CHAPTER 3

FUNCTIONAL ANALYSIS OF THE RHYNCHOKINETIC JAW APPARATUS IN THE RED KNOT (*CALIDRIS CANUTUS*)

Summary

The Pterygoid-Palatinum Complex (PPC) plays an important role in the elevation of the upper bill. However, it has never been investigated whether the type of cranial kinesis is related to a specific morphology of the PPC. Such a relationship has been suggested for the Palaeognathae, which possess a broad, rigid PPC and a special type of kinesis (central rhynchokinesis). In this paper an analysis is made of the feeding behaviour, cranial kinesis and morphology of the PPC of a distal rhynchokinetic bird. Analysis of the feeding behaviour showed that rhynchokinesis occurs throughout the feeding cycle. The feeding cycle itself resembles strongly the general neognathous feeding behaviour. Remarkable is that cranial kinesis occurs also during swallowing when no food-particles are near the bill tip. This may be the result of a combined action of both the opener and closer muscles of the lower bill. It is concluded that the type of cranial kinesis mainly determines the configuration of the bill, while the morphology of the PPC is mainly affected by the feeding behaviour.

Introduction

 A special feature of birds and some reptiles is their ability to move their upper jaw (bill). This upper bill movement, also known as cranial kinesis, is mediated by a complex system that is thoroughly described by Bock (1964). The elevation of the upper bill starts with a forward rotation of the quadrate, which is situated just behind and below the eye. The movement of the quadrate is transferred to the upper bill by two different systems. The first system consists of the jugal bars and transfers the movement onto the premaxilla. The second system, the Pterygoid-Palate Complex (PPC, Gussekloo & Zweers, 1999) is probably the most important and consists of the pterygoids, palate and vomer. The muscles that induce the movement of the upper bill all attach to the PPC or the quadrate.

Differences between types of cranial kinesis are determined by the position of the kinetic zone around which the upper bill rotates. Zusi (1984) describes three types of kinesis that occur in birds. In the most common form, prokinesis, the entire upper bill rotates around a hinge in the nasal-frontal area. The second most common type of cranial kinesis is known as rhynchokinesis. In this type the flexible zone is situated more rostrally and located within the upper bill; the nasal-frontal hinge is no longer kinetic. The third type is known as amphikinesis and can be considered a combination of prokinesis and rhynchokinesis with two flexible zones: one in the nasal-frontal area and a second one just caudal to the rostrum maxillare in the bill itself.

To make rotation in the upper bill possible a number of adaptations is found in the bill of rhynchokinetic birds. To allow rotation around a flexible zone within the upper bill, the movement of the dorsal and ventral bars of the upper bill has to be uncoupled. This uncoupling is achieved by a special arrangement of the bones in the caudal part of the nostril (the lateral bar, see Zusi, 1984). In prokinetic birds the lateral bar is fused with the dorsal bar rostral to the nasal-frontal hinge. This results in an upper bill that can only move as a single unit. In most rhynchokinetic birds the dorsal connection of the lateral bar is shifted caudally, to the area behind the nasal-frontal hinge. Furthermore, a flexible zone is present in the lateral bar and it no longer rigidly connects the dorsal bar with the ventral bar. This makes it possible to slide the ventral bar forward or backward, while the dorsal bar remains stationary. The rhynchokinetic configuration of the lateral bar is known as the schizorhinal nostril, while the prokinetic configuration is described as holorhinal (Garod, 1873).

Zusi (1984) recognised a number of different types of rhynchokinesis based on the number and position of the flexible zone(s) within the upper bill: 1) Double rhynchokinesis, with two flexible zones, 2) Distal rhynchokinesis, with a flexible zone in the distal part of the bill, 3) Proximal rhynchokinesis, with a flexible zone near the proximal end of the bill, 4) Extensive rhynchokinesis, with a large flexible zone in the centre of the upper bill and 5) Central rhynchokinesis. Central rhynchokinesis is only found in palaeognathous birds and is characterised by a narrow flexible zone in the central area of the bill (Zusi, 1984). However, a recent behavioural analysis of one of the Palaeognathae, the Rhea (*Rhea americana*), showed that the flexible zone in the upper bill of this species is large and of the extensive rhynchokinetic

type (Chapter 7). Because palaeognathous birds have a very distinct PPC (McDowell, 1948; Bock, 1963; Gussekloo & Zweers, 1999) and a special type of kinesis (Zusi, 1984) several attempts have been made to connect the two (Bock, 1963; Hofer 1954; Simonetta, 1960). However, a functional morphological analysis of rhynchokinetic feeding behaviour has never been performed and a general hypothesis about the relation between the PPC morphology and the type of kinesis is not available.

This study focuses on the relation between the morphology of the PPC and a rhynchokinetic bill as was suggested for the Palaeognathae. To find the relation between PPC morphology and
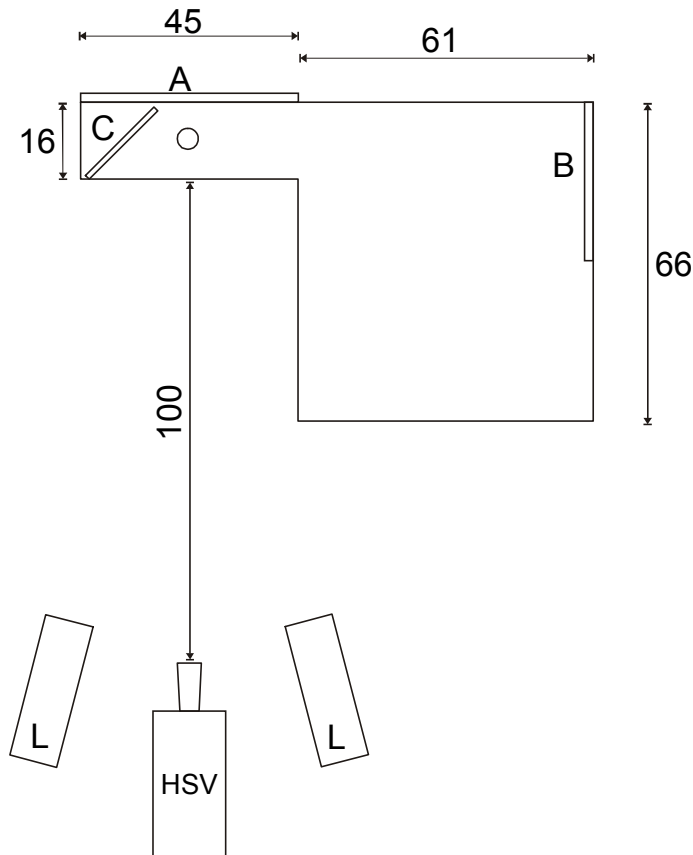

Figure 3.1. Experimental Set-up in top-view. Food-items were offered near the circle. HSV=Highspeed video, L-Cold Light Source, A=reference grid behind the feeding arena, B=reference grid behind the animal, visible in the mirror view, C=mirror at an angle of 45 degrees. All distances are given in centimetres.

a rhynchokinetic bill, an analysis was made of the osteology, myology and arthrology of the PPC of a distal rhynchokinetic bird, the Red Knot (*Calidris canutus*). We tried to identify characters of the PPC that are specific for a distal rhynchokinetic mechanism. To distinguish between features that resulted from rhynchokinesis and those that resulted from the specific feeding behaviour of the Red Knot, the feeding behaviour was analysed and specific functional demands of probing were determined.

Materials and Methods

As model for distal rhynchokinetic birds the Red Knot (*Calidris canutus*) was chosen. The natural history of the Red Knot is well known (Piersma, 1994) and part of its morphology has been described (Burton, 1974; Gerritsen, 1988). The analysis of the morphology of the jaw apparatus was based on dissection of a large number of specimens. Five osteological specimens were used to describe the skull and its elements, fifteen complete heads were used to study the myology, arthrology and osteology. Some of the dissected heads were preserved in 4% formaldehyde, while others had been freshly stored at –20 ^{o}C. All preparations were made under a dissection microscope (magnification up to 40 times). To make it easier to distinguish between muscles and other tissues 'Weigert's variation of Lugon solution' was used (Bock and Shear, 1972). This solution colours muscle tissue brown-red, while the colour of ligaments, aponeuroses, veins and nerves remains unchanged. It also simplifies the determination of fibre direction in thin muscle layers. For the nomenclature the second edition of the Nomina Anatomica Avium (Baumel *et al.*, 1993) was used.

The feeding behaviour of the Red Knot was described, and special attention was paid to rhynchokinesis. This behavioural analysis was used to describe specific functional demands related to feeding behaviour (probing) and to rhynchokinesis. For the
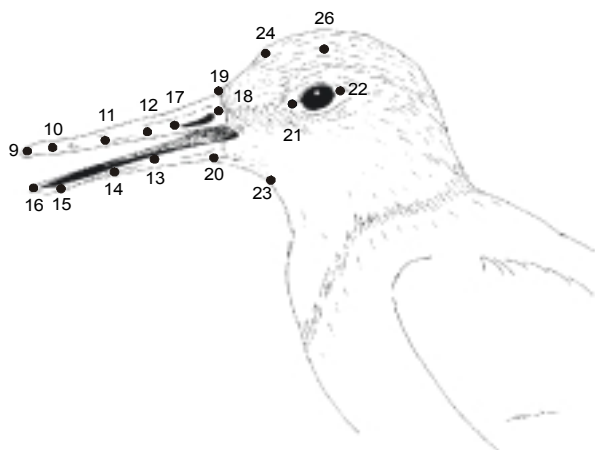

Figure 3.2. Position of the markers placed on the head of the Red Knot (Calidris canutus). Numbers refer to the numbers in table 3.1 All markers were placed on the left side only, except marker 25, which was placed on the right side opposite to marker 26 (visible in mirror view).

analysis of the feeding and drinking behaviour two specimens were used. These birds were kept in the laboratory and trained to feed in the experimental set-up (Fig. 3.1). The feeding of the birds was recorded with a high-speed video camera (500 fps). In each video-frame two images of the bird were visible: one direct image from lateral and one dorsal view obtained from a mirror, which was situated in front of the feeding area at an angle of 45 degrees. For the analysis of the feeding movements a number of white paint markers were placed on the head and bills of the birds (Fig. 3.2, Table 3.1). The position of these markers and the position of the food-item were digitised for every 1/100th of a second of the video-recordings. A reference grid positioned behind the bird, was used to digitise reference points. To assure that a wide range of feeding movements was analysed, food-items of different sizes were offered. The food-types consisted of pellets (Trouvit) to which the birds were accustomed before the experiment. The pellets were cylindrical and of three different sizes: Small, length 5 mm, diameter 0.9 mm; Medium, length 5 mm, diameter 3.5 mm; Large, length 5.0, diameter 5.0. The pellets were covered with a thin layer of chalk to facilitate digitising. Five cycles of each food-type were analysed for each individual.

The digitised points were used to calculate several parameters (Table 3.2), which describe the general movement patterns of the feeding behaviour of the Red Knot. Because of noise in the digitised points rhynchokinesis could not always be determined accurately. To verify our findings about the moments in the feeding cycle when rhynchokinesis occurred, a strain gauge was put on the upper bill of one of the birds and the feeding behaviour was again analysed. During the experiment only medium-sized food-items were offered, and only the most essential markers were digitised so that gape could be determined. The signal of the strain gauge was (pre-) amplified (10x) and digitally stored (5 kHz). The position of the strain gauge was determined after manipulating osteological specimens.

Results

1. Morphological Analysis

General descriptions of the morphology of Sandpipers have been given by Burton (1974), Gerritsen (1988) and Zweers & Gerritsen (1997). In our study we checked these descriptions for the Red Knot and collected additional information on this species where necessary. No extensive morphological description is presented here but a number of features that are related to rhynchokinesis or probing are selected and a qualitative interpretation of their functional significance is given.

1) The bill was long and slender (Fig. 3.3), which makes it possible to penetrate deep into the substrate while total reaction force of the penetration is low (Gerritsen, 1988; Zweers & Gerritsen, 1997). The laterally compressed bill in combination with the rhynchokinetic opening mechanism results also in a reduction of dorso-ventral, external forces during opening of the bill (Gerritsen, 1988). Several features of the bill are designed to resist rostro-caudal reaction forces generated during probing behaviour. Both the dorsal and ventral bar of the upper bill are compressed dorso-ventrally, which results in a lateral stabilisation of the upper bill. Dorso-

ventral stabilisation of the upper bill is achieved by a rostrally elongated inter-nasal septum. This elongated septum stabilises the caudal part of the upper bill so that bending can only occur in the distal part of the upper bill.

2) The quadrate is orientated almost rostro-caudad, in line with the lower bill. This results in a good transfer of caudally directed reaction forces from the pterygoids and palate onto the cranium. The orientation of *Pila otica* in the quadrato-squamosal articulation (Fig. 3.4) ensures that the *Processus oticus quadrati* is in line with the probing direction.

3) The rostral part of the pterygoid articulates with the *Processus basipterygoideus* (Fig. 3.3), which transfers caudally directed reaction forces directly onto the cranium, thereby

Table 3.1. Data obtained from each frame of digitised High-Speed Video. Reference points are given in figure 3.2.

No.	Group	Description
1	Calculated	Earth bound frame of reference, point 0,0.
2		Earth bound frame of reference, point 0,10 (definition y-axis).
3		Earth bound frame of reference, point 10,0 (definition x-axis).
4	Reference grid	Reference frame, point 0,0.
5		Reference frame, point 0,2 (definition y-axis).
6		Reference frame, point 2,0 (definition x-axis).
7	Holding	Food hold point, digitised on grid.
8	Food-item	Position food-item.
9	Upper Bill	Most distal upper bill marker.
10		Upper bill marker.
11		Upper bill marker.
12		Most proximal upper bill marker.
13	Lower Bill	Most proximal lower bill marker.
14		Lower bill marker.
15		Lower bill marker.
16		Most distal lower bill marker.
17	Reference Bills	Rostral border of the nostril.
18		Caudal border of the nostril.
19		Caudal border of the visible part of the upper bill.
20		Caudal border of the visible part of the lower bill.
21	Reference Cranium	Rostral border of the eye.
22		Caudal border of the eye.
23		Throat perpendicular under the eye.
24		Reference triangle, rostral.
25		Reference triangle, dorsal left.
26		Reference triangle, dorsal right.
27	Mirror view	Reference triangle, rostral: in mirror.
28		Reference triangle, dorsal left: in mirror.
29		Reference triangle, dorsal right: in mirror.
30		Upper bill most distal marker: in mirror.

reducing the forces on the pterygoid-quadrate and quadrate-cranium articulations.

4) The palate shows specific features, which can also be explained as adaptations to large caudally orientated impact forces generated during probing. Between the medial surface of the *Arcus jugale* and the connection of the *Processus maxillopalatinus* and the palate a *Pila maxillopalatina* (Fig. 3.5; Johnson, 1984) is present. The presence of this strut was first described by Lowe (1931) and later reanalysed by Zusi and Jehl (1970). They distinguish four different struts on the maxillopalatina (A, B, C, D) of which only strut C is present in the Red Knot (Fig. 3.5). The function of this rostro-caudad orientated strut is to transport caudally directed reaction forces more effectively onto the cranium.

5) The *Processus orbitalis quadrati* is well developed with a large attachment area for the *Musculus protractor pterygoidei et quadrati* (Fig. 3.3), which rotates the quadrate forward and elevates the upper bill. The *Processus orbitalis quadrati* is also relatively long compared to prokinetic birds, which results in a better moment-arm for several muscles attaching to the *Processus orbitalis quadrati*. On the mandibulae an elongated slightly ventrally orientated *Processus retroarticularis* is present (Fig. 3.3) which improves the moment-arm of the *Musculus depressor mandibulae*. This improved moment-arm of the depressor muscle might result in a larger opening force on both upper and lower bill (see Bock, 1964).

Table 3.2. Parameters obtained from the data-points given in table 3.1. These parameters were calculated for each frame of digitised High-Speed Video.

Measurement	Abbr.	Description
X-pos	X	Horizontal position of the head relative to the earth bound frame (EBF).
Y-pos	Y	Vertical position of the head relative to the earth bound frame (EBF).
Food distance	FD	Distance between the food item and the head.
Gape 1	Gp1	Distance between the upper and lower bill at markers 9 and 16.
Gape 2	Gp2	Distance between the upper and lower bill at markers 10 and 15.
Gape 3	Gp3	Distance between the upper and lower bill at markers 11 and 14.
Gape 4	Gp4	Distance between the upper and lower bill at markers 12 and 13.
Gape 5	Gp5	Distance between the upper and lower bill at markers 19 and 20.
Rhynchokinesis	Rhyn	Angle between distal tip (markers 9 and 10) and proximal part (markers 10 and11) of the upper bill.
Prokinesis	Pro	Angle between proximal part of the upper bill (markers 17 and 18) and the cranium (markers 24 and26).
Kinesis Mandibulae	KM	Angle between distal tip (markers 13 and 14) and proximal part (markers 14 and 15) of the lower bill.

6) The most prominent arthrological adaptation is the presence of bending zones (*Zona flexoria*) in the upper bill (Fig. 3.6; see also Gerritsen, 1988). In the upper bill a *Zona flexoria rostrodorsalis* and a *Zona flexoria rostroventralis* are present. The *Zona flexoria rostrodorsalis* was situated in the dorsal bar of the upper bill, the *Zona flexoria rostroventralis* in both ventral bars of the upper bill. To allow movement of the upper bill, a flexible zone was present in the lateral bars also (*Zona flexoria craniofacialis lateralis*). This flexible zone uncouples movement of dorsal and ventral bars. The bending in the lateral bar is made possible by a caudal shift of
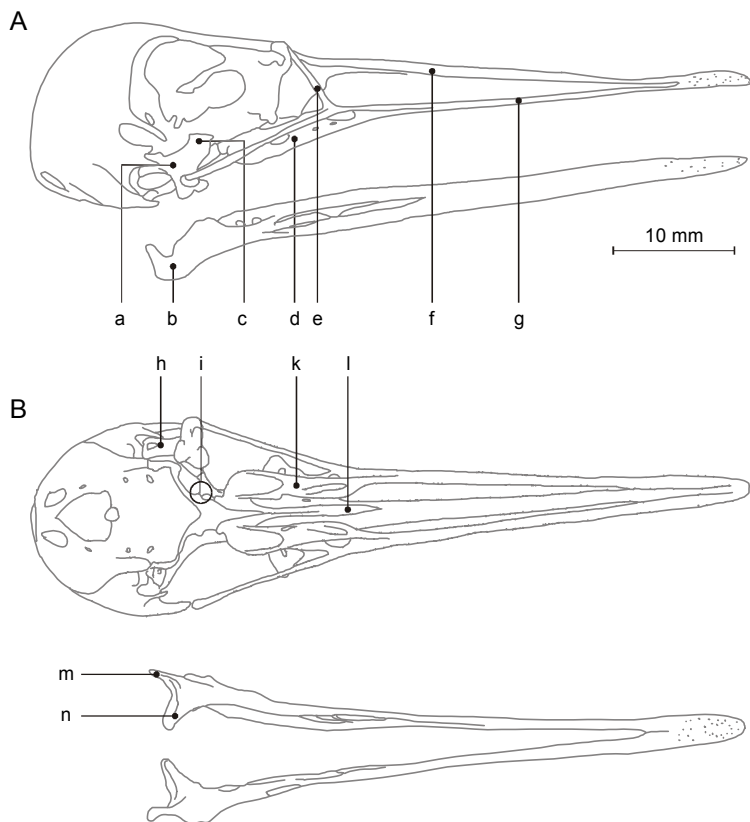

Figure 3.3. Skull of Calidris canutus in lateral (A) and ventral (B) view. The lower bill is seperated from the cranium. Quadrate and pterygoid are removed on the left side in ventral view. a) quadratum, b) Processus retroarticularis, c) Processus orbitalis quadrati, d) palatinum, e) lateral bar, f) dorsal bar, g) ventral bar, h) quadrate, I) Processus basipterygoideus articulating with the pterygoid, k) palatinum, l) vomer, m) Processus retroarticularis, n) Processus medialis.

the base of the lateral bars to a position behind the nasal-frontal hinge as found in schizorhinal skulls (Fig. 3.6; see also Zusi, 1984).

7) Two different flexible zones in the *Rami mandibulae* made mandibular kinesis possible (Fig. 3.6). These zones are the *Zona flexoria intermandibularis rostralis* and the *Zona flexoria intermandibularis caudalis*. The first is situated near the *Rostrum mandibulae*, the second near the *Fenestra rostralis mandibulae* in the most mediolateral flattened part of the ramus. The flexible zones made it possible to depress the tip of the lower bill.

8) Depression of the tip of the lower bill (mandibular kinesis) is achieved by the action of the *Musculus pterygoideus ventralis medialis*, which attached to the distal part of the *Processus medialis mandibulae* (Fig. 3.3). When the muscle contracts, the distal part of the medial process is pulled forward, which results in a outward bending of the central part of the *Rami mandibulae*. This outward bending results in a depression of the distal part of the lower bill. Other parts of the *Musculus pterygoideus* have a different line of action and operate mainly as closer-muscles of the upper jaw. This mechanism has earlier been described for other species such as the herring gull and the barn owl (Bühler, 1981).

9) Large forces for opening the upper bill are achieved by a relatively large *Musculus protractor pterygoidei et quadrati*. This muscle attached to the distal part of the *Processus orbitalis quadrati* thereby improving the moment arm and increasing the opening force on the upper bill.
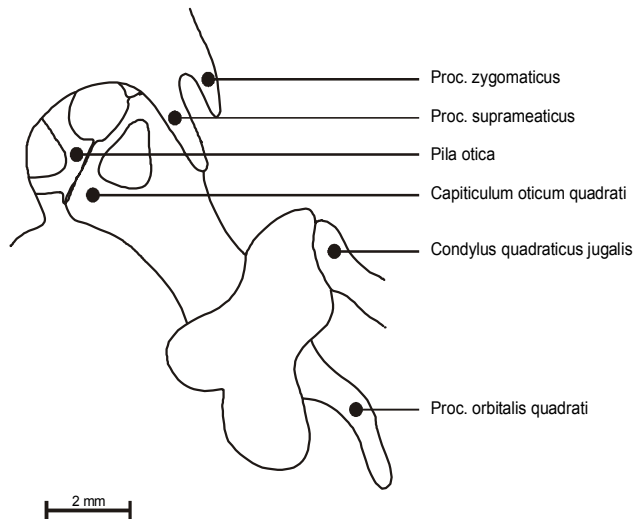

Proc. zygomaticus
Proc. suprameaticus
Pila otica
Capiticulum oticum quadrati
Condylus quadraticus jugalis
Proc. orbitalis quadrati
2 mm

Figure 3.4 Detail of the right quadrato-squamosal articulation in ventral view. Position and orientation of Pila otica in the skull of Calidris canutus
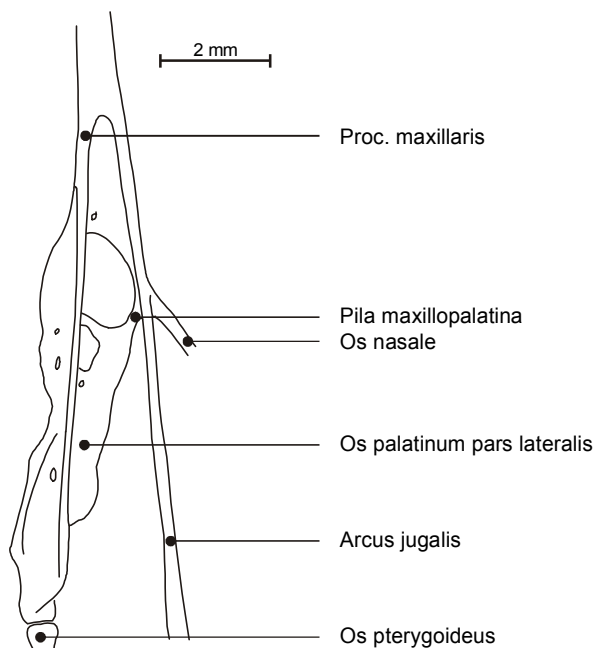
Figure 3.5. Latero-ventral view of the right palate of the Red Knot. Position and orientation of Pila maxillopalatina in Calidris canutus.

10) Even a detailed inspection of the morphology of the pterygoid/palatine/vomer complex did not show any characteristics that can be related to rhynchokinesis as such. The PPC is very similar to that of prokinetic birds, e.g. chicken (van den Heuvel, 1992), pigeon (van Gennip, 1986), or duck (Zweers, 1974). This was also found in a morphometric study of the PPC complex of a large number of birds (Gussekloo and Zweers, 1999).

2. Kinematic Analysis

2.1 General feeding behaviour

The feeding behaviour of the Red Knot follows the general avian feeding (pecking) pattern as described by Zweers *et al.* (1994). Some elements of the feeding behaviour of Sandpipers have been described by Gerritsen (1988).

Feeding behaviour of the Red Knot starts with the approach phase. Several centimetres above the food-item the head is fixated (fixation phase) for a short period. In the subsequent final head approach the bills are opened and orientated in the direction of the food-item while the head approaches the food-item. During the jaw-opening phase both the upper and lower bill show kinesis (Fig. 3.11). When the bills are around the food-item, the bills are closed and the food-item is grasped. Sometimes the bird cannot get a good grip and the food-item is dropped. When the food-item is grasped between the bills correctly, the stationing phase follows: in this phase the food-item is repositioned for intra-oral transport. The repositioning is achieved by a series of 'Catch & Throw' movements (Zweers *et al.*, 1994). During these 'Catch & Throw' movements the food-item is not transported rostrally or caudally. After the food-item is repositioned it is transported through the mouth. Two different mechanisms are used for this transport. The first is a series of 'Catch & Throw' movements, during which the food-item moves more caudally in every 'Catch & Throw' cycle. The second method is a 'Slide & Glue' mechanism (= lingual wet adhesion, Hildebrand *et al.*, 1985). When the jaws are opened the tongue is pushed forward against the food-item (Fig. 3.7). The food-item sticks to the bird's tongue with mucus and is transported backward by a retraction of the tongue. After retraction the tongue has to be repositioned under the food-item for the next retraction. Depending on the size of the food-item the food is transported through the mouth by one of these mechanisms or by a combination of the two. When small food-items are eaten, the food-item is transported with several 'Slide & Glue' movement cycles only. Between 'Slide & Glue' cycles the Red Knot often stops tongue movement to reposition the food-item. Large food-items are transported with a combination of 'Catch & Throw' and 'Slide & Glue'. One or more 'Catch & Throw' movements
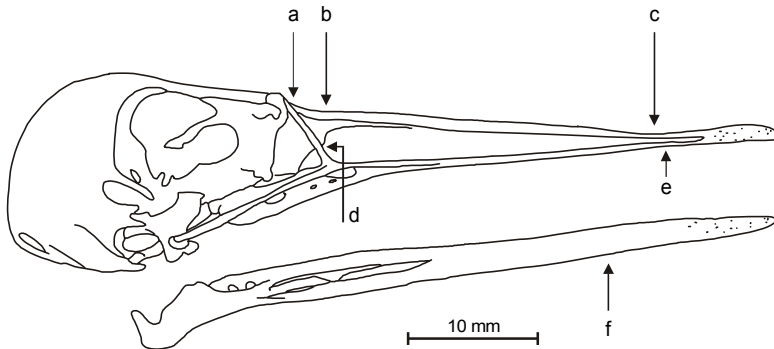

Figure 3.6. Flexible zones in the skull of Calidris canutus in lateral view. The lower bill is seperated from the cranium. a) Zona flexoria craniofacialis lateralis, b) Zona flexoria craniofacialis medialis, c) Zona flexoria rostrodorsalis, d) Zona flexoria nasalis dorsalis, e) Zona flexoria rostroventralis, f) Zona flexoria mandibularis.
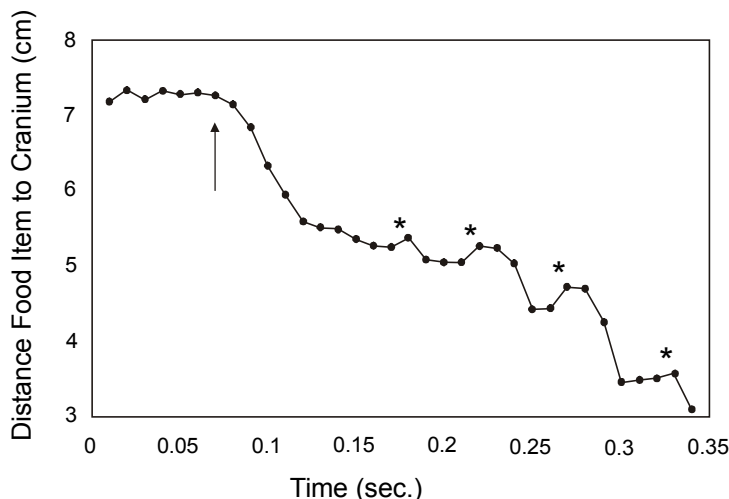
Figure 3.7. Intra-oral transport of a food item. The arrow indicates the grasp of the food item. Asteriks indicate rostral movement of the food item caused by lingual protraction.

are used to transport the food-item to a position near the rictus. Intermediate sized food-items show intermediate behaviour, with in some cases only 'Slide & Glue' behaviour and in other cases a combination of 'Catch & Throw' and 'Slide & Glue'. After the intra-oral transport the food-item is transported to the area behind the tongue and by a final retraction of the tongue and larynx into the oesophagus (swallowing).

2.2 Quantitative differences between food-types

The results from both birds are combined after a comparison between the handling times for each food-type. The handling times, defined as the time between grasping the food-item until swallowing, are not significantly different between the two birds. There are, however, significant differences between the handling times of the different food-items (Two-way ANOVA; individual: df=1, F=0.99, p=N.S.; food-types: df=2, F=14.48, p<0.001; interaction: df=2, F=1.05, p=N.S.). The average handling time for small food-items is 0.25 ± 0.13 sec., for medium sized food-items 0.54 ± 0.29 sec. and for large food-items 0.77 ± 0.19 seconds. These differences are clearly demonstrated when the position of the food-item relative to the cranium is plotted against time (Fig. 3.8). Figure 3.8 shows that the position of larger food-items remains constant for a long period of time. This constant position is due to repositioning behaviour while the food-item is situated near the bill tips. The actual transport time without repositioning of the food-items is comparable between food-types. Differences in maximum gape are also observed between the different food-types (Fig. 3.9). It is clear that during the transport phase the gape is adjusted for
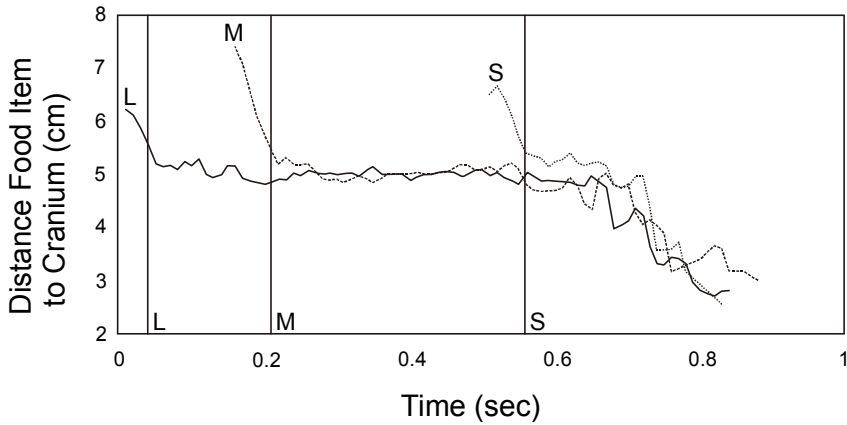
Figure 3.8. Average handling time for different food types. L=Large food items, M=Medium sized food items, S=Small food items. Ventral lines indicate moment of first food grasp.

food size. During transport of the food-item through the bill, the gape increases as the distance to the rictus level decreases.

2.3 Rhynchokinesis

Kinesis in the upper bill of the Red Knot is clearly distal rhynchokinesis. The part of the upper bill that can move relative to the cranium is the small, most rostral part of the bill (approximately 10 mm long; Gerritsen, 1988). The rhynchokinesis in the upper bill is observed mainly in feeding behaviour. During drinking only very small movements in the upper bill were observed. Measurement error in combination with the small changes of the angles in the upper bill made it impossible to quantify rhynchokinesis accurately. It was possible, however, to interpret rhynchokinesis qualitatively. In general there seemed to be a correlation between the size of the gape and the amplitude of rhynchokinesis. This is confirmed by the experiments with the strain gauge, which showed larger strain (=bending) in the upper bill during large gapes (Fig. 3.10). The largest amplitude of rhynchokinesis is observed when the bill is maximally opened.

The moments of kinesis will only be described for small and large food-items (Fig. 3.11). Moments of kinesis for intermediate sized food-items were not consistent. During grasping of large items the rostral part of the upper bill is elevated, which results in an enlargement of the gape. During repositioning the moveable part of the upper bill is depressed (ventral rhynchokinesis) to fix the food-item between the bills and elevated (dorsal rhynchokinesis) to release the food-item. The gapes produced during the transport phase show dorsal rhynchokinesis. These elevations of the bill tip are always smaller than those in the swallowing phase. During swallowing the food-item is located in the very back of the beak, and
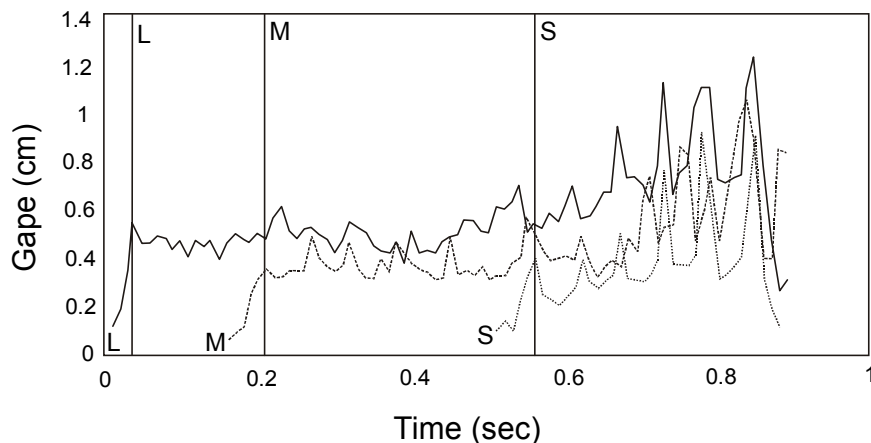
Figure 3.9. Different gapes for different food types. L=Large food item, M=Medium food item, S=Small food item. Vertical lines indicate first food handling.

elevation of the tip of the bill seems to have no direct function. For small food-items only low amplitude rhynchokinesis is observed in both the positioning phase and the swallowing phase.

Mandibular kinesis is always ventrally orientated and can be observed in several stages of the feeding behaviour. When feeding on small food-items mandibular kinesis is only observed during the transport phase. This feature is however much more prominent in the feeding on larger food-items. During feeding on large food-items rhynchokinesis is observed in the repositioning phase, the transport phase and the swallowing phase. Lower bill kinesis is also larger in amplitude during large amplitude gaping.

Discussion

The Red Knot breeds on the arctic tundra and feeds on insects and other non-burrowed prey during that period. Outside the breeding season the birds migrate south to estuary mud flat areas where their main food source becomes burrowed bivalves. During the breeding season the Red Knot is therefore a peck feeder while it becomes a probing bird during winter. The birds possess a kind of cranial kinesis that has been described as distal rhynchokinesis. Distal rhynchokinesis is considered an adaptation to probing behaviour since only a small part of the upper bill has to be elevated in the mud, which reduces the total reaction force on the moving part of the upper bill (Gerritsen, 1988).

The morphology of the jaw-apparatus of the Red Knot has been described by several authors of which the work of Burton (1974) is the most complete. In his work some adaptations for probing behaviour are described but most of them are unclear. Especially the description of the adaptations of the *Musculus depressor mandibulae* is confusing. Burton states that due to the orientation of the medial fibres of the *Musculus depressor mandibulae*, this muscle would
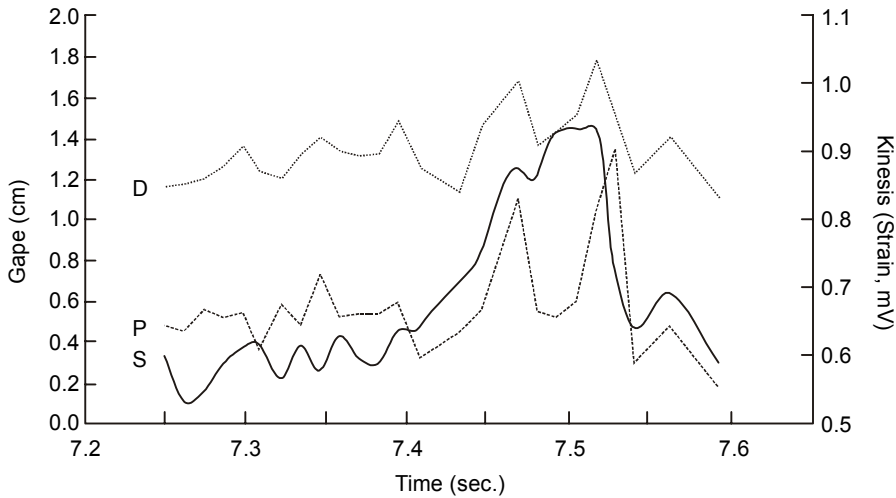
Figure 3.10. Rhynchokinesis during feeding on medium-sized food items by Calidris canutus. Rhynchokinesis is represented by the output of a strain gauge (S) on the flexible zone of the upper bill. Gape is measured from markers on a proximal (P) and a distal (D) point of the upper bill.

have a forward component. Our analysis showed that the origo of the fibres of the depressor muscle, however, was situated caudal to the *Processus retroarticularis* and the *Musculus depressor mandibulae* did not have a forward component. The nomenclature of the *Musculus pterygoideus* of Burton is different compared to ours. Burton divides the *Musculus pterygoideus* into three parts only and combines the *pars dorsalis rostralis* and *pars ventralis lateralis* into a single part called M. The two parts do have a combined insertion on the mandibulae, but the difference in origo and work-line, justifies a distinction of the two parts as separate elements in the muscle complex.

Our morphological analysis showed several adaptations to feeding behaviour within the jaw-apparatus of the Red Knot. However, a distinction must be made between adaptations specific for rhynchokinesis and adaptations to probing behaviour itself. Adaptations for probing behaviour can be divided into two groups. The first group, which facilitates penetration, is mainly found in the bill. The second group, which includes adaptations to resist large forces along the bills and enlargement of muscles that are important in opening the bills, is mainly found in the more caudal part of the jaw apparatus. A previous study of the feeding behaviour of the Red Knot (Gerritsen, 1988) already showed that the bill shape is very important for efficient probing, and that rhynchokinesis is an efficient method for catching and holding burrowed prey (Gerritsen, 1988; Zweers & Gerritsen, 1997). The actual adaptations to make rhynchokinesis possible were however never pointed out. We found that adaptations are mainly found in the bill
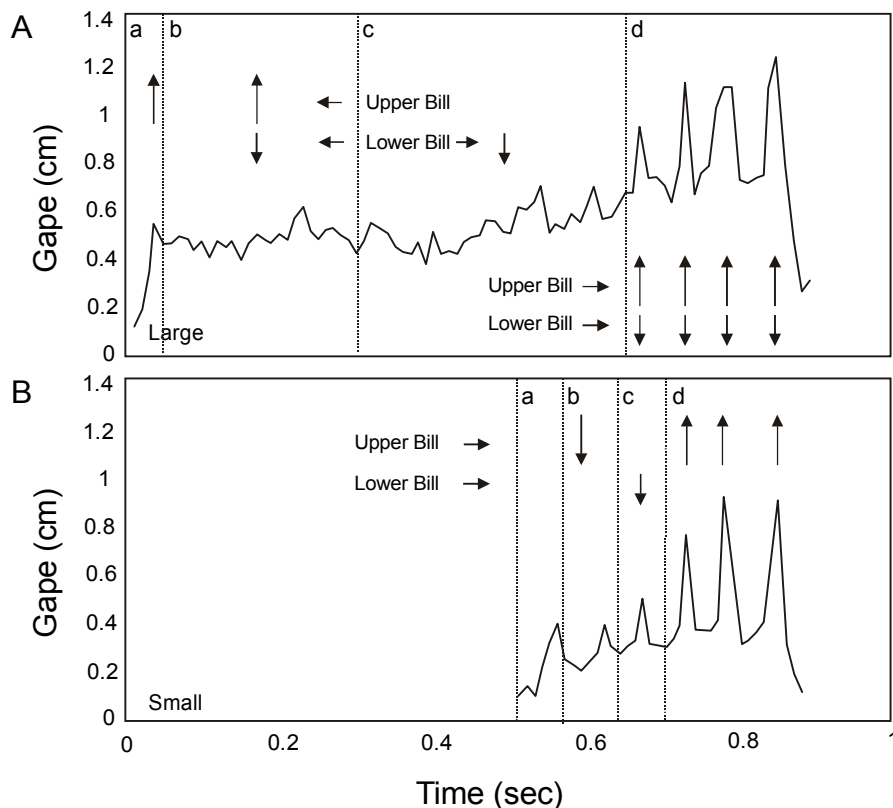
Figure 3.11. Moments of rhynchokinesis during feeding on large (A) en small (B) food items. Feeding cycles are divided in a) grasp, b) repositioning, c) transport, d) swallowing. For phases b and c only presence of kinesis during these phases is indicated (no time value). Upward arrows indicate elevation, downward arrows indicate depression of the upper or lower bill tip.

itself and no clear adaptation to rhynchokinesis could be identified in the Pterygoid-Palate Complex. The adaptations for rhynchokinesis are limited to the schizorhinal nostril, bending zones in the lateral bars and bending zones in both the dorsal and ventral bars. These adaptations have been described earlier (Zusi, 1984) and were clearly present in the Red Knot.

To find the relation between PPC morphology and rhynchokinesis, it is necessary to know the functional demands for rhynchokinesis. The different types of rhynchokinesis (distal, central, proximal, extensive and double) are associated with a large variation in feeding behaviours, and even within a single type of rhynchokinesis feeding behaviour may vary. Proximal and double rhynchokinesis are for example found in both fishing birds (Larinae) and peck-feeding birds (Columbidae; Zusi, 1984). This makes it very difficult to determine a single set of functional

demands for rhynchokinesis. Only distal rhynchokinesis is correlated with a specific type of feeding behaviour: all distal rhynchokinetic birds are probe-feeders (see Zusi, 1984). This specific relationship makes it possible to determine functional demands for the upper bill. The lack of a relationship between a specific feeding behaviour and other types of kinesis is somewhat surprising. From a mechanical point of view there is no reason to assume that relatively small differences in the position of the bending zones are associated with principally different functional demands, that is principally different mechanical loading regimes. Reports on rhynchokinesis are often based on manual manipulation of osteological specimen. It is not only very difficult to make an accurate estimate of the position of the bending zone from these manipulations, but especially in lightweight constructions as the avian skull, it is also very difficult to control the force applied. Effectively, any structure will bend if the force applied is large enough. The position of bending zones is hardly ever determined quantitatively and very little, if anything, is known about jaw opening forces that can be produced by different species of birds or the external forces that act on the bills during feeding.

This study showed that the Red Knot has a distal rhynchokinetic skull and that this type of cranial kinesis does occur during feeding behaviour. Rhynchokinesis occurs clearly when the bill is opened during the grasp phase, which can be explained as a functional adaptation to probing feeding behaviour. However rhynchokinesis also occurs in phases in which a functional explanation is not apparent. The most prominent elevation of the upper bill is observed during large swallowing gapes. During swallowing the food-item is situated in the caudal part of the oropharynx, and an elevation of the distal part of the upper bill seems to have no direct functional meaning for swallowing. Furthermore, elevation of the distal upper bill seems to increase with gape amplitude (pellet size). This suggests that in the Red Knot the elevation of the bill tip may be the consequence of a single jaw opening motor pattern In pigeon and chicken the grasp of a food-item starts with quadrate protractor activity followed by depressor activity (Bout & Zeigler, 1994; van den Heuvel, 1992). This sequence of activities is reflected in the kinematics: upper bill elevation precedes lower bill depression. During intra-oral transport and swallowing upper beak elevation is smaller than during grasping or even completely absent and upper beak elevation lags lower bill depression (van den Heuvel, 1992). As pointed out by van Gennip & Berkhoudt (1992) simultaneous activation of adductor (or passive force from stretching) and depressor muscles of the lower bill may also push the quadrate upward and forward. Although EMG's of the Red Knot are not available, co-activation of adductor and depressor muscles during jaw opening has been described in the pigeon. Especially in the Red Knot, the force generated by muscles other than the quadrate and pterygoid protractors may generate extra force to open the upper beak during probing. The rostro-caudal orientation of the quadrate in probers is very suited for the transfer of force to the quadrate and it is speculated here that adductor-depressor co-activation is a standard part of the beak opening motor pattern in the Red Knot. The effect of adductor/depressor co-activation is illustrated by a simple static model of the quadrate and mandible. The configuration (orientation and distances) of muscles and bony elements for the rest situation was measured (see fig. 3.12). By choosing the

depressor force to be 1 N in each position the free body diagram of the entire system contains three unknowns: the x and y component of the reaction force in the quadrate-skull articulation and the adductor force. The sum of the moments of adductor and depressor muscle around the quadrate-skull articulation is zero when the adductor is 0.44/0.40 = 1.1 times the depressor activity (the ratio of the moment arms). For adductor/depressor activity ratios >1.1 the quadrate will be pushed forward and elevate the upper bill. If the lower bill has to depress at the same time, the moment of the depressor around the quadrato-mandibular joint has to be larger than that of the adductor muscle. By the same reasoning, the adductor force must be < 1.3 (0.88/0.68) times the depressor force. For 1.1 F_{Depr} < F_{Add} < 1.3 F_{Depr} both beaks will open. The elastic forces generated by elevation of the upper bill will be transferred through the PPC to the quadrate and potentially counteract the quadrate movement. This force was not included in the model, but is very small over the physiological range of upper bill elevations (Nuijens & Bout, 1998; Chapter 6).
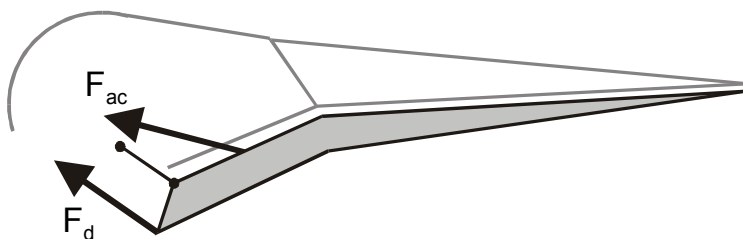

Figure 3.12. Static mathematical model in rest position. F_d=Force of the Musculus depressor mandibulae, F_{ac}=Force of the Musculus adductor mandibulae externus complex.

The evolution of the different types of cranial kinesis in birds is still unclear, but the general opinion has been that prokinesis is the most primitive condition (e.g. Bock, 1964). A recent theory states that the ancestor of all living birds was a 'transitional shorebird' (Feduccia, 1995). Based on this hypothesis an evolutionary pathway for the evolution of bills adapted to probing behaviour has been proposed which assumes a prokinetic ancestor for rhynchokinetic birds (Zweers and Gerritsen, 1997). The adaptations described in their evolutionary pathway are mainly based on the presence of rhynchokinesis and adaptation of bill shape. Our analysis showed that these are indeed the adaptations found in the Red Knot, with a number of additional adaptations in the jaw-musculature and the morphology of the bony elements to resist the large reaction forces of the mud. Our present study also showed that adaptations for rhynchokinesis are mainly found in the bill itself. If we look at evolutionary pathways from pro- to rhynchokinesis we can therefore focus on the bill itself. The changes in the bill during the transition from prokinesis to rhynchokinesis have always been described as a gradual rostral

shift of the bending zones in the bill. Besides the shift of the bending zone, another adaptation must take place to get a functional rhynchokinetic bill, which is the uncoupling of the movement in the ventral and dorsal bars. Although the shift of the bending zones is probably similar for all the types of rhynchokinesis, the uncoupling of the ventral and dorsal bars has occurred in at least two different ways. While most types of rhynchokinetic skulls possess a schizorhinal nostril, which makes uncoupling of the dorsal en ventral bars possible, in birds with central or palaeognathous rhynchokinesis this uncoupling is achieved by a gap in the lateral bar (Bock, 1963; Zusi, 1984). This indicates that these types of rhynchokinesis are probably not homologous or derived within the same lineage. The non-homology of rhynchokinesis is also confirmed by the presence of rhynchokinesis in a wide range of different systematic groups (see Zusi, 1984). A single evolutionary pathway for the origin of rhynchokinesis cannot be postulated. For the sandpiper-like distal rhynchokinesis it has been shown that certain adaptations are present which improve probing and prey handling. It is however very well possible that other types of rhynchokinesis, or the same rhynchokinesis in different habitats, may have a completely different function. We therefore conclude that the mechanism of development of rhynchokinesis is similar (rostral shift of flexible zones and uncoupling) for all types of rhynchokinesis but that the evolutionary forces responsible for each type may be different. Each potential rhynchokinetic morphology must therefore individually be checked for flexible zones in the upper bill, uncoupling of the ventral and dorsal bar, and specific functional demands. Only when these three features are known a clear evolutionary pathway can be determined.

Acknowledgements