2: F=0.198, p=N.S.; PC3: F=0.240, p=N.S.) and therefore the data from both individuals were combined. It is clear from the plot of the first principle component (PC1) against the second principle component (PC2) that drinking behaviour is remarkably different from feeding behaviour (Fig. 7.7, Table 7.6). The first principal component describes the absence of the second gape movement ('Catch & Throw' movement), differences in neck movement (duration of the neck cycle) and the duration of the total feeding cycle (Table 7.7). The second principle 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 kinesis. To investigate the differences between food-types without the 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 principle components. To test whether there are significant differences between food-types a one-way analysis of variance over the first three principle components scores was used. Differences between the food-types were tested using a t-test with Bonferroni correction. There are large differences between food-types on both the first and third principal component (df=40, PC1: F=28.678, $p<0.001$; PC2: F=0.365, p=N.S.; PC3: F=3.628, $p<0.05$). It is clear that PC1 describes the effect of food size (Fig. 7.8). The change in movement along PC1 becomes smaller when the size of the food-items increases. A difference on PC1 is only found between the seeds and all other food-types (food-type 1 vs. 2, 3 and 4, t-test, Bonferroni correction, $p<0.001$) and on PC3 between the large apple and seeds (food-type 1 vs. 4, t-test, Bonferroni correction, $p<0.05$).

The differences on the first principle 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 7.7). All these parameters increase with an increase of the size of the food-type. This indicates that the movement pattern of food uptake is relatively constant and only the duration, mainly the effect of repositioning, is variable. The third principle 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 Std) and amount of cranial kinesis (e.g. Prokinesis at Gape 1 &2, Rhynchokinesis at Gape 2, Table 7.7). Differences between food-types on PC3 are only found between large apples and seeds. However, no clear trends can be determined with a change in size of the food-types.

3. Cranial kinesis

To test the level of kinesis in the skull of the Rhea a number of measurements was taken. The movement between the cranium and the upper bill around the point were in prokinetic birds the nasal-frontal hinge would be, was measured and will be further referred to as prokinetic movement. A second measure 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. This bending region was determined by manipulating two osteological specimens (skulls) and measuring the distance between the bill tip and the point of maximal bending. Movement of the rostral part of the upper bill will be referred to as the rhynchokinetic movement. Since food-types are different in size, the kinesis of the upper bill was determined for each food-type separately. The large apple was not used for this analysis due to the small number of repeated experiments.

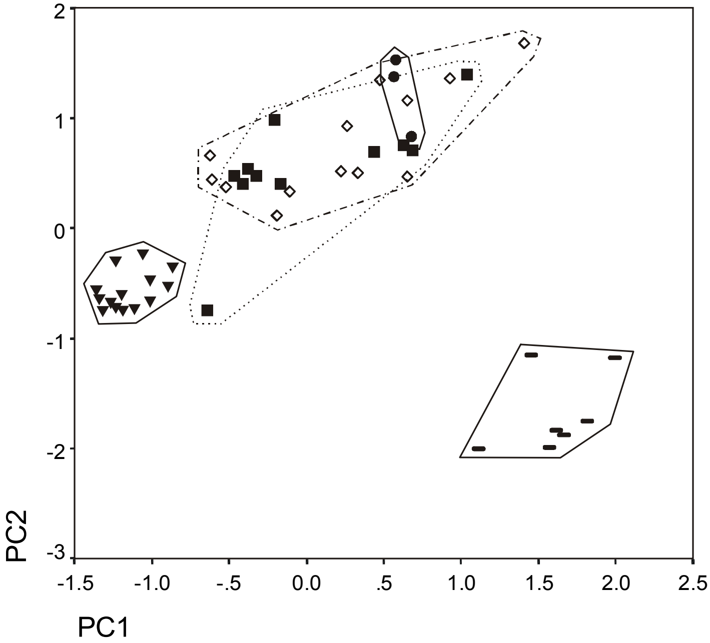

Figure 7.7. Plot of PC1 against PC2 of the analysis including drinking behaviour. Different food types are represented by different markers, and groups of a single food type are outlined. Circles: large apple, closed squares: small apple, open squares: pellets, triangles: seeds, single dashes: drinking behaviour.

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 & 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 be analysed only in the grasping phase. From repeated experiments the average pick-up cycle was calculated and plotted with the standard error. The standard error includes both measuring error and variation of the mean cycle. If time elements differ

Table 7.6. Main parameters contributing to the first three principle components of the total analysis. 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.

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 Std	0.274	0.422	0.592
Food Level Std	-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 Std	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 Std	-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

significantly from each other, the displacement in that period is larger than the measuring error and therefore the movement is significant.

The plot of gape versus time shows a clear pattern (Fig. 7.9) similar to a single food uptake cycle, and differences between the time segments are significant (ANOVA, food-type 2: df=85, $p<0.001$; food-type 3: df=90, $p<0.001$; food-type 4: df=168, $p<0.001$; food-type 5: $p<0.001$). This pattern can be found in angle-based calculations, which have a higher measurement error. A similar analysis was made for the lower bill movement expressed as the depression angle (Fig. 7.9). For all food-types the same pattern was found, and only for the largest analysed food-type (food-type 2: Small Apple) the differences between times were not significant due to large

Table 7.7. Main parameters contributing to the first three principle components of the food type analysis. 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.

Parameter	**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	0.000	-0.474
Prokinesis Level	-0.635	0.089	0.469
Difference Neck Neck	0.230	0.390	0.437
Food Level Std	0.028	-0.298	-0.427
Food Level	0.457	-0.317	-0.419

variation (ANOVA, food-type 2: df=86, p=N.S.; food-type 3: df=89, p<0.05; food-type 4: df=168, p<0.05; food-type 5: df=100, p<0.05). Angular measurements were also used to test the response of the prokinetic and the rhynchokinetic movement during the feeding cycle. Prokinetic movement showed a pattern similar to the lower bill movement but with a much smaller amplitude (Fig. 7.9). However, the prokinetic movement pattern is not significant for any food-type or drinking (ANOVA, food-type 2, df=87, p=N.S.; food-type 3: df=89, p=N.S., food-type 4: df=167, p=N.S.; food-type 5: df=102, p=N.S.). The rhynchokinetic movement patterns can be clearly recognised except in the drinking behaviour (Fig. 7.9). The rhynchokinetic movement is only significant for the two largest food-types: small apple (food-type 2) and pellets (food-type 3)(ANOVA, food-type 2: df=84, p<0.05; food-type 3: df=88, p<0.05; food-type 4: df=166, p=N.S.; food-type 5: df=98, p=N.S.). In table 7.8 the maximal changes in the means angles of the different types of kinesis are given which shows an increase in cranial kinesis with an increase in food size.

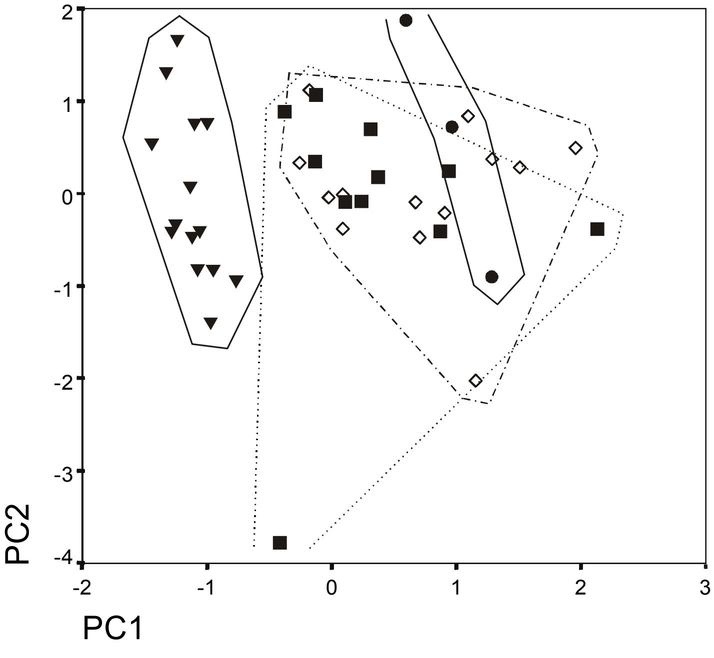

Figure 7.8. Plot of PC1 against PC2 of the analysis of food types only. Different food types are represented by different markers, and groups of a single food type are outlined. Circles: large apple, closed squares: small apple, open squares: pellets, triangles: seeds.

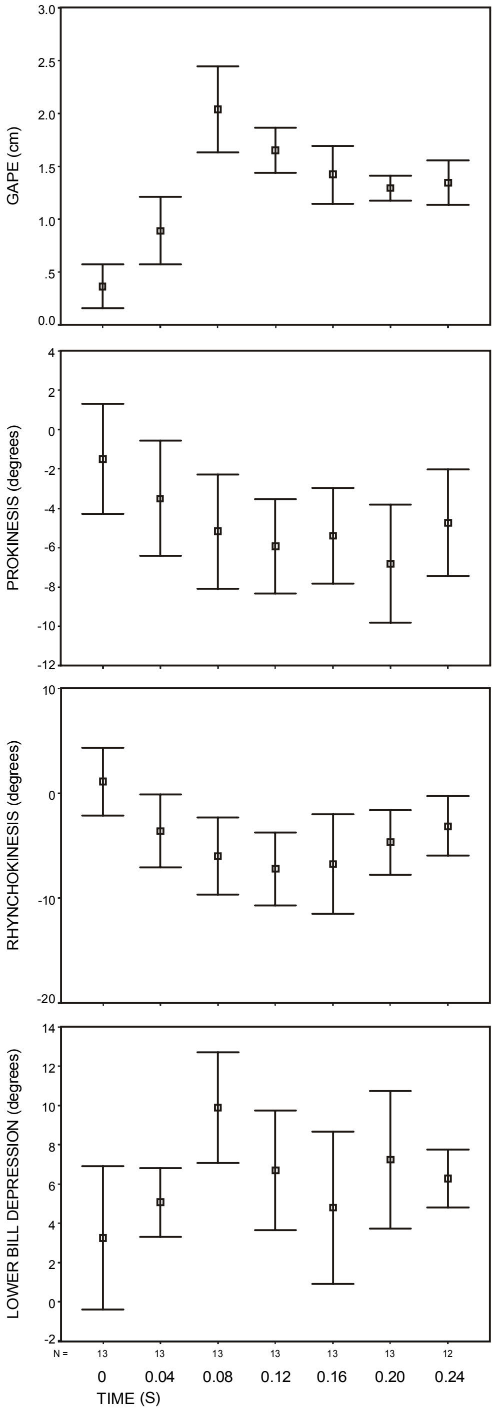

Figure 7.9. Kinesis in the upper bill of the Rhea. Squares indicate mean values (n=13) for each parameter at a certain time for the peck up phase with a medium sized food type. (3: pellets). Vertical lines indicate 95% confidence intervals. The gape is represented as the distance between the bill tips. Prokinesis, rhynchokinesis and lower bill depression 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.

Discussion

Feeding behaviour has been described for a large number of neognathous birds. In a comparative study a general feeding sequence has been described for the neognathous birds (Zweers *et al.*, 1994). Zweers and co-workers describe the most general form of avian feeding as pecking behaviour. This general pecking behaviour is divided into a number of elements. The first elements are preliminary head fixation, preliminary head approach and final head fixation. None of these elements are observed in the Rhea. A number of elements of the general neognathous pattern are characteristic for the feeding behaviour of the Rhea also. These elements are: 1) final head approach, 2) catch at jaw tips, 3) stationing and repositioning, 4) catch at jaw tips, 5) intra-oral transport (‘Catch & Throw’), 6) intra pharyngeal transport.

The complete intra-oropharyngeal phase as described for palaeognathous birds is

Table 7.8. Maximal change in mean of all feeding cycles of kinesis-parameters. Changes in gape are given in centimetres (cm), all other parameters are given in degrees (dg). Values between brackets indicate non-significant changes. L.=lower, Pro.=Prokinese, Rhyncho.=Rhynchokinese

Food	n	Gape (cm)	L. Bill (dg)	Pro. (dg)	Rhyncho. (dg)
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)

achieved by a single ‘Catch & Throw’ movement in the Rhea. This is in large contrast with the complicated ‘Slide & Glue’ mechanism and complex swallowing to transport food through the oropharynx often used by neognathous birds. However, in the case of large food-items neognathous birds may also use a single ‘Catch & Throw’ movement, but still show complex intra-pharyngeal transport (Zweers *et al.*, 1994). The difference between the single ‘Catch & Throw’ movement of neognathous and palaeognathous birds is that the neognathous birds use this movement to transport the food-item onto the lingual base, while palaeognathous birds use it to transport the food-item to the area caudal to the lingual base. The palaeognathous single ‘Catch & 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 oropharynx. Recently, a tongue muscle, the *Nervus hypoglossus* [XII] innervated *Musculus geniohyoideus*, was described, which is only found in Palaeognathae (Müller & Weber, 1998). Note that this muscle should not be confused with the *Nervus glossopharyngeus* [IX] innervated *Musculus geniohyoideus* as described by Zweers (1974) in the duck. The muscle described by Müller and Weber runs dorsal from to the *Musculus intermandibularis* from the *Rostrum mandibulae* to the ventral and latero-rostral side of the ceratobranchiale. The orientation of the muscle is such that it contributes to the large depression of the tongue during the characteristic ‘Catch & Throw’ movement in Palaeognathae. When the lower bill is slightly depressed and the *Musculus geniohyoideus* activated, it will pull the tongue ventro-rostral and will thereby strongly depress the mouth floor and enlarge the pharyngeal cavity. The pharyngeal cavity will become larger when the lower bill is more depressed. This mechanism is confirmed by roentgen-film observations that show protraction of the tongue during gaping (Tomlinson, 1997). Tomlinson (1997) also showed that 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 & Throw’ movement and the retraction during swallowing are the only functions of the tongue during feeding. This indicates a difference from neognathous birds in which the tongue is often used during intra-oral transport (Zweers *et al.*, 1994).

To determine whether the feeding behaviour of the Palaeognathae is derived or primitive within modern birds a comparison must be made with the general feeding patterns found in other tetrapods. The method of feeding highly 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 & Gans, 1994). Avian ‘Catch & Throw’ is an inertial feeding technique, while the feeding pattern of snakes consists of left-right alternating mandibular retractions. Inertial feeding is found in many species of reptilia and can be considered the most general pattern of non-lingual feeding. Comparison of the feeding behaviour of the Rhea with the nearest living sister group of birds, the crocodilians, shows that the feeding behaviour of the Rhea is more similar to reptilian inertial feeding than the general feeding pattern of neognathous birds as described by Zweers *et al.* (1994). Crocodilian feeding is also divided in a number of elements: 1) killing/crushing, 2) transport and 3) swallowing (Cleuren & de Vree, 1992). These three elements can easily be compared with the different elements of the general avian pecking behaviour. The killing/crushing element is comparable to the grasp at the bill tips and repositioning. The transport phase can be compared to the intra-oral transport, and finally swallowing with intra-pharyngeal transport.

The similarity between the transport and swallowing phase in crocodilians and the intra-oral and intra-pharyngeal transport phases in the Rhea is remarkable. In crocodilian intra-oral transport the tongue elevates the food-item until it presses against the palate. Then a cycle occurs which is similar to a ‘Catch & Throw’ movement. The gape is rapidly increased, while simultaneously the tongue pushes the prey slightly upward. Then the cranium is lifted and moved forward and the tongue is depressed. In crocodilian feeding, tongue depression also results in a larger buccal cavity, which facilitates the transport of the food-item by inertial forces. The final transport of the food-item into the oesophagus in palaeognathous birds is also very similar to the crocodilian feeding behaviour. In the Rhea this transport is achieved by a retraction of the hyolingual apparatus (Tomlinson, 1997), similar to the transport in crocodilians.

For neognathous birds a general drinking pattern is also postulated (Zweers, 1992). This pattern consists of the following elements: 1) the fixation in which the bird orientates its head, 2) the down-stroke in which the head is lowered towards the water, 3) the immersion in which the actual water intake takes place, 4) the upstroke in which the head is positioned in such a way that gravitational forces facilitate transport of the water from the pharynx into the oesophagus (swallowing). In the general neognathous pattern (Zweers, 1992) the immersion phase can be divided into three elements that are different in the Rhea. In the first sub-phase (beak tip adhesion) the head is fixed and water enters the bill due to adhesion. In the Rhea there is no stationary phase, and in the immersion phase the bill is widely opened which makes adhesion forces negligible. The second phase in the general neognathous pattern is the intra-oral transport, which always includes pro- and retraction of the tongue. In the Rhea no tongue movement was observed in this phase and the main mode of intra-oral transportation is by means of a scooping motion of the head. In the third or storage phase, which is similar in

Palaeognathae and Neognathae, the water is kept in the oropharynx while the head is lifted during the upstroke.

The upstroke in the general pattern is also divided into subsequent elements: 1) the head elevation, also found in Rhea, 2) an elevation stop in combination with a swallowing cycle and 3) tipping up in which only the tips of the bill are elevated and gravitational forces transport the water into the oesophagus. In the Rhea we found no clear elevation stop. The head elevation movement gradually turns into a low amplitude tip-up phase in which a single protraction of the tongue facilitates the movement of the water into the oesophagus.

Although several differences in the feeding behaviour of Palaeognathae and Neognathae can be determined, most of them are reductions relative to the general neognathous feeding pattern. This indicates that no additional or different functional demands for the palaeognathous PPC can be expected relative to those of neognathous birds.

The food preferences of the Greater Rhea in the wild (Martella *et al.*, 1996) suggest that no fundamentally different feeding behaviours will be performed, than the ones analysed in our study. The feeding and food-acquisition behaviour of all Palaeognathae, except the Kiwi (*Apteryx* spec.), can be described as browsing. The diet consists of a wide variety of food-items, but is mainly vegetarian (Mosa, 1993; Martella *et al.*, 1996; Quin, 1996). There are some differences between the diets of the various palaeognathous species but these seem due to food availability, and not to preference or performance. This indicates that the main addition to our analysis might be that the Palaeognathae pull leaves of plants, which may add additional functional demands during food-acquisition. The removal of leaves is mainly achieved by neck motion, which generates external forces that will open the upper bill. These external forces might indicate a difference between the Palaeognathae and Neognathae but are not related to active cranial kinesis as found in neognathous birds.

The feeding behaviour of the Rhea resembles the feeding behaviour of the crocodilians, and lacks certain elements found in the general feeding pattern of neognathous birds. This suggests that the feeding behaviour of the Rhea is either primitive within birds or highly adapted to inertial feeding. A large problem in determining whether a feeding pattern is primitive or derived is that feeding is highly flexible and adaptive (de Vree & Gans, 1994). However, lingual feeding is found in the more primitive amphibians and inertial feeding is only found in cases where the tongue serves another function (de Vree & Gans, 1994). It is suggested here that lingual feeding is the most primitive avian feeding mechanism and we therefore conclude that the feeding behaviour of the Rhea should be regarded as general tetrapod inertial feeding which has evolved many times independently within vertebrates (de Vree & Gans, 1994).

The drinking behaviour of the Rhea lacks the tongue movement present in neognathous drinking. Although this very simple movement pattern suggests a basal position of the palaeognathous drinking behaviour, the absence of tongue movement may be the consequence of a reduction in size of the tongue in relation to an optimal ‘Catch & Throw’ feeding behaviour.

Our study showed that cranial kinesis in Palaeognathae is not limited to a single hinge or narrow bending zone. Kinesis is found both between the rostral and caudal part of the upper bill, and to a lesser extent between the caudal part of the upper bill and the cranium. Although the type of cranial kinesis of Palaeognathae has been described as central rhynchokinesis (Zusi, 1984) this study indicates that the movement in the upper bill of Palaeognathae is neither rhynchokinetic nor prokinetic but is flexible over its full length. The elevation amplitude of the bill tip relative to the cranium in the Rhea is similar to the elevation of the upper bill as found in prokinetic neognathous birds (approximately 5-10 degrees; Kooloos & Zweers, 1989; Heidweiller & Zweers, 1990; van den Heuvel, 1992). Because the bending zone is large in the Rhea these elevation angles are only achieved at the very tip of the upper bill. The actual elevation angle of the upper bill will gradually decline more caudally in the upper bill.

One hypothesis about the role of rhynchokinesis states that it can improve the holding of food-items as found in certain Charadriiformes (Zusi, 1984). These birds sometimes depress their upper bill tip around a food-item to improve holding. No upper bill depression is observed in the Rhea, which indicates that this cranial kinesis is not used in this way in Palaeognathae.

According to some authors cranial kinesis is the key character that played a role in the large radiation of birds. (Zweers *et al.*, 1997; Zweers & Vanden Berge, 1997b). In their view cranial kinesis has been a key-factor that resulted in the survival of certain species of birds during the mass-extinction at the Cretaceous-Tertiary transition. During this transition many non-kinetic species became extinct while the kinetic species survived. Zweers *et al*. assume that cranial kinesis resulted in the release of the horizontal component of the *Musculus pterygoideus* resulting in extra biting force. This extra biting force should increase the capacity to acquire food during the K-T transition. One of the groups that is assumed to have benefited from the cranial kinesis are the Palaeognathae. A previous study (Chapter 6) showed that the contribution of cranial kinesis to improved food manipulation is very limited.

Alternative hypotheses about the function and the origin of the palaeognathous PPC configuration have been postulated. The palaeognathous PPC is more robust than the neognathous configuration. One hypothesis states that the special morphology of the palaeognathous PPC is an adaptation to the large impact forces generated when the bill hits the ground during pecking (Bock, 1963). However, in our analysis it was found that impact forces on the bill are relatively low, which indicates that the birds are probably capable of reducing the impact force by reducing the speed at which the ground is hit. Large external forces from hitting the ground are therefore not very likely. During grazing, however, dorso-ventral forces reaction forces are present on the upper bill. It is possible that the morphology of the upper bill of the Palaeognathae is adapted to oppose these reaction forces.

Three hypotheses about the origin of the Palaeognathae agree with the assumption that feeding behaviour is primitive within this group. The first hypothesis is the most widely accepted one on the evolution of the Palaeognathae. It states that the Palaeognathae are the oldest offshoot in the phylogeny of modern birds (Bock, 1963; Meise, 1963, Parkes & Clark, 1966; Cracraft, 1974; de Boer, 1980; Prager and Wilson, 1980; Sibley & Ahlquist, 1981; McGowan, 1984; Feduccia, 1985; Handford & Mares, 1985; Elzanowski, 1986, Houde, 1986, Bledsoe, 1988; Caspers *et al.*, 1994, Lee *et al.*, 1997). The second hypothesis states that Palaeognathae have evolved through neoteny from a flying ancestor (de Beer, 1956). The hypothesis on the neotenous origin of the Palaeognathae is recently revived by physiological/ontogenetic data (Dawson *et al.*, 1994) and molecular systematics (Mindell *et al.*, 1997; Härlid & 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 Palaeognathae. A third hypothesis on the origin of the special morphology of the palaeognathous PPC suggests 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 when these birds increased in size. This unstable upper bill configuration was reinforced by creating a more rigid ventral plane of the upper bill. This plane is mainly formed by the PPC. The reinforcement of the ventral plane of the upper bill limited the active kinesis in the upper bill. This limited kinesis without clear bending zones might be an adaptation to protect the very well developed olfactory organs in the nasal cavity. Absence of bending and the presence of the broad PPC might protect the nasal cavity from movement damage.

Although our results cannot discriminate between these three hypotheses it is clear that the Palaeognathae have a very typical feeding behaviour with very little variation that indicates that the feeding behaviour is either basal within birds or highly adapted to ‘Catch & Throw’ feeding. The role of active cranial kinesis in palaeognathous feeding behaviour is not very large, and it can also not be described as rhynchokinesis since flexibility is observed throughout the upper bill. This also points at a primitive condition, which limits the discussion of the origin of the Palaeognathous feeding apparatus to the question, how to discriminate between primitive and neotenous conditions.