The bill of evolution : trophic adaptations in anseriform birds

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THE BILL OF EVOLUTION

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THE BILL OF EVOLUTION
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The beak of a shoveller-duck is a … beautiful and complex structure.

Charles Darwin, Origin of Species (1859)

Contents

Chapter 1

General Introduction

Wildfowl are a well known, globally distributed (except Antarctica) and diverse group of birds, adapted to various habitats and foods and exploiting a vast variety of ecological niches.
The about 150 species belonging to this group (Anatidae) are the ducks, geese and swans, and with the three screamer species (Anhimidae) and the magpie goose (Anseranatidae), make up the avian order Anseriformes.

Wildfowl feed by widely varying methods that are directly related to the habitat in which feeding occurs and the type of food exploited (reviews in Kear, 2005 and Krapu and Reinecke, 1992), examples are depicted in figure 1.1. Most of the methods are found in each subfamily, often as ecological equivalents in different geographic areas. Foods differ in their profitability due to differences in availability, the time needed to obtain them and the energetic costs involved in collecting food.

- Dabbling is used in aquatic environments, at the water surface but also at larger depths. At large depth the head or head and neck are submerged (dipping), or even the entire anterior part of the body, with the tail pointing upwards (upending). Food items may range from invertebrates, seeds, to parts of vegetation, and may be determined by both habitat type, in combination with species occurrence (Kear, 2005), and foraging depth. Many duck species and swans (e.g. Brazil, 2003) obtain their foods by dabbling. In geese this feeding method is used much less and in some species perhaps not at all.

- Grazing is typically used on land to feed on leafy plant parts, but it may also be employed when foraging on aquatic vegetation. Terrestrial grazing is characteristic of geese, sheldgeese, wigeon and maned duck.
  Swans also include terrestrial vegetation in their diet, but they forage mainly on aquatic vegetation. Some duck species are known to feed on aquatic vegetation, and even fewer are observed to include terrestrial vegetation in their diet.

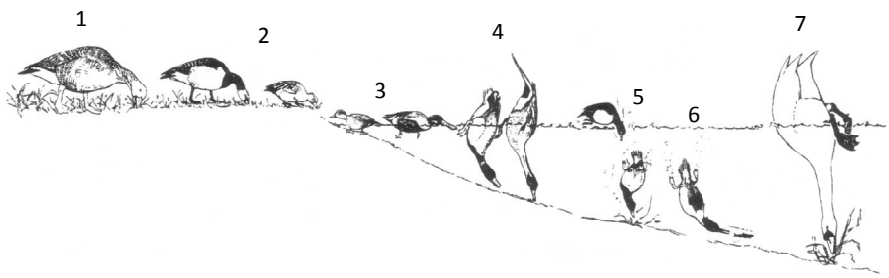


Figure 1.1. Feeding methods of anseriform birds. 1. grubbing (greylag goose), 2. grazing (barnacle goose and Eurasian wigeon), 3. dabbling (Eurasian teal and shoveler), 4, upending (mallard and pintail), 5. diving (tufted duck and common pochard), 6. pursuit diving (goosander), 7. upending (mute swan). Modified from Kear (2005).

- Grubbing (i.e. digging in sediments for roots and tubers) is restricted to areas of soft ground. Some goose species, swans and ducks are known to broaden their diet with subterranean plant parts in this way. Among the northern geese, the small and medium-sized species feed by grazing, while only the larger species include grubbing in their feeding methods.

- Pecking is considered the most general method of feeding in birds (Zweers et al., 1994) and is employed by all anatid species. This feeding method is applied in agricultural environments in wintering areas where grains, potatoes and/or turnips are collected. Switching from feeding in natural to feeding in agricultural habitats may have occurred as early as such crops were cultivated (Bossenmaier and Marshall, 1958). Agricultural crops and grains provide an easily accessible source of energetically rewarding food (Kear, 2005), thus allowing many species to reduce daily feeding time significantly.

The many species of wildfowl and their diversity in feeding methods and habitat use are believed to represent an example of adaptive radiation. Adaptive radiation involves the rapid divergence of a single ancestral species into a group of species with diverse phenotypic traits, enabling each one to exploit different environments. Ecological speciation is the final process of adaptive radiation and occurs as a consequence of divergent natural selection (Schluter, 2001). For divergent selection to occur, there must be trade-offs in the ability of individuals with different phenotypes to exploit different resources (Doebeli, 1996; Taper and Case, 1992). Performance trade-offs create variation in fitness between phenotypes because adaptations to the preferred resource must come at the cost of reduced performance exploiting a less preferred resource. Performance trade-offs also allow co-existence of species due to differences in exploitation of resources, a process known as resource partitioning.

The most well studied phenotypic traits in anseriform species with respect to feeding diversifications are body size and bill morphology, in which trade-offs however are not yet found. Body length in non-diving aquatic feeding species constrains how deep each species can forage when upending, leading to vertical partitioning of resources (Pöysa et al., 1994; Pöysa, 1983a, 1983b). As large species can also forage on depths small species can, there is however, no clear advantage in being small, and therefore body length alone does not provide a trade-off leading to divergent selection.

Many ducks filter food items from water using lamellae on the edges of both bills (Kooloos et al., 1989; Zweers et al., 1977). The distances between lamellae within a row are thought to be directly related to interspecific differences in size of prey taken (Crome 1985; Kooloos et al. 1989; Mott 1994). While some studies have documented correlations between lamellar density and prey size (Nummi, 1993; Nudds and Bowlby, 1984; Guillemain et al., 2002; Thomas, 1982), other studies did not find such a relationship (Nummi and Väänänen, 2001) or found that bill size and shape were more important than lamellar density (Lagerquist and Ankney, 1989; Pöysa 1983a).

Although already Darwin (1998) and Lack (1971, 1974) speculated about the implications of variation in bill morphology, in particular of variation in the number and form of lamellae, on foraging ecology, the interaction between lamellar density and prey size

alone does not provide a trade-off (Bethke and Nudds unpublished in Gurd (2005)). Species with high lamellar density can forage on large and small invertebrates, while species with low lamellar density can feed only on large invertebrates (e.g. Kooloos et al., 1989), leaving the advantage of having large lamellar spacing open to question.

Detailed kinematical and X-ray analyses (Zweers et al., 1977; Kooloos et al., 1989; Gurd, 2005) of different feeding methods, especially filter-feeding, together with model studies suggest that the 'mesh-width' used during filter-feeding is not independent of the volume pumped through the bill, and that food intake rate is related to selected food size in a complex way. These findings demonstrate the necessity to gain a mechanistic understanding of how phenotypes interact with different environments in order to determine resource use (Wainwright, 1996; Moermond, 1986; Schoener, 1986; Werner, 1984).

Filter-feeding in ducks is based on a so-called 'under-tongue' transport mechanism in which the rostral part of the tongue is used as a piston to draw water and suspended food items into the bill. Food items are then transported along the sides of the caudal part of the tongue, which is held against the roof of the oral cavity to avoid the ingestion of water. This way of collecting and transporting food through the oral cavity is limited to relatively small (suspended) food items. For terrestrial feeding and feeding on large food items in an aquatic environment other mechanisms have to be used. For terrestrial feeding on large food items (e.g., acorns) and grazing in the mallard an inertial transport mechanism ('catch-and throw') is used to transported food items through the oral cavity. The mechanism underlying both grazing and pecking in the domestic goose, however, is quite different from the inertial transport mechanism used by the mallard. A different coordination of tongue and bill movements enables the domestic goose to transport clipped vegetation or seeds over the tongue ('over-tongue' transport mechanism), instead of along the sides of the tongue. During retraction of the depressed tongue food items are carried caudad. During subsequent protraction the tongue is elevated and food items are retained behind small caudally pointing spines on the inner surface of the maxilla. Occasionally, geese obtain food items from the water by filter-feeding, and then they use the same 'over-tongue' mechanism instead of the 'under-tongue' mechanism seen in dabbling ducks.

Selection may operate on both morphological characters of tongue and bill, as well as on the transport mechanism. Considering the feeding mechanisms for filter-feeding and grazing, a performance trade-off seems likely. There are very few data on feeding performance in anatids, but the performance of grazing in the mallard compared to the domestic goose is very low. The inertial transport mechanism used by the mallard is slow and a considerable amount of grass is lost from the bill. Vice versa, the performance of filter-feeding is much higher in the mallard than in the domestic goose. As the lingual cushion must be depressed to let food items pass, separate feeding cycles for collection and for transport of food particles, slow down intake rate. Morphological characters associated with the main feeding mechanism used by these species may offer an explanation for this trade-off, e.g. spines on the inside of the upper beak facilitate the transport of grass in the goose but may prevent a proper piston function of the tongue, resulting in a 'leaky' pump system.

Performance data on anatids, however, are scarce and our understanding of the relationship between cranial morphology and feeding mechanism is limited.

Outline thesis

This thesis aims to increase our understanding of the functional trade-off between grazing and filter-feeding. As the feeding apparatus forms an integrated complex of elements, I examined a large number of skull characters in detail, including muscle size and the morphology of the oral cavity in a range of anseriform species.

In *chapter 2* shape differences in the skull of a number of grazing and specialized filter-feeding wildfowl are studied using a geometric morphometric approach. The size and position of skull bones may indicate adaptations to particular force regimes. Grazing specifically puts a load on the moveable upper beak, while filter-feeders experience drag forces when they move their bills through the water.
Grazing has evolved several times within the Anatidae, and in addition to differences in skull shape between filter-feeding and grazing species, I assessed whether the mechanical demands of grazing has resulted in similar skull shape in all grazing species or whether skull shape (also) reflects phylogenetic history.

In the same vein adaptations to either aquatic or terrestrial feeding may be reflected in the relative size of jaw muscles and this is investigated in *chapter 3*. Larger muscle sizes are expected in aquatic feeding species than in terrestrial feeding species.

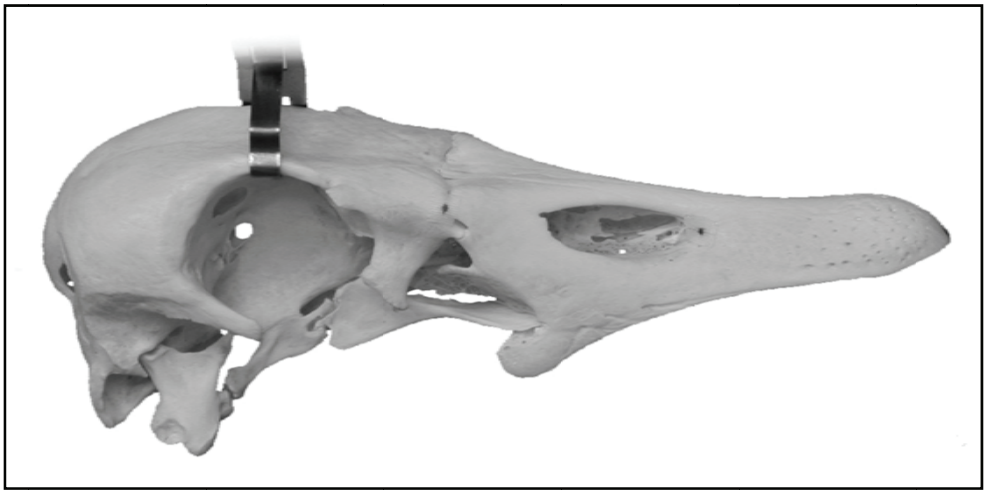
As the relationship between morphology of bills and tongue and feeding mechanism is based on detailed studies on a limited number of species, I examined the consistency of the association between main feeding method and oral morphology in *chapter 4*. Species of every anseriform genus in which terrestrial grazing has evolved is studied, as well as of about 20 aquatic feeding species, including species which are known to feed mainly on large food items.

In *chapter 5* the performance of grazing, defined as intake rate over a short period of time, is studied in three terrestrial and in one aquatic grazing anserine species. Intake rate is examined by determination of bite size, amount of leaves lost during food transport, and bite rate and compared to data on the performance of ducks.

The performance of filter-feeding is assessed in *chapter 6*. Filter-feeding performance is determined by the percentage of food-items retained as well as by the amount of water and suspended food particles pumped through the bill. Both parameters were recorded for geese and swan (grazing) species and compared to literature data on aquatic feeding duck species.

Chapter 2

Cranial geometric morphometrics of wildfowl (Aves: Anatidae) indicate trophic adaptations



Summary

In a number of vertebrate taxa trophic specializations have led to distinct differences in cranial shape. The design of the trophic system determines the efficiency and boundaries of resource use, and in turn resource use directly or indirectly influences fitness, upon which natural selection can act. Wildfowl (Anatidae) have diverged into a number of specialised feeding niches and in this study we investigated whether trophic specialization in anatid birds is reflected in cranial design.

Cranial shape of several grazing and filter-feeding anatid species was examined and we tried to identify the characters that are related to differences in feeding habits. A geometric morphometric approach was used to analyse 33 three-dimensional cranial landmarks. Principal component analysis of these data describes two independent components that may be related to grazing. The first component describes co-variance of relative height of the neurocranium, the position of the craniofacial hinge, and the relative lengths of pterygoids and palatines. The second component describes co-variation of length and width of the bill and width of the cranium. A third component indicates a number of allometric shape changes.

While the cranial characters indicated by the PC analysis seem to be related to bite force and the reaction forces in the joints with the upper bill, the bill characters are related to the bite and pulling forces required during grazing. Efficient grazing requires a short narrow bill for an efficient transfer of forces and is incompatible with efficient filter-feeding, which requires a large pump capacity and therefore a long and broad bill.

A comparison of grazing species within the Anatidae suggests that the degree of adaptation to grazing reflects evolutionary history. Recent clades possess modifications in bill dimensions only, while the more basal clades show large differences in cranial shape as well.

Introduction

Foraging performance and cranial morphology are functionally linked. In a number of vertebrate taxa, trophic specializations have led to distinct differences in cranial shape, e.g., in bats (for review see Van Cakenberghe et al., 2002), ungulates (Pérez-Barbería and Gordon, 1999), rodents (Courant et al., 1997), turtles (Herrel et al., 2002), fishes (Wainwright et al., 2004) and seed-cracking birds (van der Meij, 2004; Herrel et al., 2005a). The design of systems determines how efficiently behaviors can be performed, and the limits of performance set the ultimate boundaries within which an animal must operate. For foraging this means that design and performance determine individual patterns of resource use. In turn, resource use directly or indirectly influences fitness, upon which natural selection can act (Arnold, 1983).

The feeding mechanisms in wildfowl (Anatidae) provide an example of the link between morphological modification and performance. Anatid species have diverged into specialized feeding niches ranging from piscivory to herbivory, presumably from either a filter-feeding ancestor (Olson and Feduccia, 1980; Zweers and Vanden Berge, 1997) or an ancestor exploiting submerged vegetation (Van der Leeuw et al., 2003). Terrestrial grazing is considered a secondarily derived feeding mechanism and has evolved several times independently within the anatid clade.

Efficiency of grazing and filter-feeding are believed to impose conflicting demands on the oropharyngeal epidermal morphology (see also chapter 3). Filter-feeding is performed through repeated rapid opening and closing movements of the jaws with a frequency up to 20 Hz (Kooloos et al., 1989) to generate a waterflow with food particles through the beak. This foraging mechanism requires a bald palatal surface, and well developed cushion-like thickenings of the tongue, which acts as a piston within the opened bill and sucks water into the oral cavity. Food that is filtered out of the water is transported along the tongue (so-called ‘under-tongue’ transport) so that a continuous waterflow can be generated. In many grazing species, however, grass or seeds filtered from the water are transported over the tongue during a series of for/backward movements of the tongue. During these movements food is retained by small spines on the inner surface of the upper bill (Van der Leeuw et al., 2003). Without these spines the transport of grass becomes very inefficient (e.g., mallard), while grazing species have a very low pump capacity during filter-feeding (see chapter 4 and 5).

The mechanisms of grazing and filter-feeding in wildfowl may also pose opposite demands on the shape of the skull. In several vertebrate taxa it has been shown that cranial dimensions are related to the amount of bite force generated during feeding (Van Cakenberghe et al., 2002; Pérez-Barbería and Gordon, 1999; Courant et al., 1997; Herrel et al., 2002; Wainwright et al., 2004; van der Meij, 2004; Herrel et al., 2005a). The feeding system of most vertebrates produces bite force by the jaw adductor muscles acting on a fairly simple lever system. The theory of force transmission defines the mechanical advantage of a muscle as the ratio of the muscle force moment arm (in-lever) relative to the bite force moment arm (out-lever). Bite force ability will thus improve at short out-lever lengths (e.g. Schenk and Wainwright, 2001; Westneat, 1990). In grazing anseriforms,

a forceful closure of the bill is necessary to hold grass firmly in the bill so that when the head and neck are drawn backwards, the grass will snap off, rather than be pulled out of the bill. Furthermore, the backward movement of the head will result in forces that elevate the upper bill, which is moveable with respect to the neurocranium. While grazing species may benefit from relatively short bills, filter-feeders may benefit from large bills to increase their pump volume capacity. However, filter-feeding is performed at high frequencies up to 20 Hz and the drag forces generated during high velocity opening and closing movements may be considerable.

The differences in force regimes acting on the bill during grazing and filter-feeding may be related to both skull geometry (relative positions of joints and muscles) and the size of jaw musculature. To investigate whether the functional demands of filter-feeding and grazing are matched by cranial morphology several groups of anatid birds (geese, swans, sheldgeese and ducks) are studied. To investigate the extent and nature of cranial morphological diversity between anatid groups, we constructed a morphospace (Foote, 1997) of cranial features using landmark-based morphometric methods. These methods allow size and shape to be considered independently, preserve geometric information, and offer powerful techniques for studying variation in form (Rohlf and Marcus, 1993; Parsons et al., 2003; Adams and Rohlf, 2000).

We also investigated whether there is significant overlap in skull geometry of herbivores between the two subfamilies Anatinae and Anserinae, which would suggest that skull geometry has evolved along similar pathways to meet the mechanical demands of grazing. Alternatively, differences in skull geometry may reflect selection pressures related to different foraging habits, differences in constraints that influence the evolution of herbivory among groups, or the time of independent evolution.
Phylogenetic analyses (Madsen et al., 1988; Sraml et al., 1996; Donne-Goussé et al., 2002; Sorenson et al., 1999; Livezey, 1997a) suggest the following succession of events (figure 2.1). From a common ancestor two groups originated: the true geese (*Anser* and *Branta*) and swans (*Cygnus*) (Anserinae) and the duck-like birds (Anatinae). Subsequently, specialized grazing species have diverged within the Anatinae clade. First the sheldgeese (*Chloephaga*, *Alopochen*, *Neochen* and *Cyanochen*), and last, within the genus of dabbling ducks (*Anas*), the wigeon (*Anas penelope*). Not specialized, but known to graze occasionally is the omnivorous mallard (*Anas platyrhynchos*) (Arzel and Elmberg, 2004; Nummi, 1993; Combs and Fredrickson, 1996; Drilling et al., 2002). The mallard is included in our study as least specialized grazer. Straining specialists are found only within the Anatinae and a number of *Anas* species (shovelers) are included in our analyses.

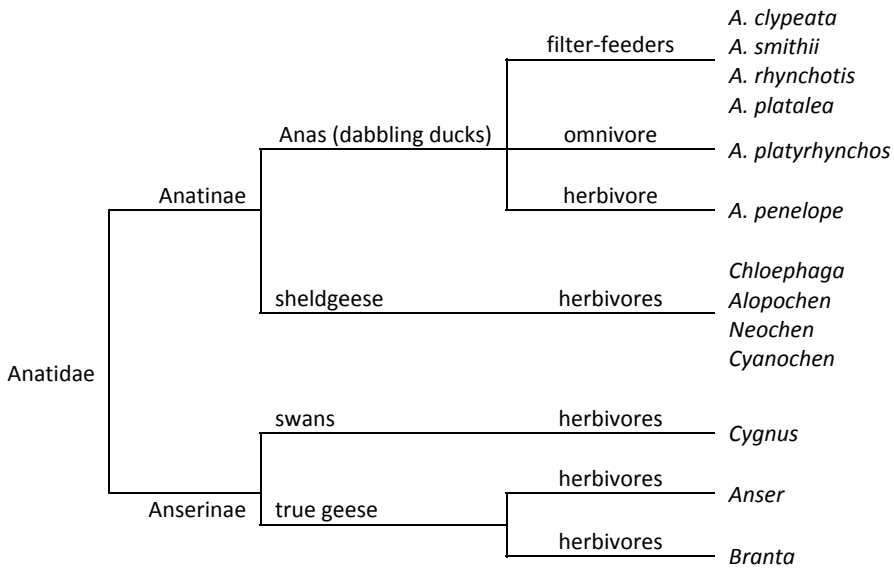


Figure 2.1. Phylogenetic relationships (compiled from Livezey, 1996a, 1997b; Sraml et al., 1996; Madsen et al., 1988; Donne-Goussé et al., 2002; Johnson and Sorenson, 1999) and trophic characterization of the anatid species examined in this study.

Materials and Methods

Specimens

This study is based on 150 skulls of adult anseriform specimens. Specimens belong to the private collection of G. Niklaus (Padingbüttel, Germany), the collection of Naturalis (National Museum of Natural History, Leiden, The Netherlands) and W. van Gestel (Wageningen University). Grazing specialists are represented by all 15 species of true geese (*Anser* and *Branta*), and all but one species of sheldgeese (*Alopochen*, *Neochen* and *Chloephaga*), and by the Eurasian wigeon (*Anas penelope*). Filter-feeding specialists are represented by 4 shoveler species (*Anas clypeata*, *Anas platalea*, *Anas smithii*, and *Anas rhynchotis*). The study further comprised all 7 species of swans (*Cygnus*) and the mallard (*Anas platyrhynchos*). The exact number of specimens per species (subspecies are pooled) are listed in table 2.1.

Table 2.1. Identification and number of Anseriform species studied.

Scientific name		Common name	#
Anser		grey geese	43
	A. cygnoides	Swan goose	1
	A. fabalis	Bean goose	9
	A. brachyrhynchus	Pink-footed goose	3
	A. anser	Greylag Goose	6
	A. albifrons	Greater White-fronted goose	4
	A. erythropus	Lesser White-fronted goose	3
	A. indicus	Bar-headed goose	3
	A. canagicus	Emperor goose	2
	A. caerulescens	Snow goose	8
	A. rossii	Ross' goose	4
Branta		black geese	29
	B. bernicla	Brent goose	10
	B. leucopsis	Barnacle goose	6
	B. canadensis	Canada goose	6
	B. sandvicensis	Hawaiian goose (Nene)	3
	B. ruficollis	Red-breasted goose	4
Cygnus		Swans	30
	C. atratus	Black swan	4
	C. melancoryphus	Black-necked swan	5
	C. olor	Mute swan	4
	C. buccinator	Trumpeter swan	3
	C. columbianus	Whistling swan	1
	C. columbianus bewickii	Bewick's swan	4
	C. cygnus	Whooper swan	9
		Sheldgeese	25
	Cyanochen cyanoptera	Blue-winged goose	1
	Alopochen aegyptiaca	Egyptian goose	2
	Neochen jubata	Orinoco goose	4
	Chloephaga melanoptera	Andean goose	3
	Chloephaga picta	Magellan (Upland) goose	6
	Chloephaga poliocephala	Ashy-headed goose	6
	Chloephaga rubidiceps	Ruddy-headed goose	3
Anas		dabbling ducks	23
	A. penelope	European wigeon	4
	A. platyrhynchos	Mallard	3
	A. smithii	Cape shoveler	5
	A. platalea	Red shoveler	4
	A. rhynchotis	Australian shoveler	5
	A. clypeata	northern shoveler	2

Landmarks

The variation of anseriform cranial morphology is analysed using landmark-based geometric morphometry. Landmarks for this analysis were chosen to cover the geometric form of the skull, to encompass linear measurements used in a previous study (Goodman and Fisher, 1962), and to include landmarks related to lever lengths of the jaw muscle system. Essential to the geometric morphometric technique is the biological homology of the landmarks (Bookstein, 1991) between specimens. Most of the landmarks were digitised at intersections of bony structures. For each specimen, 33 landmarks were recorded in the form of three-dimensional (3D) coordinate data. The landmarks used are shown in figure 2.2 and listed in table 2.2 (see next page). Although most of the landmarks are only unilateral in order to reduce the number of variables by taking advantage of symmetry, some contralateral landmarks were included for orientation of the skulls in the morphometric analyses (see below).

The x, y, and z coordinates of each landmark were collected from a series of photographs of each skull. A skull was clamped at the orbits in a rotating device (figure 2.3) and rotated stepwise around the longitudinal axis with intervals of 30 degrees. At a fixed distance of 50 cm and perpendicular to the longitudinal axis of the skull, a digital photograph (Nikon Coolpix 950) was made. All photographs had a resolution of 1200 x 1600 pixels. Starting from a dorsal viewpoint, a total of 8 pictures were taken for each skull.

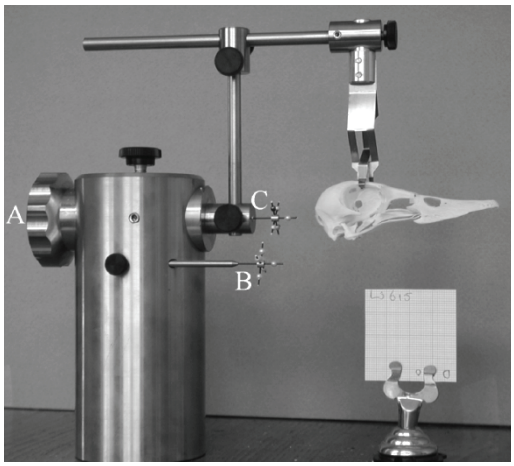


Figure 2.3. Experimental set-up. Eight digital pictures were taken from a 30 degree gradual rotation starting from a dorsal view of the anatid skull. Each picture included the total skull, part B and C, and part of the graph paper. A: knob of rotating device to rotate anatid skull around its longitudinal axis, B: XYZ frame attached to stationary part, C: XYZ frame attached to rotating part.

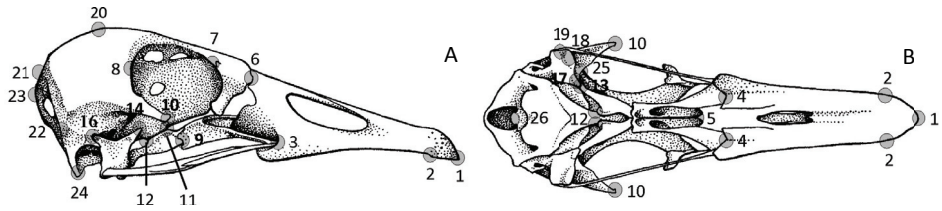


Figure 2.2. Position and number of landmarks used to represent anatid skull morphology. Numbers correspond to table 2.2. A: lateral view, *B*: ventral view (modified from Delacour, 1964).

Table 2.2. Number and description of landmarks. See also figure 2.2. Points marked with [c] were also measured contralaterally. Terminology according to (Baumel et al., 1993).

Number of landmark	Description of landmark
1	tip of the maxilla
2/2[c]	largest width maxilla just caudal from maxillary nail
3	connection jugale with maxilla
4/4[c]	connection palatinum with maxilla
5	connection vomer with maxilla
6/6[c]	articulation frontal nasal hinge with maxilla
7/7[c]	most rostral point of lining of the orbit
8	most caudal point of lining of the orbit
9	articulation palatinum with pterygoid
10/10[c]	tip postorbital process
11	most rostral point of basipterygoid surface on skull
12/12[c]	most caudal point of basipterygoid surface on skull
13	articulation pterygoid with quadrate
14	tip of orbital process of quadrate
15	medial condyle of processus oticus quadratii
16	lateral condyle of processus oticus quadratii
17	condylus medialis quadratii
18	condylus lateralis quadratii
19	articulation jugale with quadrate
20	highest point cranium
21	caudalmost point on the crista nuchalis transversa
22	lateralmost point on crista nuchalis transversa
23	posteriormost point on the prominentia cerebellaris
24/24[c]	ventralmost point of the paroccipital process
25	base of postorbital process
26	middle of occipital condyle

Custom software (R. G. Bout) written in Matlab (The Mathworks Inc., Natick) was used to digitise and subsequently compute the three coordinates of each landmark. To check for unintended translation of the skull and rotation errors with respect to the camera, the tips of a XYZ metal coordinate frame fixed to the stationary part of the device (B in figure 2.3) and the tips of a XYZ metal coordinate frame fixed to the rotating part (C in figure 2.3) were digitised in each of the 8 pictures. A piece of graph paper was used to calculate the scaling factor for the images.

The 3D coordinates of each landmark were reconstructed as follows. For each landmark a first estimate of its unknown third coordinate was chosen. A search matrix was created by adding a random component to a series of 10 values of the first estimate for each individual measurement. The series of pictures containing the landmark were then all rotated to the same (lateral) orientation after a correction for the projection angle. The combined standard deviation over all x, y and z measurements in the lateral rotation plane was used as a cost function that was minimized with a steepest gradient descent method (Nelder and Mead simplex method; (Bunday, 1984)) by adjusting the z-value. This effectively gave the same result as starting with random y and z-values in the lateral rotation plane (x does not change under the rotation scheme used) and minimizing the difference with the measured x, y values after rotation of the initial coordinate towards the plane in which they were measured. The number of cycles required for the algorithm to converge to accurate values (95% of the coordinates less than 0.002 mm from their true value) was estimated from a data set with known values and variance. After convergence of the algorithm, the final set of values for each landmark was averaged to estimate its coordinates.
Not all landmarks were visible in all photographs. To estimate 3D-coordinates a landmark has to be digitised in at least two photographs, although the accuracy increases with the number of times a landmark is measured. Most points of the skull were visible in 3 or 4 photographs, occasionally coordinates were estimated from 2 or more than 4 photographs.
The overall standard deviation after convergence for a stationary point was 0.1 mm in both x and y direction. However, for rotating points the (pooled) standard deviation was clearly higher and slightly different in x (0.24 mm) and y direction (0.17 mm).

Geometric morphometrics

The three-dimensional set of 33 landmarks (also called configurations) for all 150 specimens were analysed by geometric morphometrics (Marcus et al., 1996; Bookstein, 1991; Rohlf and Marcus, 1993; Dryden and Mardia, 1998; Rohlf, 1998) which allows size and shape to be considered as two independent components. A generalized least-squares Procrustes superimposition (GLS) (Gower, 1975; Rohlf and Slice, 1990) generates shape variables from the set of homologous landmarks recorded on each specimen, after differences in specimen position, orientation, and size have been mathematically removed. Each specimen is translated onto a common centroid, then all specimens are scaled to the average centroid size (square root of the sum of squared distances from all landmarks to the centroid of the configuration), and lastly each specimen is rotated to a common orientation that minimizes the squared differences between corresponding

landmarks (Rohlf and Slice, 1990; Adams et al., 2004). Details of this method are given in Bookstein (1991) and Rohlf (1990). Unlike linear distance measurements, geometric morphometric shape variables preserve the geometry of the anatomical structure throughout the analysis.

The Generalized Procrustes Superimposition was performed using PAST-software (Hammer et al., 2001) and custom written software (R.G. Bout). GPS with sets of exclusively ipsilateral landmarks showed that the best fit for ipsilateral points may negatively affect the fit of points on the less intensively sampled contralateral side. Moreover, the construction of the avian skull with its many fused and poorly delineated neurocranial elements does not allow an even distribution of landmarks on the ipsilateral side either, which may also affect the fit of the landmarks. The GPS was therefore performed on a subset of the landmarks. The three landmarks (1, 2, 2^{c}) of the bill were excluded to avoid the Pinocchio-effect (Walker, 2000), as bill length showed much larger variation between groups than neurocranial landmarks. To obtain the most even distribution of cranial landmarks a number of medial (5, 26) and all bilaterally (4, 6, 7, 10, 12, 24) measured landmarks were included, as well as half of the ipsilateral measured points (3, 9, 13, 15, 16, 17, 18, 19). The remaining landmarks (8, 11, 14, 20, 21, 22, 23, and 25) were not used to determine the best fit but translated, scaled and rotated in the same way as the landmarks used for the GPS.

Statistical procedures

After superimposition, transformed coordinates were treated as variables (3 for each landmark) and subjected to statistical analysis. Statistical procedures were performed with SPSS10 (SPSS Inc. Chicago), unless stated otherwise.
To test differences between groups a multivariate general linear model was used (MANOVA). Differences between coordinates of landmarks were assessed through a series of univariate ANOVA's. This involves a large number of univariate tests (99 for 33 landmarks). Although the use of Bonferroni adjustment in our type of analyses may be questioned (Perneger, 1998), we also calculated the Bonferroni-Holm test. This resulted in a study wide (type I) error rate of $p = 0.001$

To reduce the dimensionality of the data set of aligned coordinates we used principal component analysis. Only ipsilateral landmarks were entered in the PCA. To test whether the data were suitable for factor analyses, both the Kaiser-Meyer-Olkin measure of sampling adequacy tests and Bartlett's test of sphericity were performed. Both diagnostic tests (KMO = 0.80, Bartlett: $p = 0.000$) confirmed that the data were suitable for factor analysis. The PCA was performed on the correlation matrix. Standardization is recommended if variances are very different (Quinn and Keough, 2002). To simplify the interpretation of the factors, a varimax rotation was performed. This minimizes the number of variables with high loadings on a factor. The first three components were used for further analysis.

While differences in geometric scale are removed during the GPS, aspects of shape variation correlated with size (i.e. allometric components of shape) are not. To check for

allometric effects, the correlation between PC scores of sample means per species and centroid size were computed.
The scores of each specimen on the three principal components were used in an ANOVA to determine significant differences among the anseriform groups. When the ANOVA proved to be significant, post-hoc tests on group means were used to assess which groups differed from one another. For statistical reasons, both wigeon and mallard were added to the shoveler species to form a single *Anas* group.

Finally, a morphological distance tree was estimated using the matrix of Procrustes distances between each pair of skull configurations of landmarks. Tangent space coordinates were approximated by Procrustes residuals and two phenetic trees were computed on unweighted pair-group averages (UPGMA) using PAST (Hammer et al., 2001). Both trees were based on all ipsilateral landmarks, for the second tree a subset of these landmarks was used in which the landmarks of the bill were excluded.

Results

Relative lengths of cranial bone elements in wildfowl

After Procrustes fitting and standardizing skull size, a first exploration of shape differences was done by calculation the relative lengths of a number of bone elements.
ANOVA's on groups with species means, followed by post-hoc tests, were performed to check for differences between groups. The results are listed in table 2.3.

Groups differ in skull length and in skull width at the craniofacial joint and at the postorbital processes. *Anser*, *Branta*, *Cygnus* and sheldgeese species all have shorter skulls compared to *Anas* species, and a broader skull at the craniofacial joint. Only *Anser* and *Branta* species have significantly wider skulls than *Anas* at the postorbital level. The variation in skull width at the occipital processes is less than at more rostral levels and is largest in *Branta* and smallest in *Anas* and *Cygnus*. Within the *Anas* group the wigeon has a relatively short skull, although not as short as the grazing species in the other anatid groups. Both mallard and wigeon have a relatively wide craniofacial hinge within the *Anas* group. In the wigeon the width of the hinge is similar to the width in sheldgeese. For the other two skull width measures, both mallard and wigeon show larger values than the 4 specialised filter-feeding ducks, but the differences are small.

Differences in skull length are not reflected in palatine and pterygoid lengths. In *Anser* species, the palatine is shorter than in the other groups (except *Branta*), which do not differ among each other. Similarly, the pterygoid bone is longer in *Anser* species than in the other groups, but only differs significantly from *Cygnus* and *Anas* species. Note, that the two grazing *Anas* species, mallard and wigeon, have clearly longer pterygoids than the other *Anas* species, but only the mallard has a relatively short palatine.
Sheldgeese and *Branta* species posses the relatively shortest bills among all anatid groups followed by *Anse*r, *Cygnus* and *Anas* species. Sheldgeese, *Branta* and *Anser* species also

have narrower bills tips compared to *Cygnus* and the long-billed *Anas* species. Maxilla height is significantly larger in *Anser* and *Branta* species than in all other groups. Within the *Anas* group, the mallard and especially the wigeon have shorter and narrower (but not higher) bills than the filter-feeding ducks. In the wigeon relative bill length is only slightly larger than in the *Branta* species.

The quadrate is longer in both true geese genera compared to sheldgeese and *Anas* species, with *Cygnus* taking an intermediate position. The distance between the two joints of the quadrate with the skull and the two condyles of the quadratomandibular joint are largest in *Cygnus, Anser* and *Branta* species and smallest in sheldgeese and *Anas*. However, the differences in quadrate width are very small at both articulations, few comparisons show significant differences, and there seems to be no obvious relationship with foraging mechanism.

Orbit size in *Cygnus* species is significantly smaller than in all other groups and the wigeon seems to have the largest orbit size of all anatid species measured.

Table 2.3. Mean lengths with standard deviations of skull elements of anseriform groups at average centroid size. To compare filter-feeders and grazers within the *Anas* group data for the northern shoveler and wigeon are given separately. When not stated otherwise all three coordinates are used for calculations. Superscript numbers indicate significant differences between groups. Tamhane (T) instead of Bonferroni tests are used when Levene's test indicates inhomogeneity of variance.

	1. *Anser* (n = 10)	2. *Branta* (n = 5)	3. *Cygnus* (n = 7)	4. sheldgeese (n = 7)	5. *Anas* (n = 6)	northern shoveler	wigeon
skull length							
mid 6 - 23	58.11 ± 2.43$^{4, 5}$	60.99 ± 1.20^{5}	60.17 ± 1.30^{5}	61.82 ± 1.07$^{1, 5}$	66.91 ± 1.73$^{1, 2, 3, 4}$	67.34	64.22
5 - 23	59.15 ±1.54^{5}	61.00 ± 0.78^{3}	57.22 ± 1.27^{2,5}	58.72 ± 1.50^{5}	61.35 ± 1.47$^{1, 3, 4}$	59.30	63.59
skull width							
6z - 6^{c}z	17.95 ± 1.08$^{3, 4, 5}$	16.36 ± 1.13^{5}	14.88 ±1.16$^{1, 5}$	14.35 ± 1.05$^{1, 5}$	12.18 ± 1.58$^{1, 2, 3, 4}$	11.08	14.39
10z - 10^{c}z	34.97 ± 2.34$^{3, 5}$	35.09 ± 0.63$^{3, 5}$	31.14 ± 1.35$^{1, 2}$	32.97 ± 1.37	30.43 ± 1.77$^{1, 2}$	28.47	31.92
24z - 24^{c}z	23.66 ± 0.99	25.02 ± 0.82$^{3, 5}$	22.54 ± 0.70^{2,4}	24.36 ± 0.63$^{3, 5}$	22.48 ± 0.85$^{2, 4}$	21.82	22.25
Maxilla length							
1 - mid 6	57.83 ± 5.43$^{2, 4}$	49.12 ± 2.91$^{1, 3, 5}$	57.21 ± 2.90$^{2, 4}$	45.25±3.05$^{1, 3, 5}$	68.55 ± 9.69$^{2, 4}$	79.05	51.42
Maxilla width							
2z - 2^{c}z	17.69 ± 1.96$^{3, (5)}$	17.41 ± 0.83$^{3, 5}$	21.54 ± 0.99$^{1, 2, 4}$	16.28 ± 2.28$^{3, 5}$	31.64 ± 7.40$^{(1), 2, 4}$	40.81	20.21
Maxilla height							
mid 6y – 5y	15.79 ± 1.63$^{3, 4, 5}$	14.43 ± 0.65	12.21 ±0.56^{1}	13.47 ± 1.45^{1}	12.85 ± 1.22^{1}	13.37	10.57
Palatine length							
4 - 9	29.38 ± 1.99$^{3, 4, 5}$	30.89 ± 1.93	34.43 ± 1.85^{1}	33.67 ± 2.85^{1}	33.84 ± 2.31^{1}	34.43	33.83
pterygoid length							
9 - 13	14.20 ± 0.91$^{3, 5}$	13.23 ± 0.64	12.11 ± 2.05^{1}	12.44 ± 1.13	11.88 ± 1.59^{1}	11.07	13.52
Basipterygoid							
11 - 12	6.36 ± 0.61	6.33 ± 0.47	6.12 ± 0.31	6.73 ± 0.78^{5}	5.65 ± 0.29	5.78	5.88
quadrate length							
16-18	14.32 ± 0.67$^{4, 5}$	14.18 ± 0.46^{4}	13.87 ± 0.66	12.90 ± 0.70$^{1, 2}$	13.00 ± 0.78^{1}	12.62	13.54
15-17	13.86 ± 0.90$^{4, 5}$	14.00 ± 0.37$^{4, 5}$	13.21 ± 0.60	12.67 ± 0.72$^{1, 2}$	12.68 ± 0.58$^{1, 2}$	12.25	12.70
quadrate width							
15 - 16	4.11 ± 0.45^{5}	3.97 ± 0.32	4.30 ± 0.32^{5}	3.60 ± 0.48	3.24 ± 0.54$^{1, 3}$	4.27	3.31
17 - 18	5.05 ± 0.42	4.88 ± 0.25	5.06 ± 0.20	4.53 ± 0.30	4.67 ± 0.48	4.95	4.86
orbit size							
7 – 8	23.16 ± 1.40^{3}	24.55 ± 0.44^{3}	17.71 ± 0.76$^{1, 2, 4, 5}$	22.81 ± 1.46^{3}	23.02 ± 1.30^{3}	22.58	25.48

Differences in anatid skull shape based on landmark coordinate configurations

After scaling and superimposition (figure 2.4), large differences between groups exist in the position of the coordinates of the bill and of the dorsal part of the cranium, while the landmarks at the ventral side of the skull show smaller differences. In table 2.4, the mean 3D-coordinates per group after superimposition are listed.

Not surprisingly, multivariate analysis of variance of the coordinates of each landmark shows significant differences in head shape between the five groups ($p = 0.000$).
The comparison of individual landmarks shows that almost all landmarks differ in at least one coordinate and contribute to the shape difference between the groups. Of the 99 tests 81 show a significant difference between the groups according to the conventional criterion $p < 0.05$, and 61 are significantly different according to the Bonferroni-Holm test ($p < 0.001$) (table 2.4).
All except one coordinate of the contralaterally measured landmarks behave like their ipsilateral counterpart. As expected, the z-coordinates of landmarks in the medial plane of the skull (points 1, 5, 23, 26) do not differ among groups.

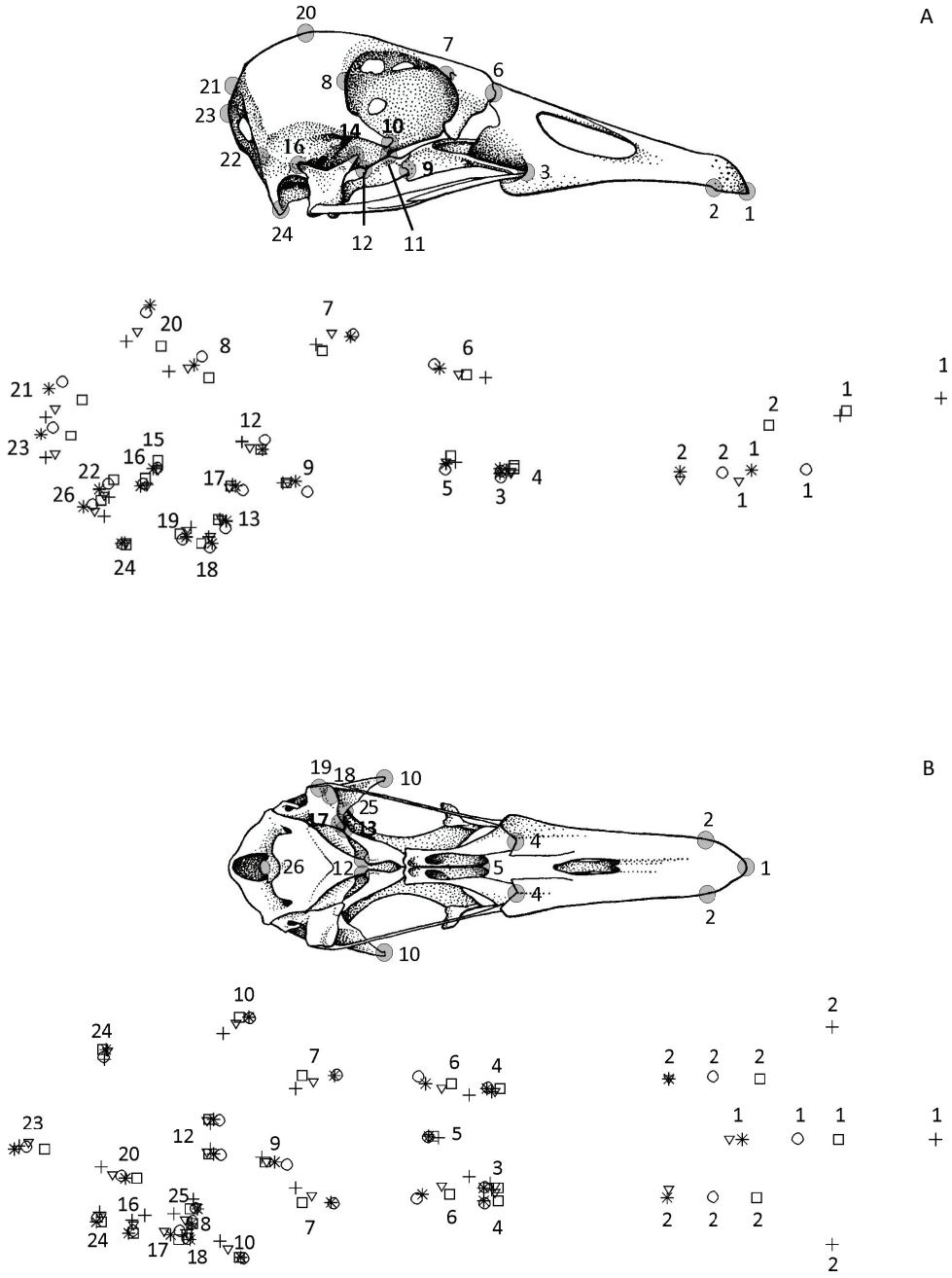


Figure 2.4. Positions of the cranial landmarks and representation of the mean landmark configuration per group after superimposition procedures, the latter depicted in scaled mm (not shown). A: Upper part: lateral view of skull, lower part: corresponding projection of superimposed skull configurations, B: Upper part: ventral view of skull, lower part: corresponding dorso-ventral projection. *: *Anser*, ○: *Branta*, □: *Cygnus*,▽: Sheldgeese, and +: *Anas*.

Table 2.4. Means and standard errors of landmark coordinates after superimposition for each taxon. P-values indicate the probability that the samples are statistically identical according to a univariate ANOVA, * indicate significance according to the Bonferoni-Holm test ($p < 0.001$).

	Anser (n = 10) mean ± s.e.	*Branta* (n = 5) mean ± s.e.	*Cygnus* (n = 7) mean ± s.e.	Sheldgeese (n = 7) mean ± s.e.	*Anas* (n= 6) mean ± s.e.	p-value
1X	77.69 ±1.94	69.79 ±1.59	83.77 ±1.08	67.91 ±1.51	98.11 ±4.59	**0.000** *
1Y	-0.056 ±0.46	0.23 ±0.92	-8.67 ±1.43	1.96 ±0.89	-10.51 ±0.88	**0.000** *
1Z	0.26 ±0.27	0.35 ±0.22	-0.04 ±0.26	0.38 ±0.14	0.35 ±0.27	0.705
2X	65.25 ±1.33	58.89 ±1.61	72.28 ±1.17	58.95 ±1.04	82.93 ±4.06	**0.000** *
2^{c}X	65.28 ±1.37	58.78 ±1.62	71.82 ±1.20	58.89 ±1.11	83.04 ±4.25	**0.000** *
2Y	0.48 ±0.37	0.50 ±0.65	-6.57 ±1.14	1.63 ±0.69	-7.93 ±0.82	**0.000** *
2^{c}Y	0.41 ±0.37	0.46 ±0.64	-6.54 ±1.14	1.60 ±0.67	-7.94 ±0.85	**0.000** *
2Z	-8.98 ±0.48	-8.43 ±0.26	-10.71 ±0.31	-8.41 ±0.45	-15.96 ±1.47	**0.000** *
2^{c}Z	8.71 ±0.24	8.986 ±0.18	10.81 ±0.17	7.87 ±0.46	15.68 ±1.56	**0.000** *
3X	31.97 ±0.40	31.97 ±0.49	33.97 ±0.15	33.63 ±0.63	33.09±0.52	**0.011**
3Y	0.19 ±0.38	0.09 ±0.38	-0.01 ±0.30	0.86 ±0.49	0.24 ±0.25	0.609
3Z	9.76 ±0.14	9.34 ±0.18	8.22 ±0.08	8.25 ±0.25	7.77 ±0.27	**0.000** *
4X	31.97 ±0.56	32.00 ±0.40	34.04 ±0.15	33.62 ±0.65	32.87 ±0.47	**0.022**
4^{c}X	32.24 ±0.53	32.31 ±0.39	34.13 ±0.18	33.64 ±0.66	33.00 ±0.48	0.053
4Y	1.21 ±0.31	0.75 ±0.26	-0.47 ±0.16	0.57 ±0.25	0.17 ±0.30	**0.002**
4^{c}Y	0.62 ±0.24	0.25 ±0.23	-1.11 ±0.18	-0.16 ±0.30	-0.80 ±0.25	**0.000** *
4Z	7.33 ±0.14	7.51 ±0.15	7.17 ±0.17	7.21 ±0.19	6.90 ±0.16	0.172
4^{c}Z	-7.42 ±0.15	-7.02 ±0.16	-7.23 ±0.16	-6.68 ±0.30	-6.51 ±0.21	**0.027**
5X	23.64 ±0.18	23.88 ±0.05	24.66±0.33	23.88 ±0.30	25.23 ±0.45	**0.002**
5Y	-0.03 ±0.26	-0.70 ±0.23	-1.93 ±0.18	-0.79 ±0.32	-0.80 ±0.28	**0.002**
5Z	-0.02 ±0.07	0.08 ±0.11	-0.09 ±0.13	0.17 ±0.05	0.11 ±0.06	0.193
6X	22.05 ±0.35	23.05 ±0.34	26.86 ±0.42	25.74 ±0.29	29.66 ±0.67	**0.000** *
6^{c}X	22.23 ±0.30	23.39 ±0.28	27.06 ±0.33	25.85 ±0.25	29.70 ±0.62	**0.000** *
6Y	-15.80 ±0.30	-14.94 ±0.19	-14.09 ±0.26	-14.10 ±0.40	-13.61 ±0.27	**0.000** *
6^{c}Y	-15.83 ±0.33	-15.30 ±0.16	-14.17 ±0.23	-14.42 ±0.36	13.70 ±0.28	**0.000** *
6Z	8.95 ±0.19	8.52 ±0.31	7.98 ±0.36	7.29 ±0.23	5.99 ±0.14	**0.000** *
6^{c}Z	-8.99 ±0.21	-7.82 ±0.27	-6.89 ±0.22	-7.05 ±0.24	-6.19 ±0.57	**0.000** *
7X	9.66 ±0.31	9.61 ±0.37	5.34 ±0.26	6.65 ±0.45	4.41 ±0.64	**0.000** *
7^{c}X	10.12 ±0.32	10.04 ±0.35	5.36 ±0.28	6.95 ±0.36	4.30 ±0.60	**0.000** *
7Y	-20.18 ±0.37	-19.64 ±0.60	-17.67 ±0.24	-20.19 ±0.69	-18.60 ±0.58	**0.013**
7^{c}Y	-20.07 ±0.36	-20.17 ±0.72	-17.60 ±0.36	-20.10 ±0.63	-18.83 ±0.37	**0.005**
7Z	9.53 ±0.16	9.60 ±0.15	8.98 ±0.18	8.73 ±0.18	7.41 ±0.16	**0.000** *
7^{c}Z	-9.25 ±0.20	-8.99 ±0.25	-8.13 ±0.21	-8.08 ±0.18	-7.10 ±0.36	**0.000** *
8X	-12.86 ±0.23	-14.09 ±0.31	-11.65 ±0.15	-14.89 ±0.28	-17.84 ±0.19	**0.000** *
8Y	-16.91 ±0.53	-15.56 ±0.42	-13.51 ±0.38	-14.91 ±0.59	-14.55 ±0.39	**0.000** *
8Z	13.69 ±0.33	14.46 ±0.29	11.57 ±0.18	13.97 ±0.44	11.54 ±0.44	**0.000** *
9X	2.88 ±0.31	1.37 ±0.46	-0.15 ±0.62	0.19 ±0.54	-0.67 ±0.52	**0.000** *
9Y	3.26 ±0.14	1.86 ±0.40	2.15 ±0.22	2.10 ±0.22	2.15 ±0.50	**0.006**
9Z	3.96 ±0.17	3.86 ±0.14	4.28 ±0.15	3.75 ±0.20	3.00 ±0.24	**0.001** *
10X	-3.48 ±0.22	-3.58 ±0.63	-3.90 ±0.30	-5.61 ±0.22	-6.65 ±0.28	**0.000** *
10^{c}X	-2.54 ±0.23	-2.39 ±0.70	-3.82 ±0.26	-4.41 ±0.30	-6.22 ±0.48	**0.000** *
10Y	-4.35 ±0.34	-2.67 ±0.24	-2.84 ±0.31	-2.92 ±0.34	-3.97 ±0.35	**0.005**
10^{c}Y	-4.86±0.26	-3.18 ±0.30	-3.36 ±0.28	-3.47 ±0.36	-4.48 ±0.24	**0.002**
10Z	17.63 ±0.33	17.65 ±0.11	15.66 ±0.23	16.56 ±0.21	15.35 ±0.31	**0.000** *
10^{c}Z	-17.32 ±0.43	-17.42 ±0.20	-15.47 ±0.29	-16.38 ±0.31	-15.06 ±0.41	**0.000** *

	Anser (n = 10) mean ± s.e.	*Branta* (n = 5) mean ± s.e.	*Cygnus* (n = 7) mean ± s.e.	Sheldgeese (n = 7) mean ± s.e.	*Anas* (n= 6) mean ± s.e.	p-value
11X	-0.85 ±0.26	-1.78 ±0.30	-2.65 ±0.29	-2.30 ±0.41	-2.95 ±0.49	**0.002**
11Y	0.95 ±0.12	0.34 ±0.22	0.27 ±0.22	0.46 ±0.26	0.18 ±0.24	0.070
11Z	2.20 ±0.06	2.14 ±0.15	2.07 ±0.13	1.62 ±0.19	1.35 ±0.15	**0.001** *
12X	-6.82 ±0.23	-7.67 ±0.17	-8.29 ±0.25	-8.47 ±0.34	-8.11 ±0.42	**0.002**
12^{c}X	-6.96 ±0.20	-7.75 ±0.12	-8.44 ±0.25	-8.63 ±0.32	-8.16 ±0.38	**0.001** *
12Y	3.05 ±0.12	2.57 ±0.22	2.59 ±0.13	2.92 ±0.22	2.35 ±0.24	0.083
12^{c}Y	2.80 ±0.12	2.31 ±0.29	2.29 ±0.23	2.65 ±0.15	2.37 ±0.19	0.289
12Z	2.55 ±0.08	2.52 ±0.07	2.00 ±0.07	2.31 ±0.03	1.95 ±0.07	**0.000** *
12^{c}Z	-2.63 ±0.11	-2.71 ±0.15	-2.10 ±0.12	-2.41 ±0.09	-2.00 ±0.03	**0.000** *
13X	-9.22 ±0.25	-9.02 ±0.14	-10.12 ±0.13	-9.68 ±0.21	-9.89 ±0.10	**0.001** *
13Y	8.64 ±0.14	7.92 ±0.05	7.57 ±0.20	7.65 ±0.17	7.55 ±0.22	**0.000** *
13Z	8.87 ±0.17	9.28 ±0.12	8.49 ±0.09	8.77 ±0.17	7.98 ±0.26	**0.000** *
14X	-8.07 ±0.34	-8.04 ±0.21	-8.83 ±0.38	-8.22 ±0.26	-9.74 ±0.40	**0.005**
14Y	0.50 ±0.36	0.70 ±0.32	-0.13 ±0.53	0.80 ±0.34	1.02 ±0.19	0.430
14Z	5.96 ±0.41	6.31 ±0.28	6.90 ±0.17	6.25 ±0.31	5.32 ±0.41	0.050
15X	-21.81 ±0.13	-22.02 ±0.11	-21.40 ±0.18	-21.00 ±0.13	-21.03 ±0.22	**0.000** *
15Y	2.14 ±0.10	2.61 ±0.11	1.40 ±0.13	2.54 ±0.09	2.44 ±0.29	**0.000** *
15Z	11.07 ±0.11	11.77 ±0.12	10.65 ±0.15	10.92 ±0.17	10.75 ±0.15	**0.000** *
16X	-19.75 ±0.15	-20.10 ±0.21	-19.49 ±0.21	-19.38 ±0.11	-19.60 ±0.21	0.119
16Y	-0.26 ±0.13	0.03 ±0.13	-1.03 ±0.15	0.21 ±0.17	0.04 ±0.15	**0.000** *
16Z	13.63 ±0.21	14.08 ±0.11	13.62 ±0.14	13.04 ±0.17	12.22 ±0.20	**0.000** *
17X	-10.51 ±0.23	-9.95 ±0.15	-11.15 ±0.08	-10.35 ±0.16	-10.61 ±0.07	**0.001** *
17Y	10.05 ±0.17	9.59 ±0.08	9.66 ±0.21	9.33 ±0.16	9.37 ±0.24	0.056
17Z	10.26 ±0.18	10.55 ±0.04	9.71 ±0.08	10.40 ±0.14	9.17 ±0.23	**0.000** *
18X	-11.76 ±0.20	-11.18 ±0.15	-12.71 ±0.08	-11.51 ±0.11	-11.58 ±0.24	**0.000** *
18Y	11.49 ±0.17	11.00 ±0.12	11.05 ±0.20	10.28 ±0.18	10.13 ±0.43	**0.003**
18Z	14.93 ±0.26	15.04 ±0.15	14.31 ±0.13	14.66 ±0.20	13.59 ±0.27	**0.000** *
19X	-15.96 ±0.12	-15.23 ±0.15	-16.06 ±0.18	-15.17 ±0.10	-14.41 ±0.55	**0.001** *
19Y	10.31 ±0.13	10.16 ±0.17	9.68 ±0.10	9.23 ±0.17	8.70 ±0.55	**0.002**
19Z	16.24 ±0.17	16.68 ±0.20	15.86 ±0.05	15.92 ±0.22	15.31 ±0.13	**0.000** *
20X	-21.20 ±0.38	-20.65 ±0.47	-18.88 ±0.76	-22.43 ±0.47	-24.18 ±0.50	**0.000** *
20Y	-23.45 ±0.47	-24.33 ±0.65	-18.19 ±0.21	-20.41 ±0.26	-19.05 ±0.69	**0.000** *
20Z	5.60 ±0.25	6.13 ±1.07	5.33 ±0.41	5.72 ±0.41	4.40 ±0.74	0.393
21X	-33.88 ±0.61	-35.60 ±0.65	-30.66 ±0.23	-34.66 ±0.53	-36.14 ±0.24	**0.000** *
21Y	-13.12 ±0.33	-11.94 ±0.68	-10.19 ±0.55	-8.85 ±0.78	-7.78 ±0.45	**0.000** *
21Z	1.26 ±0.26	2.69 ±0.40	0.53 ±0.27	0.98 ±0.53	1.65 ±0.93	**0.034**
22X	-26.83 ±0.22	-28.01 ±0.20	-26.09 ±0.20	-27.35 ±0.25	-26.74 ±0.18	**0.000** *
22Y	2.25 ±0.19	3.15 ±0.34	1.72 ±0.20	4.03 ±0.15	4.23 ±0.19	**0.000** *
22Z	12.25 ±0.11	12.62 ±0.09	11.00 ±0.17	11.35 ±0.25	10.16 ±0.18	**0.000** *
23X	-35.14 ±0.56	-36.93 ±0.34	-32.46 ±0.24	-34.79 ±0.40	-36.10 ±0.29	**0.000** *
23Y	-6.27 ±0.15	-5.18 ±0.31	-4.85 ±0.44	-2.16 ±0.70	-1.51 ±0.20	**0.000** *
23Z	1.44 ±0.19	1.98 ±0.26	1.10 ±0.22	1.04 ±0.40	1.37 ±0.32	0.740
24X	-24.87 ±0.13	-24.92 ±0.22	-24.07 ±0.16	-24.02 ±0.26	-24.30 ±0.23	**0.013**
24^{c}X	-23.89 ±0.16	-23.39 ±0.12	-23.88 ±0.21	-23.13 ±0.16	-23.60 ±0.20	0.097
24Y	11.08 ±0.16	11.12 ±0.19	11.31 ±0.22	10.84 ±0.32	11.10 ±0.09	0.757
24^{c}Y	11.21 ±0.16	11.17 ±0.20	11.37 ±0.15	10.47 ±0.33	10.95 ±0.17	0.130
24Z	11.83 ±0.09	12.36 ±0.17	11.34 ±0.18	11.84 ±0.10	11.13 ±0.20	**0.000** *
24^{c}Z	-11.80 ±0.28	-12.61 ±0.22	-11.19 ±0.13	-12.50 ±0.21	-11.32 ±0.17	**0.000** *
25X	-10.85 ±0.21	-10.92 ±0.26	-10.82 ±0.10	-11.95 ±0.18	-13.63 ±0.33	**0.000** *

	Anser (n = 10) mean ± s.e.	*Branta* (n = 5) mean ± s.e.	*Cygnus* (n = 7) mean ± s.e.	Sheldgeese (n = 7) mean ± s.e.	*Anas* (n= 6) mean ± s.e.	p-value
25Y	-6.15 ±0.40	-4.42 ±0.10	-5.98 ±0.39	-4.73 ±0.48	-4.30 ±0.33	**0.004**
25Z	12.27 ±0.29	12.66 ±0.16	11.90 ±0.30	12.26 ±0.13	11.24 ±0.16	**0.002**
26X	-29.25 ±0.21	-30.47 ±0.22	-27.84 ±0.21	-28.79 ±0.22	-27.43 ±0.38	**0.000 ***
26Y	5.27 ±0.27	5.59 ±0.09	4.81 ±0.18	6.49 ±0.16	7.22 ±0.19	**0.000 ***
26Z	0.02 ±0.15	-0.18 ±0.12	0.10 ±0.13	-0.17 ±0.13	-0.11 ±0.08	0.382

In order to detect co-variation among landmarks as well as to reduce the number of variables of the dataset, a PCA was performed. The principal components were calculated from the correlation matrix with varimax rotation. The first three PC's accounted for 41% of the variation in shape (table 2.5). PC1 accounted for 15.4% of the variance, PC2 explained 13.8% of the variation of the superimposed normalized cranial landmarks and PC3 explained 12.4% of the variation. In figure 2.5 the location of each measured specimen in principal component space is shown.

Table 2.5. Loadings of Procrustes fitted landmark coordinates on the first three principal components after varimax rotation. Percent of variance explained between brackets. Bold values indicate high loadings on that axis.

Land mark	PC1 (15.4%)	PC2 (13.8%)	PC3 (12.4%)	Land mark	PC1 (15.4%)	PC2 (13.8%)	PC3 (12.4%)
1x	0.047	**-0.927**	-0.153	14x	0.326	0.467	0.338
1y	-0.173	**-0.869**	0.041	14y	0.041	-0.118	0.100
1z	0.184	0.107	-0.093	14z	-0.078	0.108	0.211
2x	-0.022	**-0.914**	-0.143	15x	-0.261	-0.225	-0.194
2y	-0.205	**-0.857**	0.031	15y	0.116	-0.317	0.490
2z	-0.128	**-0.794**	-0.398	15z	0.064	0.394	-0.057
3x	**-0.723**	-0.068	0.102	16x	-0.037	-0.134	0.094
3y	-0.210	-0.078	0.088	16y	0.201	-0.352	**0.610**
3z	**0.587**	0.232	0.166	16z	0.264	0.345	0.476
4x	**-0.775**	-0.023	0.099	17x	0.103	0.204	-0.347
4y	**-0.566**	-0.263	0.136	17y	**-0.702**	-0.056	-0.248
4z	0.191	0.054	0.036	17z	0.100	0.445	0.080
5x	-0.310	**-0.506**	0.045	18x	0.050	0.166	**-0.564**
5y	**0.643**	0.089	0.216	18y	**-0.688**	-0.163	-0.434
5z	0.084	0.184	-0.202	18z	0.296	0.336	0.211
6x	**-0.457**	**-0.607**	-0.371	19x	-0.257	-0.231	**-0.654**
6y	**0.651**	0.265	0.261	19y	-0.461	-0.228	-0.337
6z	0.396	0.257	**0.525**	19z	0.199	0.214	0.146
7x	0.493	**0.627**	0.153	20x	-0.057	0.178	**0.737**
7y	**0.591**	0.339	-0.170	20y	**0.574**	**0.564**	-0.039
7z	0.190	0.484	0.410	20z	0.034	0.159	0.169

Land mark	PC1 (15.4%)	PC2 (13.8%)	PC3 (12.4%)	Land mark	PC1 (15.4%)	PC2 (13.8%)	PC3 (12.4%)
8x	0.065	0.225	**0.871**	21x	-0.107	-0.199	**0.810**
8y	**0.793**	0.220	-0.041	21y	**0.545**	0.235	0.465
8z	0.113	**0.694**	-0.120	21z	0.005	0.192	-0.103
9x	**0.747**	0.220	0.258	22x	0.056	-0.389	0.380
9y	-0.302	0.002	-0.172	22y	0.283	-0.111	**0.772**
9z	-0.188	0.106	0.448	22z	0.327	**0.645**	0.180
10x	0.432	0.166	**0.636**	23x	-0.164	-0.218	**0.655**
10y	**0.831**	-0.177	-0.023	23y	0.424	0.152	**0.623**
10z	**0.641**	**0.517**	0.090	23z	-0.057	0.203	-0.046
11x	**0.799**	0.243	0.277	24x	-0.319	0.008	-0.177
11y	-0.154	-0.053	-0.084	24y	-0.190	0.261	-0.114
11z	0.119	0.217	0.287	24z	0.196	0.450	-0.084
12x	**0.831**	0.069	0.194	25x	0.240	0.387	**0.718**
12y	-0.152	-0.119	-0.175	25y	0.485	-0.067	0.359
12z	0.325	0.479	0.042	25z	0.114	0.491	0.094
13x	0.468	0.228	-0.077	26x	-0.141	**-0.659**	0.028
13y	**-0.703**	-0.145	-0.101	26y	0.016	0.128	**0.851**
13z	0.176	0.376	0.148	26z	-0.073	0.004	0.181

Extraction Method: Principal Component Analysis.
Rotation Method: Varimax with Kaiser Normalization.

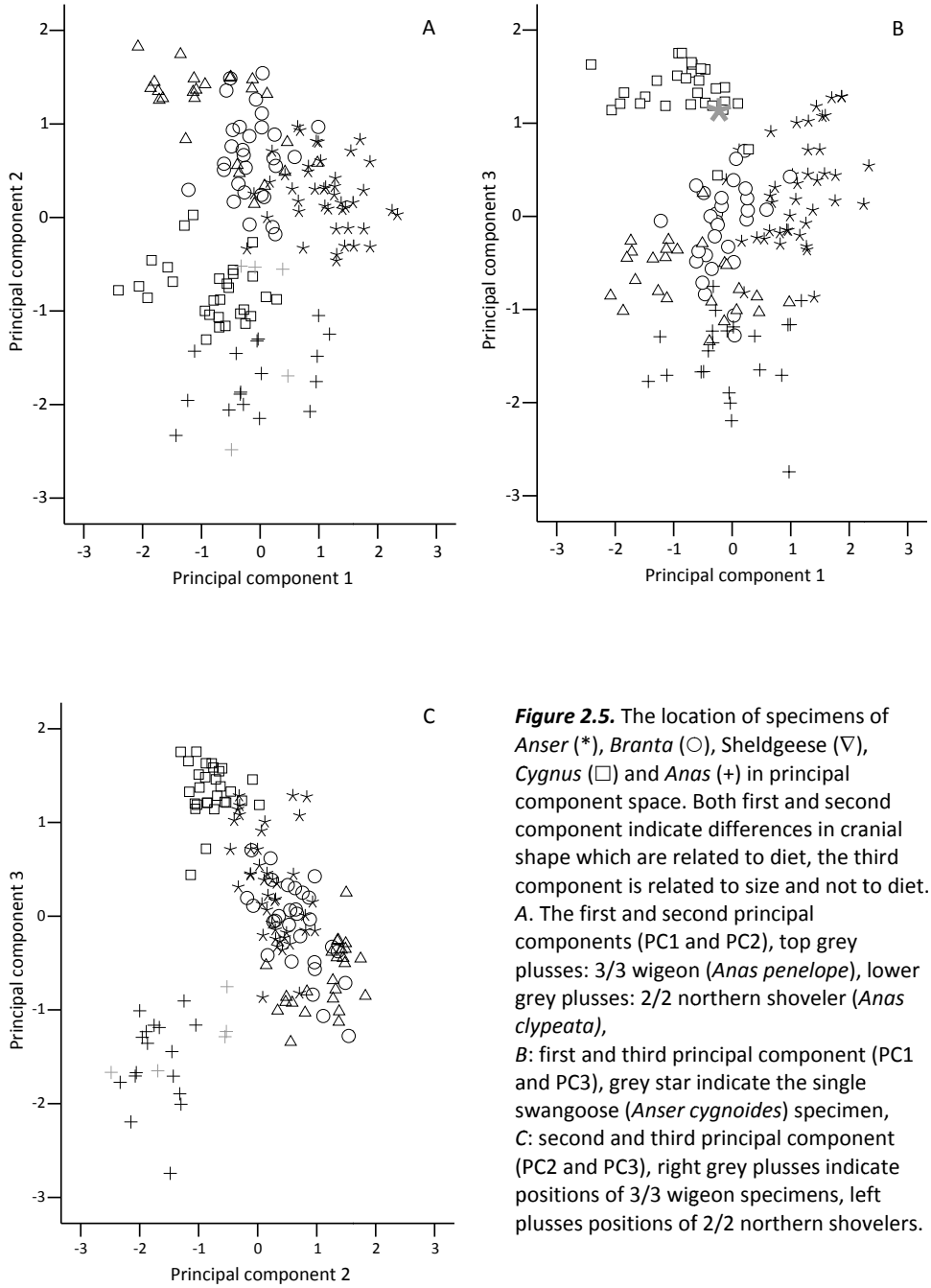


Figure 2.5. The location of specimens of *Anser* (*), *Branta* (○), Sheldgeese (▽), *Cygnus* (□) and *Anas* (+) in principal component space. Both first and second component indicate differences in cranial shape which are related to diet, the third component is related to size and not to diet. *A*. The first and second principal components (PC1 and PC2), top grey plusses: 3/3 wigeon (*Anas penelope*), lower grey plusses: 2/2 northern shoveler (*Anas clypeata)*,
B: first and third principal component (PC1 and PC3), grey star indicate the single swangoose (*Anser cygnoides*) specimen,
C: second and third principal component (PC2 and PC3), right grey plusses indicate positions of 3/3 wigeon specimens, left plusses positions of 2/2 northern shovelers.

For the first two PC's the factor scores were not correlated with centroid size (r = -0.298, n = 35, p = 0.096 and r = -0.182, n = 35, p = 0.296 respectively), but a significant negative correlation was found for the third PC (r = -0.805, n = 35, p = 0.000), indicating an allometric effect on shape.

Species with high positive scores on the first PC tend to have a relatively high and short neurocranium, a high upper beak and a more dorsal position of the orbit. Landmarks with high loadings for height on PC1 are the highest point on the neurocranium (20y), both landmarks indicating the orbit (7y and 8y), the craniofacial hinge (6y), both the base (25y) and the tip (10y) of the postorbital process, and the landmarks indicating the back of the skull (21y, 23y). Other high loadings for height on this axis indicate a relatively long quadrate (e.g., a more ventral position of the quadratomandibular joint (17y and 18y), the pterygoid-quadrate (13y) and the jugal-quadrate joints (19y)), and a high upper beak (e.g., a more ventral position of the vomer (5y) and the palatine-maxilla joint (4y), and a more dorsad position of the craniofacial hinge).
The skull is shorter due to more caudal positions of the landmarks representing the connections of the cranium and bill. High loadings on PC1 are found for the rostro-caudal position of both jugal-maxilla (3x) and palatine-maxilla (4x) joints, and the craniofacial hinge (6x).
More caudally, the position of the palatine-pterygoid joint (9x), both landmarks indicating the position of the basipterygoid articulation with the pterygoid (11x and 12x), and the pterygoid-quadrate joint (13x) vary in a direction opposite to the direction of the rostral cranial landmarks. Consequently, the length of the palatine varies with skull length, while the length of the pterygoid remains more or less the same along PC1. Only two landmarks have high scores for the z-coordinate, the jugal-maxilla joint (3z) and the tip of the postorbital process (10z).

Among the species with the highest PC1 scores (high and short skull, with a high upper beak) are most species of the genus *Anser*. Many sheldgeese species have low scores on PC1 (figure 2.5A). *Branta*, *Cygnus* and *Anas* species take a more intermediate position on this axis. Note the relative position of the wigeon along PC1, which is not very different from many *Anser* species.

A nested ANOVA performed on the factor scores showed significant differences between groups. To identify which anseriform groups differ significantly Bonferroni corrected post-hoc tests based on the mean factor score of each species for PC1 are performed (table 2.6).
Significant differences are present between *Anser* and *Cygnus* and between *Anser* and sheldgeese. Tukey's homogenous subsets give two sets: *Cygnus*, sheldgeese, *Branta* and *Anas*, and *Anas* and *Anser.*

PC2 is characterized by high loadings of the landmarks of the bill and the width of the skull. The birds are characterized by variation in the length and width of the beak, differences in the angle between the beak and neurocranium, a more caudal position of the craniofacial hinge, and the width of the cranium. Variation in bill length and width, and the angle of the bill with the cranium are described by the position of the bill tip (1x, 1y) and the coordinates of the landmarks just behind the bill tip (2x, 2y, 2z). The rostro-caudal

position of both the vomer-maxilla connection (5x), the craniofacial hinge (6x), and the height of the skull (20y) covary with bill length (1x).

Other PC2 related landmarks represent the width of the skull at the orbit (7z and 8z), at the postorbital process (10z, 25z), and caudally at the most lateral point of the crista nuchalis transversa (22z). The occipital processes (23z, 24z) and the coordinates indicating the lateral position of the quadrate (15z, 16z, 17z, 18z, 13z, 19z) all show relatively low loadings on PC2. Although there are significant differences between groups for all these quadrate landmarks, the increase in width is only 0.6 times the increase of the other cranial landmarks.
Other landmarks that vary along PC2 are the rostro-caudal position of the rostral corner of the orbit (7x) and occipital condyle (26x), and the height of both otical processes of the quadrate (15y and 16y), and the length of the orbital process of the quadrate (14x).

Sheldgeese and most species of both *Anser* and *Branta* have positive scores on the axis described by PC2. These species are characterized by a shorter and a more ventral pointing and narrower maxilla, a more caudal position of the craniofacial hinge and occipital condyle. Furthermore, the most caudal and rostral part of the cranium is wider. Ducks and swans show negative scores on PC2. The most extreme positions are held by the specialized filter-feeding ducks. Note that the three wigeon specimens have less negative values than most swan specimens (figure 2.5A and 2.5C).

Table 2.6. Mean score per anseriform group per principal component and post-hoc comparisons of mean scores. Numbers in bold indicate significant difference at the 0.05 level.

		PC1		PC2		PC3	
		Mean difference	(std error)	Mean difference	(std error)	Mean difference	(std error)
Anser	*Branta*	1.01	(0.33)	-0.467	(0.22)	0.40	(0.21)
	Cygnus	**1.67**	(0.30)	**1.00**	(0.20)	**-1.04**	(0.19)
	sheldgeese	**1.51**	(0.30)	**-0.77**	(0.20)	**1.04**	(0.19)
	Anas	0.85	(0.32)	**1.78**	(0.21)	**1.78**	(0.20)
Branta	*Cygnus*	0.66	(0.36)	**1.45**	(0.23)	**-1.44**	(0.22)
	sheldgeese	0.50	(0.36)	-0.31	(0.23)	0.64	(0.22)
	Anas	-0.16	(0.37)	**2.23**	(0.24)	**1.38**	(0.23)
Cygnus	sheldgeese	-0.160	(0.33)	**-1.76**	(0.21)	**2.08**	(0.20)
	Anas	-0.821	(0.34)	**0.78**	(0.22)	**2.82**	(0.21)
Sheldgeese	*Anas*	-0.661	(0.34)	**2.55**	(0.22)	**0.75**	(0.21)

A nested ANOVA performed on the factor scores showed significant differences between groups. Bonferroni corrected post-hoc tests on the mean factor score of each species show that for PC2 both *Cygnus* and *Anas* are different from each other and all other groups, while *Anser* and *Branta*, and *Branta* and sheldgeese do not differ on this axis (table 2.6). Tukey's homogenous subsets gives four sets: *Anas*, *Cygnus*, *Anser* and *Branta* and *Branta* and sheldgeese.

The shape differences along PC3 describe differences in the shape of the back of the head, which involve rostro-caudal positions as well as the height of landmarks. PC3 also has the highest loading on the width of the craniofacial hinge.
Variation is found in rostro-caudal positions of the landmarks indicating the caudal corner of the orbit (8x), the most dorsal point of the crista nuchalis transversa (21x), the highest point on the skull (20x) and the most caudal point of the skull on the prominentia cerebellaris (23x), and for the base and tip of the postorbital process (25x, 10x). Differences in height coordinates are found at the posterior part of the skull, the occipital condyle (26y), the most rostral point of the crista nuchalis transversa (22y) and the most caudal point on the prominentia cerebellaris (23y). The lateral side of the quadrate shows a rostro-caudad shift (18x, 19x), and the quadratocranial joints a dorso-ventrad shift. Note, however, that the effects are very small, and also partly described by PC1. Width-coordinates of the craniofacial joint (6z) are related to this PC as well.

Cygnus species have high scores on PC3 and are characterized by a relatively broad craniofacial hinge and a short but high neurocranium, with a more rostrad position of landmarks on the caudad part on the skull, the caudal corner of the eye and postorbital process (small eye), and the base of the occipital condyle. As may be expected from the correlation between factor score and body size *Anas* species have the most negative scores on PC3. Sheldgeese, *Branta* and *Anser* specimens occupy intermediate positions.

A nested ANOVA on the factor scores showed significant differences between groups. Bonferroni corrected post-hoc tests based on the mean factor score of each species, show that for PC3 both *Cygnus* and *Anas* are different from all other groups, while *Anser* and *Branta*, and *Bran*ta and sheldgeese do not differ on this axis (table 2.6). Tukey's homogenous subsets gives four sets: *Anas*, sheldgeese, *Branta* and *Anser*, and *Cygnus*.

Phenetic clustering

To illustrate the overall similarity between species two phenetic trees were created using the UPGMA-method based on Euclidean distances between Procrustus fitted landmarks, one including and one excluding the landmarks of the bills. Both trees are given in figure 2.6.
Using all ipsilateral landmarks, the specialized filter-feeding ducks are different from all other measured anatid species, including mallard and wigeon. Within the remaining species two other groups may be recognized, a goose-like and a swan-like group. The swan-like group comprises all *Cygnus* species, the one *Anser cygnoides* specimen, and all specimens of *Anas platyrhynchos* and *Anas penelope*. The goose-like group comprises two subgroups: one is formed by the *Chloephaga* sheldgeese species and the other by all remaining *Anser*, *Branta* and sheldgeese species.

Omitting the landmarks of the bill, the neurocranium landmarks yield a somewhat different tree. Two large groups are formed, a duck-swan group and a group consisting of all but one of the true geese species. Within the duck-swan group four out of the seven sheldgeese species cluster with *Anas platyrhynchos* and *Anas penelope. Anser cygnoides* is more similar to the swans than to the other geese. The filter-feeding specialists form a separate subgroup. The goose-like group comprises all *Anser*, (except *A. cygnoides*) and *Branta*.

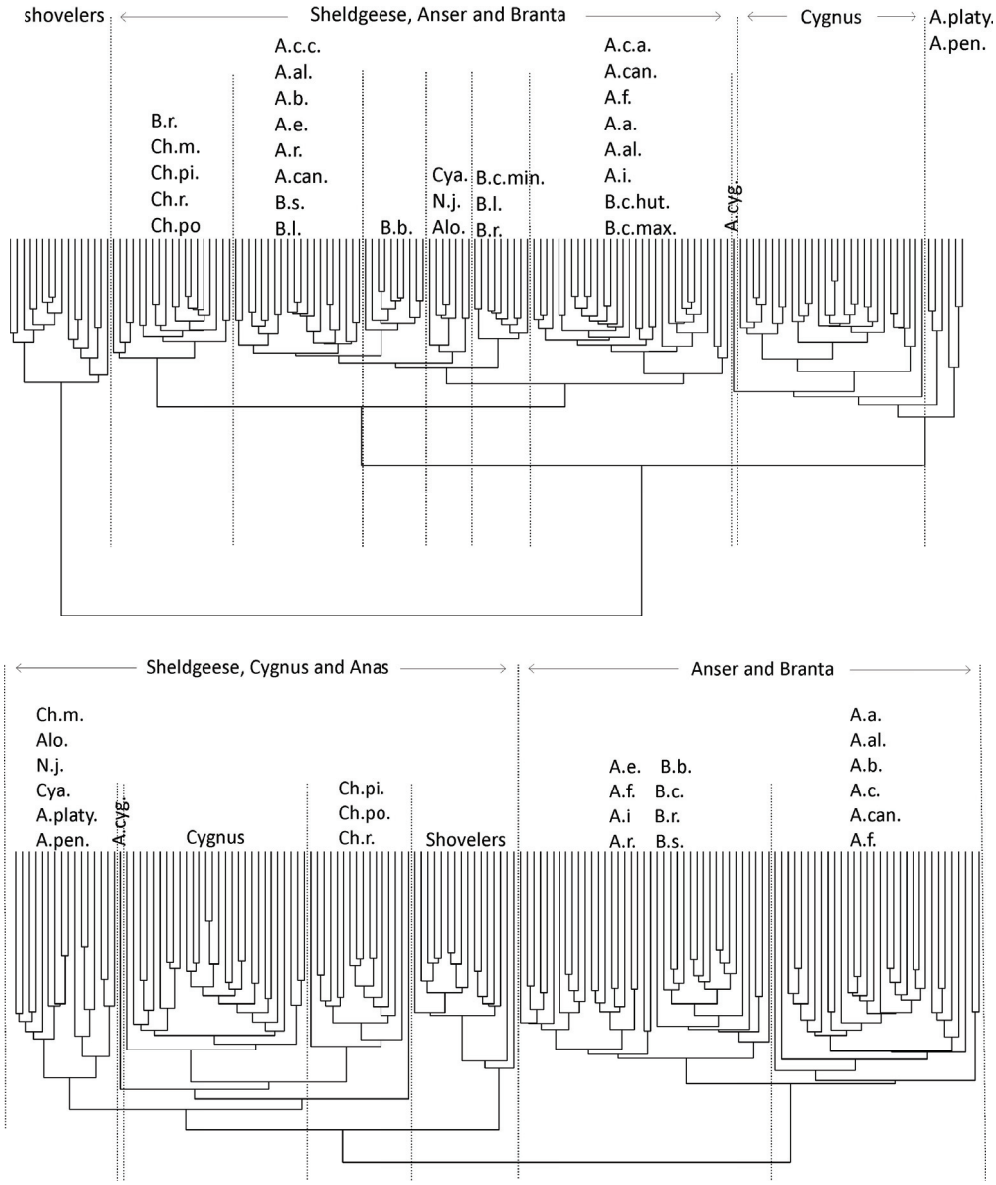


Figure 2.6. Phenetic trees of studied anatid species based on UPGMA clustering of Procrustes fitted coordinates. The tree in the upper panel is based on all ipsilateral cranial landmarks; the tree in the lower panel is based on the same set of landmarks, but without the bill. Abbreviations: A.a: *Anser anser*, A.al: *Anser albifrons*, A.b: *Anser brachyrhynchus*, A.c.a*: Anser caerulescens atlantica*, A.c.c: *Anser caerulescens caerulescens*, A.can: *Anser canagicus*, A. cyg: *Anser cygnoides*, A.e: *Anser erythropus*, A.f: *Anser fabalis*, A.i: *Anser indicus*, A.pen: *Anas penelope*, A.platy: *Anas platyrhynchos*, A.r: *Anser rossi*, B.b: *Branta bernicla*, B.c.max: *Branta canadensis maxima*, B.c.hut: *Branta Canadensis hutchinsii*, B.c.min: *Branta canadensis minima*, B.l: *Branta leucopsis*, B.r: *Branta ruficollis*, B.s: *Branta sandvicensis*, Ch.m: *Chloephaga melanoptera*, Ch.pi: *Chloephaga picta*, Ch.po: *Chloephaga poliocephala*, Ch.r: *Chloephaga rubidiceps*, Cya.: *Cyanochen cyanochen*, N.j: *Neochen jubata*.

Discussion

Feeding specializations such as herbivory are an example of convergent and adaptive evolution (e.g. Westneat et al., 2005; Pérez-Barbería and Gordon, 1999). In the present study we focus on cranial adaptations to grazing in waterfowl. To identify adaptations to grazing several anatid species are compared, including filter-feeding specialists of the genus *Anas*.

Grazing in anatids involves the coordinated action of the jaw and neck system. During grazing a bite of grass is severed by a short pulling movement from the top of the neck and head. Differences in bite size or strength of the plants may be related to differences in head and neck morphology. During the grazing movement grass must be clamped firmly between the bills so that the grass will snap off, rather than be pulled out of the bill. Furthermore, the backward movement of the head will result in forces that elevate the upper bill, which is moveable with respect to the neurocranium (figure 2.7).

In studies on a number of dietary specialists bite force appears to be directly related to differences in cranial structure (Van Cakenberghe et al., 2002; Pérez-Barbería and Gordon, 1999; Courant et al., 1997; Herrel et al., 2002; Wainwright et al., 2004; van der Meij, 2004; Herrel et al., 2005a). There are different ways in which evolution may modify bite force produced by the adductor and pterygoid muscles of the jaw apparatus. Bite or pulling force may be increased by larger muscles (cross sectional area), but also by a large angle of attachment, or a relatively long power arm (the distance between quadrate-mandibular articulation and the attachment of the muscle) and a short work arm (the distance from the tip of the mandible to the pivot) (figure 2.7). Increasing the mechanical advantage of the jaw adductors results in the ability to produce high bite forces or to produce a given bite force with less muscular effort. On the other hand, relatively long power arms decrease the closing speed of the jaws, and may therefore affect the efficiency of other feeding mechanisms, e.g., filter-feeding.

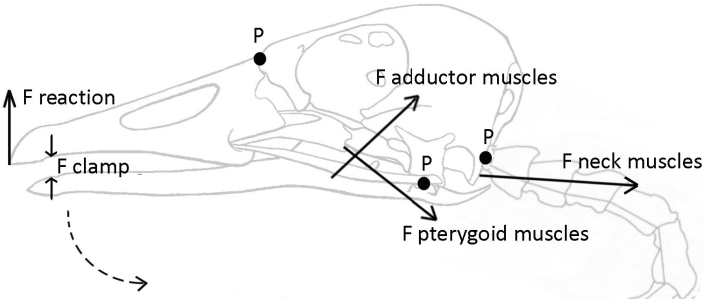


Figure 2.7. Schematic representation of forces and lever systems of the head and jaws involved in grazing. The dotted arrow indicate direction of movement when severing vegetation (i.e. pull). This downward rotation of the head is realized by the neck muscles (m. rectus capitus). As a result the vegetation exerts an upward reaction force onto the upper bill, which is counteracted by the jaw muscles. In order to clamp the vegetation tightly between the bills to prevent slipping, both adductor and pterygoid muscles forces are needed. P: pivot, F: force.

Although neck movement in birds is complicated (Bout, 1997; Van der Leeuw et al., 2001), the rotation of the head on top of the neck may also be described by a simple lever system (figure 2.7). In this system the rectus capitus muscle, which attaches to the basicranium (basitemporal plate), rotates the head around the occipital condyle downwards during the pulling movement of grazing. As the overall design of the craniocervical system limits the variation in the length of the (relatively short) power arm, the relative length of the work arm (basically head length) may be expected to determine the mechanical advantage of the system.

In the present study the PCA analysis suggests that bill length and neurocranial length are independent (PC1 and PC2). The first principal component (PC1) describes the covariation between length and height of the neurocranium. However, the variation in length of the neurocranium is almost completely the result of the variation in position of the craniofacial hinge. The rostrocaudal position of the vomer-maxilla connection, and the position of the connection between the bill and jugal and palatine vary very little. With respect to the efficient transfer of pulling force the variation in cranium length seems therefore immaterial, because head length does not change. The relationship between neurocranial length and height results from the fact that our definition of cranium length involves the relatively variable position of the craniofacial hinge, rather than, for instance, the connection between palatine and upper beak.
The second principal component relates the variation in bill length independent of the position of the craniofacial hinge ('cranium length'), to bill width and vertical position of the bill tip, and to the width of the (caudal part) of the cranium. In short bills the tip of the bill is narrower and is pointing more to ventral than in long bills.

For the second PC a relationship between skull shape and main feeding technique seems evident. Specialized filter-feeding ducks are characterized by a long, broad bill, while the grazing *Anser*, *Branta* and especially sheldgeese species have relatively short and narrow bills. *Cygnus* species occupy an intermediate position. It has been shown that in filter-feeding species a long, wide bill allows a larger body of water to enter the bill and more food particles can be pumped through the bill per unit of time (chapter 5). The terrestrial grazing species (*Anser*, *Branta*, and sheldgeese) have short bills, which increases both the force exerted by the neck muscles on the grass during pulling and bite force at the tip of the beak. Relative bill length is approximately 60% shorter in sheldgeese than in the *Anas* species, which reduce the work arm of the pulling force by a factor 1.3. In some grazing species, the work arm may be further reduced by taking vegetation between the edges of the bill instead of at the tip (Cope et al., 2005). Why grazing species should have more ventrally directed bills is less evident, but static force modelling in finches has shown that a more ventrally directed beak increases bite force (van der Meij, 2004).

In a study comparing insectivorous and omnivorous (partly herbivorous) lizards, only shape related modifications in the neurocranial part of the skull were found, but no changes in the jaw lever system (Herrel et al., 2004). On the other hand, studies on avian clades demonstrated high evolutionary flexibility of bill morphology (Grant, 1986; Lovette et al., 2002), as found in the present study. Avian neurocranial shape is less well studied but width of the skull proved to be a better predictor for bite force than head length in Darwin's finches (Herrel et al., 2005b).

There is a less evident relationship between the variation in characters and feeding mechanism for the first PC. However, variation in the position of the craniofacial hinge may be expected to affect the efficiency of the upper jaw closer muscles. During grazing an external force exerted by the grass acts to lift the upper bill and must be resisted (see above). Static 2D force modelling of a mallard skull suggests that the maximal external force (acting at the tip of the bill and perpendicular to its length axis) that a mallard is able to resist increases (1.2 times) as the craniofacial hinge is moved to an *Anser*-like position. This effect is much smaller than the effect of shortening the length of the bill. When bill length in the model is reduced by 60% the maximum external force at the bill tip that may be resisted by the jaw muscles increases 4.8 times.

Because of the tapered shape of the frontal bone a caudal shift of the hinge will also increase its width. A wider craniofacial hinge may be necessary to resist larger reaction forces in the hinge during grazing. This is again demonstrated by static 2D modelling. Filter-feeding may be represented by a closed beak at a maximum closing force. When an external force is applied at the upper bill to simulate the grazing situation, maximum closing force generates reaction forces in the craniofacial hinge that are 1.3 times higher than without external force. As a more robust construction of the hinge would interfere with movement of the upper jaw, the width and position of the kinetic hinge may therefore be an adaptation to grazing. Filter-feeding specialists have a very narrow hinge, while *Anas* species that graze (wigeon, mallard) have a hinge width that is comparable to the hinge width of sheldgeese. Note that in grazing anatids there is not only a dorsad shift of the craniofacial hinge causing a deepening of the maxilla, but also a correlated lateral shift of the jugals (PC1), resulting in a wider bill. Beak width and depth have been shown to correlate positively with bite force in studies on finches (Herrel et al., 2005b; Herrel et al., 2005a; van der Meij, 2004).

Much of the variation in hinge width is described by PC1 but there is also a contribution of PC3, which combines differences in height and rostro-caudal position of landmarks at the back of the skull with the rostro-caudal position and width at the craniofacial connection. As this variation described by PC3 is related to allometric differences, PC1 seems to describe additional variation, not related to body size. *Cygnus* species have a more rostral and less wide hinge width than may be expected for their body size, while in *Branta* the craniofacial hinge is relatively wider and situated more caudally.

While the variation of the craniofacial hinge may be interpreted as a contribution to the variation in bite force, the variation in height of the skull described by PC1 may be interpreted as a way to increase the available space for muscle tissue. Relative skull height is one of the morphological modifications reported to improve bite capacity in other vertebrates (Stayton, 2005; Herrel et al., 1999; Herrel et al., 2001; Claude et al., 2004; Herrel et al., 2004; Van Cakenberghe et al., 2002). Posterior to the orbit a higher skull may increase the available area for the attachment of adductor muscle fibers. According to this interpretation *Anser* and *Branta* species are expected to have large adductor muscles, while *Anas*, most *Cygnus* and some sheldgeese species should have relatively small muscles. However, an analysis of the jaw musculature in a number of anseriform species does not show a systematic difference in the size of the adductor muscles among groups (chapter 3). Alternatively, the increase in height of the cranium and the more dorsal

position of the eye results in more space between the eye and the palatine and pterygoid, as the pterygoid-palatine joint does not shift dorsad. This may increase the space available for either the part of the adductor complex just below the eye (m. pseudotemporalis superficialis), or the more ventrally situated pterygoid muscles. The increase in space is not occupied by a larger eye as relative eye size is similar in most groups, except in swans, which have relatively small eyes. Unlike the adductor muscles, the pterygoid muscles do differ in relative size among groups (chapter 3). However, only the *Branta* species differ from all other species and have relatively smaller and not larger pterygoid muscles, as one would expect.
The absence of a direct relationship between jaw muscle size and the differences in cranial morphology is also illustrated by the size of the depressor muscles. While aquatic feeding species (e.g., *Anas*) have larger depressor muscles than terrestrial grazers, the *Anas* species in our study have a narrower and lower cranium than grazing species (chapter 3).

As mentioned above the rectus capitus muscle rotates the head downwards during the pulling movement of grazing. This muscle attaches to the basicranium (basitemporal plate). The dorsoventral position of the occipital condyle in *Anser*, *Branta* and *Cygnus* may increase the area available for muscle attachment. However, Goodman and Fisher (1962) did not find any evidence for differences in relative neck muscles mass among anseriform species. As the dorsoventral position is related to body size (PC3) variation in the position of the occipital condyle may be related to differences in relative neck length, which also increases with body weight, and the way the head is positioned on top of the neck: more ventrally or more caudally (Van der Leeuw, 2002; Duym, 1951; Bookstein, 1996; Marugán-Lobón and Buscalioni, 2006).

An alternative explanation for some of the cranial differences among the trophic groups may be related to the reaction forces generated in the palatine and jugal connections with the upper bill during feeding. As the craniofacial hinge these connections are cartilaginous joints, which may be more prone to wear and failure than the synovial joints. Static 2D force modelling of a mallard skull suggests that grazing generates higher reaction forces in these joints than filter-feeding (see above). PC1 indicates that the rostrocaudal shift of the craniofacial hinge is accompanied by a shift of the joint between pterygoid and palatine: in *Anser* and *Branta* the pterygoid is relatively longer and the palatine is shorter than in *Anas*, *Cygnus* and sheldgeese. Interestingly, the same variation is found within *Anas*. While the straining specialists have the relatively shortest pterygoid of all measured species, the pterygoid of the partly grazing species, wigeon and mallard, is as long as the pterygoid of the true geese. Shortening the pterygoid of the mallard (and increasing the length of the palatine) in the static force model increases the relatively low reaction force in the palatine-maxilla connection, but decreases the high reaction forces in the jugal-maxilla connection at maximal bite force and no external force present. Whether such changes in reaction forces are related to (dominant) feeding habits remains to be seen and require estimates of true pulling and bite forces.

Differences in skull geometry are related to clearly different foraging techniques (e.g. filter-feeding vs. grazing), but there are also (quantitative) differences in skull geometry between herbivores of the two subfamilies Anatinae and Anserinae. If skull geometry has evolved along similar pathways to meet the mechanical demands of grazing one would

expect a large overlap between groups, as for instance found for two families of seed cracking finches (van der Meij, 2004). Alternatively, differences in skull geometry among different grazing groups may reflect differences in selection pressures related to different foraging habits, differences in constraints that influence the evolution of herbivory among groups, or the time of independent evolution.
Phylogenetic analyses (Madsen et al., 1988; Sraml et al., 1996; Donne-Goussé et al., 2002; Sorenson et al., 1999; Livezey, 1997a) suggest the following succession of trophic specialisations. From a common, possibly aquatic feeding ancestor (Van der Leeuw et al., 2003; Zweers and Vanden Berge, 1997) two groups originated: the Anserinae (*Anser, Branta* and *Cygnus*), and the Anatinae, duck-like birds. The geese of the Anserinae are all terrestrial grazers. Subsequently, specialized grazing species have diverged within the Anatinae clade. First the sheldgeese (*Chloephaga*, *Alopochen*, *Neochen* and *Cyanochen*) and last, within the genus of dabbling ducks (*Anas*), the wigeon (*Anas penelope*). Within each group generalist species that use several foraging techniques may be present (e.g. mallard), but often detailed ecological knowledge on the relative importance of different foraging techniques is not available.
Within the phylogenetically oldest group, the true geese, no sharp distinction between *Anser* and *Branta* is found for cranial shape (figure 2.6). Both genera show relatively short bills with a narrow bill tip, a caudal shift and larger width of the kinetic hinge, a higher and wider skull, and a relatively longer pterygoid and shorter palatine than filter-feeding specialists. *Anser* shows most of these modifications more clearly than *Branta* species, but bill length is relatively longer than in *Branta* or sheldgeese species. Although species of both the *Anser* and *Branta* genus exploit above ground plant parts, i.e. grazing (Weller, 1964; Owen, 1980), most *Anser* species forage on underground plant parts as well, i.e. grubbing (e.g. Aerts et al., 1996; Alisauskas and Ankney, 1992; Budeau et al., 1991; Eisenhauer and Kirkpatrick, 1977; Gauthier, 1993; Mayes, 1991; Zhang and Liu, 1999). Grubbing refers to the tearing out by the bill of tubers, rhizomes and other underground parts of plants growing in wet soil (Glazener, 1946). This feeding technique may require longer bills for probing the wet soil. The swan goose is a remarkable exception within the *Anser* genus. The foraging habits of the swan goose seem to be similar to that of other *Anser* species, and it is even known to use grubbing (see http://www.birdskorea.org/Birds/Significant_Records/New_Birds/BK-NB-Bar-headed-Goose.shtml). The head, however, does not show the characters for grazing very clearly, and is more similar to the head of swans than to geese in the phenetic analyses.

Compared to filter-feeding specialists, swans show the same modifications in cranial morphology as the true geese, but to a lesser extent. In the phenetic analyses swans cluster with *Anas* and sheldgeese species, rather than the true geese. This may be due to the fact that their main feeding technique is different from geese. Swans tear off parts of aquatic plants (Grant et al., 1994; Gillham, 1956; Earnst and Rothe, 2004; Chisholm and Spray, 2002; Earnst, 2002; Bollinger and King, 2002), which are subsequently strained out of the water (pers. obs.). Although tensile strength does not differ for aquatic and terrestrial plants (Henry et al., 1996; Zhang et al., 2004; Schutten et al., 2005), the lower bulk density of submerged vegetation involves smaller bites with accompanying smaller bite forces. The effect of an increase in body size on bite force might thus be sufficient for aquatic grazing. Yet, some swan species include terrestrial vegetation in their diet (Grant et al., 1994; Gillham, 1956; Petrie et al., 2002; Crawley and Bolen, 2002; Colhoun and Day,

2002; Chisholm and Spray, 2002; Earnst, 2002), and most, if not all, species are able to feed on swards in aviculture. Moreover, in a separate study we found that intake rates on grass scaled to metabolic need is very similar in mute swan and goose species (chapter 4).

Sheldgeese branched off earlier within the Anatinae subfamily than the wigeon (Sraml et al., 1996; Donne-Goussé et al., 2002; Sorenson et al., 1999)). These terrestrial grazing birds (Summers and Grieve, 1982; Summers, 1985; Kriese, 2005) show a different balance of characters related to grazing than geese. The cranial characters (e.g. position of the craniofacial hinge, the length of pterygoid and palatine, and skull height and width) are often more similar to (grazing) *Anas* species than to geese (figure 2.6, lower panel), while the bill of sheldgeese is the shortest of all grazing species.
The most recently specialized grazer is the wigeon (Rijnsdorp, 1986; Owen and Thomas, 1979). The cranial characters of the wigeon are similar to those of sheldgeese, but the length of the bill is relatively longer.
The efficiency of grazing in sheldgeese is not known, however in the wigeon the scaled intake rate is lower than the intake rate in a number of geese and swan species (chapter 4).

Considering the differences in the amount of time grazing anatid species have had to develop adaptations to grazing, some characters appear to be more apt to modification than others. Bill characters tend to change faster than the position of the craniofacial hinge and height of the skull, as species evolve towards a grazing life style. A high evolutionary flexibility in bill morphology may be an intrinsic, clade-specific trait (Lovette et al., 2002), and may also differ for different characters within the same species. Whether apparent differences in flexibility are intrinsic or reflect differences in the contribution of characters to the efficient use of resources remains to be seen.

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Chapter 3

Jaw muscle size in aquatic and terrestrial feeding wildfowl

Summary

Wildfowl exploit many trophic resources ranging from filter-feeding small aquatic food items to terrestrial grazing. Aquatic feeding birds usually feed with their bills submerged and especially in filter-feeding species with fast repetitive bill movement. Under water such movements may generate resisting forces that are much larger than for terrestrial feeders. To investigate possible differences in muscle size related to the environment in which species forage we categorized a number of anseriform species as aquatic or terrestrial feeders based on literature data and determined the mass of several functionally different jaw muscle groups.

We found that total jaw muscle mass scales negatively allometric with respect to body mass in both trophic groups. The exponent is the same for aquatic and terrestrial feeders, but total jaw muscle mass are 1.5 times higher in aquatic feeding species. Not all muscle groups contribute to the difference in total jaw muscle mass. The openers of the lower jaw, the openers of the upper jaw and the pterygoid muscles (closers of upper and lower jaw) are larger in aquatic than in terrestrial feeding species. No differences are found for the two remaining jaw-closing muscle groups.

The jaw opener muscle groups of aquatic feeding anatids were also heavier when compared to a sample of non-anseriform birds, which did not differ from anseriform terrestrial feeders. The pterygoid muscles, however, were much larger in the non-anseriform birds than in both anseriform groups.

As the bill of aquatic feeders is larger than in terrestrial feeders the difference in relative size of the jaw opener muscles cannot be simply explained as an adaptation to large resisting forces in an aquatic environment. Longer and wider bills result in a larger moment of inertia. If angular acceleration and density of the environment remain the same, having a larger bill also requires larger jaw opener muscles. The difference in size of the jaw opener muscles is estimated to be approximately sufficient to compensate for the difference in bill size and there is no indication that muscle size increases to compensate for the larger resisting forces in an aquatic environment.

Introduction

Wildfowl (ducks, geese and swans) exploit many trophic resources ranging from filter-feeding small aquatic food items to terrestrial grazing. These two extremes are characterized by different types of food as well as a different environment in which food has to be secured by and transported through the bill. Both require a specific morphology of the jaw apparatus. Terrestrial grazers, for instance, use short spines on the roof of the mouth to transport vegetation, while filter-feeders require a bold lining of the oral cavity to generate a waterflow through the mouth using their tongue, which is pressed against the roof of the mouth and acts as a piston (Van der Leeuw et al., 2003; Kooloos et al., 1989; Zweers et al., 1977). Similarly, the bill is shorter and narrower in terrestrial grazers than in filter-feeders, resulting theoretically in higher bite and pulling forces in grazers (chapter 2 and chapter 3), but a larger volume pumped through the beak per movement cycle in filter-feeders (Van der Leeuw et al., 2003 and chapter 6). These differences in trophic morphology, in turn, are reflected in foraging performance. Species specialized in terrestrial grazing have a low performance for filter-feeding, while in species with a high filter-feeding performance the inefficient transport of grazed vegetation through the bill results in a low intake rate (Van der Leeuw et al., 2003; chapter 5, chapter 6).

Not only bill and tongue morphology may be related to resource use but jaw muscle size may be expected to be associated with resource use as well. In filter-feeding species the jaws open and close at a high rate, up to a frequency of 20 Hz (Kooloos et al., 1989). Forces acting on a moving bill under water are drag force plus acceleration reaction forces. The reaction forces consists of the force required to accelerate the mass of the moving part of the beak plus the force required to accelerate an added mass of water moving with the beak. The forces generated during bill movements in water may be of importance; especially since the bill surface area of filter-feeders is relatively large. Such resisting forces are much less or absent in terrestrial grazers, which also open and close the bill at a much lower rate, up to maximal 2 Hz for the barnacle goose on short pasture (Durant et al., 2003). One may therefore expect larger opening muscles in aquatic feeding species than in terrestrial grazers. Whether aquatic versus terrestrial feeding also affects the size of jaw closers is less clear. In grazing a forceful closure of the bill is necessary to hold grass firmly in the bill so that when the head and neck are drawn backwards, the grass will snap off, rather than be pulled out of the bill. The backward movement of the head results in forces that elevate the upper bill, which is moveable with respect to the neurocranium. On the other hand aquatic feeders have to push water out off their beak during closing. To investigate possible differences in muscle size between aquatic and terrestrial feeders we categorized a number of anseriform species as aquatic feeder or terrestrial grazer based on literature data on their foraging habits. The aquatic feeding group was not limited to filter-feeders but also included species feeding on larger items such as water plants, molluscs, fish, etc. A regression analysis was used to evaluate differences in muscle size between the two groups.

Material and Methods

Assignment of species to trophic group are based on literature data and are listed in table 3.1 (Austin et al., 1998; Drilling et al., 2002; Dubowy, 1996; Dugger et al., 1994; Eadie et al., 1995; Hohman and Lee, 2001; James and Thompson, 2001; Johnson, 1995; Kear, 2005; Mallory and Metz, 1999; Mowbray, 1999; Mowbray, 2002; Mowbray et al., 2000; Mowbray et al., 2002; Petersen et al., 1994; Reed et al., 1998; Robertson and Savard, 2002; Rylander and Bolen, 1974; Savard et al., 1998).

Complete specimen or loose heads of 34 species of Anseriformes were obtained from a commercial supplier. After determining body mass (g) the jaw muscles were dissected from one side of the head and weighed (mg) on a balance (Sartorius, H51, Göttingen, Germany). When just the head was available body mass was taken from the literature. The jaw muscles were subdivided into five groups: the adductors (closers) of the mandible, the depressors (openers) of the mandible, the protractors of the quadrate and pterygoid, which act as openers of the upper jaw, and two groups (the pterygoid muscles and the adductors originating on the quadrate) that are able to close both jaws. Although each of these muscle complexes encompasses several distinct muscles (figure 3.1 and Zweers, 1974) muscles with similar lines of action were taken to form a single functional unit.

To increase our data-set we included some of the species that were not already in our own data set from the study by Goodman and Fisher (1962). All species used in the analyses are given in table 3.1.
To allow a comparison between the data on Anseriformes and non-anseriform birds we also used previously published data on jaw muscle mass of 16 bird species with body mass ranging from 12 to 12000 g (Burger, 1978; van der Meij and Bout, 2004).

Table 3.1. Jaw muscle weights of wildfowl species examined.

Species	Common name	trophic group	body mass (g)	adductor muscles (mg)	quadrate adductor muscles (mg)	pterygoid muscles (mg)	protractor muscles (mg)	depressor muscles (mg)
Anas specularis	Spectacled duck	aquatic	1134.0	1298.6	426.5	694.5	227.1	1091.5
Anas hottentota	Hottentot teal	aquatic	200.0	223.6	69.7	116.5	56.1	268.7
*Anas carolinensis**	Green-winged teal	aquatic	350.0	291.0	67.0	128.0	97.0	316.0
Anas platyrhynchos	Mallard	aquatic	1206.0	1375.8	404.1	641.9	377.1	1757.4
Anas rhynchotis	Australian shoveler	aquatic	320.0	267.3	87.3	168.4	60.6	293.5
*Anas clypeata**	Northern shoveler	aquatic	735.0	254.0	93.0	172.0	154.0	479.0
Anas formosa	Baikal teal	aquatic	320.0	481.1	117.6	228.9	105.8	432.4
Anas bahamensis	White-cheeked pintail	aquatic	440.0	469.7	127.4	165.0	99.9	435.1
Anas americana	American wigeon	terrestrial	740.0	439.4	134.1	205.1	83.9	245.9
*Aythya affinis**	Lesser scaup	aquatic	825.0	498.0	128.0	279.0	193.0	637.0
*Aythya valisneria**	Canvasback	aquatic	1178.0	932.0	244.0	529.0	414.0	1458.0
Aythya nyroca	Ferrugineous duck	aquatic	520.0	487.9	104.3	192.7	78.3	448.5
Anser anser	Greylag goose	terrestrial	4204.0	3919.2	839.3	1762.2	430.0	1233.1
Anser indicus juv	Bar-headed goose	terrestrial	1140.0	928.6	339.2	545.3	122.8	411.7
Anser erythropus	Lesser white-fronted goose	terrestrial	1640.0	909.9	264.5	422.7	106.9	372.3
Anser caerulescens	Snow goose	terrestrial	3900.0	3808.5	915.8	1462.9	540.2	1455.3
Anser cygnoides	Swan goose	terrestrial	2800.0	2752.0	796.6	1567.4	303.4	1025.2
Anser canagicus juv	Emperor goose	terrestrial	1060.0	1231.4	308.6	596.9	151.7	539.6
Branta canadensis	Canada goose	terrestrial	3480.0	2388.5	550.4	743.6	236.8	617.5
*Branta bernicla nigricans**	Brent goose	terrestrial	1424.0	739.0	145.0	244.0	124.0	215.0
Branta ruficollis	Red-breasted goose	terrestrial	920.0	470.1	110.4	150.0	35.9	196.1
Branta leucopsis	Barnacle goose	terrestrial	1850.0	709.9	255.2	292.1	90.7	420.2

Species	Common name	trophic group	body mass (g)	adductor muscles (mg)	quadrate adductor muscles (mg)	pterygoid muscles (mg)	protractor muscles (mg)	depressor muscles (mg)
Chenonetta jubata	Maned duck	terrestrial	500.0	387.5	98.8	144.3	48.4	146.0
Neochen jubatus	Orinoco goose	terrestrial	1350.0	793.9	241.1	254.9	83.7	311.5
Alopochen aegypticus	Egyptian goose	terrestrial	1880.0	1271.3	324.4	558.9	163.8	791.0
Chloephaga hybrida *	Kelp goose	terrestrial	2324.0	791.0	266.0	486.0	174.0	441.0
Chloephaga poliocephala	Ashy-headed goose	terrestrial	720.0	348.7	146.7	173.1	41.0	172.0
*Bucephala clangula**	Common goldeneye	aquatic	906.0	573.0	130.0	278.0	168.0	931.0
*Clangula hyemalis**	Long-tailed duck	aquatic	725.0	565.0	136.0	286.0	141.0	786.0
Dendrocygna autumnalis	Black-bellied whistling-duck	terrestrial	620.0	823.9	195.7	384.9	179.9	516.7
Dendrocygna viduata	White-faced whistling-duck	aquatic	480.0	815.3	202.6	392.7	139.2	491.9
Dendrocygna eytoni	Plumed whistling-duck	terrestrial	780.0	918.5	251.2	359.4	125	471.1
Dendrocygna bicolor	Fulvous whistling-duck	aquatic	600.0	1211.3	234.4	576.2	186.6	619.6
*Melanitta perspicillata**	Surf scoter	aquatic	950.0	1226.0	310.0	556.0	255.0	1023.0
*Lophodytus cucullatus**	Hooded merganser	aquatic	610.0	477.0	78.0	317.0	72.0	355.0
*Mergus merganser**	Common merganser	aquatic	1400.0	1311.0	217.0	851.0	202.0	550.0
Tachyeres pteneres	Flightless steamer-duck	aquatic	2620.0	2587.8	830.8	1057.1	380.4	1606.6
Tadorna cana	South-african shelduck	aquatic	1660.0	1179.8	318.7	444.2	148.9	870.3
Tadorna ferruginea	Ruddy shelduck	aquatic	1460.0	724.0	249.0	376.8	147.8	649.6
Cygnus olor	Mute swan	aquatic	6780.0	3768.3	1213.8	1850.7	579.1	2570.2
Cygnus bewicki	Bewick's swan	aquatic	5100.0	3463.2	1221.1	1858.4	900.2	2915.9
Cygnus atratus	Black swan	aquatic	4880.0	2297.3	599.3	985.3	428.4	1354.3
Netta peposaca	Rosy-billed pochard	aquatic	910.0	1163.4	260.0	546.7	233.9	794.6
Netta rufina	Red-crested pochard	aquatic	1179.0	744.2	226.4	405.1	216.7	685.1

Species	Common name	trophic group	body mass (g)	adductor muscles (mg)	quadrate adductor muscles (mg)	pterygoid muscles (mg)	protractor muscles (mg)	depressor muscles (mg)
Marmaronetta angustirostris	Marbled teal	aquatic	480.0	452.6	114.9	228.6	114.3	461.7
Non-anseriforms								
Padda oryzivora	Java sparrow		30.4	85.7	15.8	86.3	4.1	23.6
Carduelis chloris	Greenfinch		28.3	138.7	21.1	89.5	10.5	33.7
Mycerobas affinis	Collared grosbeak		70.0	322.4	23.8	212.9	14.6	47.1
Serinus mozambicus	Yellow-fronted canary		12.0	39.4	6.9	26.8	5.1	9.5
Calidris canutus	Knot		130.9	41.4	23.7	54.3	11.3	49.0
Columba palumbus	Woodpigeon		368.5	66.1	33.4	104.4	22.4	83.1
Emberiza citrinella	Yellowhammer		28.9	47.5	16.2	43.5	4.0	14.1
Euplectus afer	Yellow-crowned bishop		15.0	36.8	8.3	28.6	2.7	8.1
Fulica atra	Eurasian coot		450.1	266.5	69.2	233.2	30.5	142.1
Larus ridibundus	Black-headed gull		189.1	390.0	120.7	385.5	35.5	161.1
Parus major	Great tit		15.2	24.3	3.6	20.3	1.8	7.6
Passer domesticus	House sparrow		27.0	94.6	22.6	58.0	11.2	41.6
Phalacrocorax africanus	Reed cormorant		756.0	2076.0	168.0	896.0	232.0	348.0
Rhea americana	Greater rhea		12500.0	3600.0	600.0	3200.0	500.0	2000.0
Sicalis flaveola	Saffron finch		25.1	40.7	11.7	48.0	2.7	12.4
Vidua chalybeata	Village indigobird		11.9	15.4	4.9	12.2	1.6	15.5

* From Goodman and Fisher (1962)

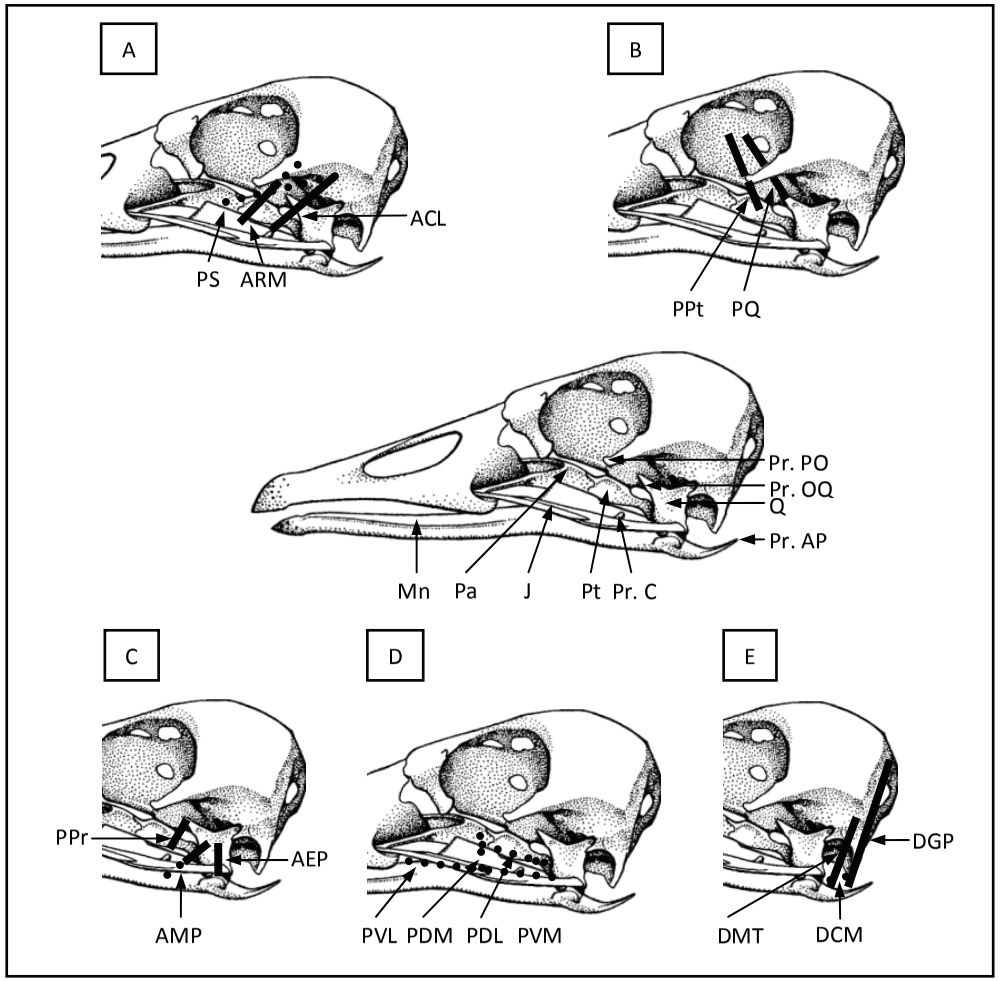

Figure 3.1. Bones of the skull (middle figure) and work lines of individual jaw muscles, dotted lines indicate that (part of) a muscle runs behind other structures. Muscle names according to Zweers (1974).

A: Skull adductor muscles: ACL, ARM and PS
B: Protractor muscles: PPt and PQ
C: Quadrate adductors: AMP, AEP, PPr
D: Pterygoid muscles: PVL, PVM, PDL, PDM
D: Depressors: DGP, DMT and DCM

ACL: musculus adductor mandibulae externus pars caudolateralis, *AEP*: musculus adductor mandibulae externus profundus, *AMP*: musculus adductor mandibulae posterior, *ARM*: musculus adductor mandibulae externus pars rostromedialis, *DCM*: musculus depressor mandibulae, *DGP*: musculus depressor mandibulae grandis pyramidalis, *DMT*: musculus depressor mandibulae triangularis, *J*: jugal, *Mn*: mandible, *O*: orbit, *Pa*: palatine, *PDL*: musculus pterygoideus dorsalis, lateralis, *PDM*: musculus pterygoideus dorsalis medialis, *PPr*: musculus pseudotemporalis profundus, *PPt*: musculus protractor pterygoidei, *PQ*: musculus protractor quadrati, *Pr. AP*: processus angularis posterior, *Pr. C*: processus coronoideus, *Pr. OQ*: processus orbitalis quadrati, *Pr. PO*: processus postorbitalis, *PS*: musculus pseudotemporalis superficialis, *Pt*: pterygoid, *PVL*: musculus pterygoideus ventralis lateralis, *PVM*: musculus pterygoideus ventralis medialis, *Q*: quadrate.

Data analysis

All data were log transformed to obtain normality. Basic statistical tests were performed in SPSS 12.0 (SPSS Inc. Chicago, IL, USA). For the analysis of muscle data the standardized major axis routine (S)MATR (v1) (Falster et al., 2003) was used. This routine implements the algorithms developed by Warton and Weber (2002).
Independent contrasts were calculated with Compare v4.6b (Martins, 2004) with all branch lengths set to unit length, as has been recommended for clades that have undergone adaptive radiations through the occupation of diverse niches (Mooers et al., 1999).
Phylogenetic hypotheses were based on studies by Livezey (1991, 1995, 1996a, 1996a) and Donne-Goussé et al. (2002).

Results

The data on species body mass and weights of individual groups of jaw muscles are listed in table 3.1. The log-transformed data of total jaw muscle mass (1-side; mg) and the mass of each functional muscle group (figure 3.1) are all highly correlated with body mass (g) for both aquatic feeders (n = 27) and terrestrial grazers (n = 18; all p = 0.000). A regression II analysis of the total jaw muscle mass and body mass shows that the slope of this relationship is not different for the two trophic groups (p = 0.072). The common slope for the two groups of anseriforms is 0.873 and suggests negative allometric growth of jaw muscle mass, although the 95% confidence interval includes 1, be it only just. However, the intercepts do differ significantly (p = 0.000; figure 3.2 and table 3.2). For a given body mass total jaw muscle mass is on average 1.5 times higher in aquatic feeding birds than in terrestrial feeding anseriforms, but there is a large overlap between groups.

To determine which functional muscle groups contribute to this difference in relative jaw muscle mass between the two trophic groups each muscle group was analysed separately. Terrestrial and aquatic feeders have similar slopes and intercepts for skull and quadrate adductor muscles (table 3.2). Jaw closing muscles therefore seem to have the same size relative to body mass in aquatic and terrestrial feeders. The size of the pterygoid muscles and openers of the upper or lower jaw, however, differs between the two groups. As for the adductor muscle groups the slopes for the opener muscle groups and pterygoid muscle group are statistically similar but for the jaw opener and pterygoid muscles the intercepts are different. Both the openers of the upper (protractors) and lower jaw (depressors) are approximately 2 times larger in aquatic feeders than in terrestrial grazers. The pterygoid muscles are on average 1.4 times heavier in aquatic feeders.

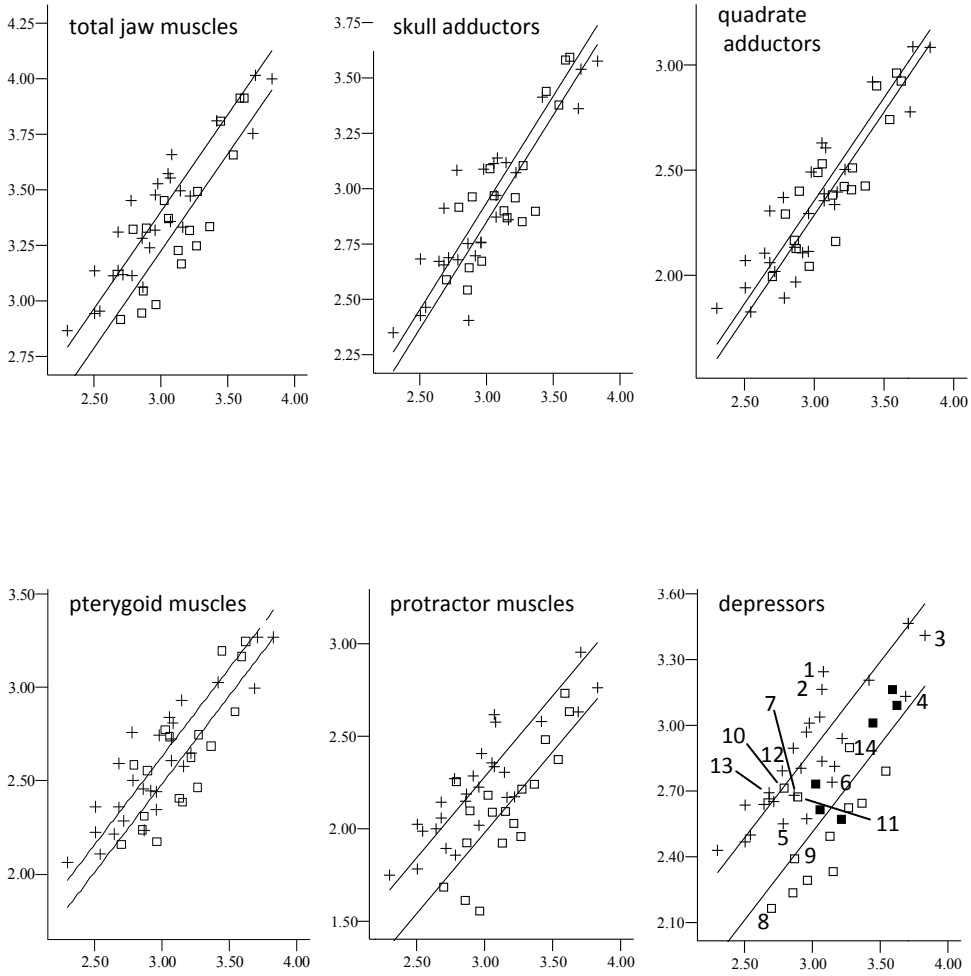

Figure 3.2. Regression lines for log body mass and log jaw muscles mass (x-axis: log body mass (g), y-axis: log muscle mass (mg)).
Legend: +: aquatic feeders, □: terrestrial feeders. Species of interest are indicated in depressor graph (see text). Filled squares: *Anser* species, 1: mallard (*Anas platyrhynchos*), 2: canvasback (*Aythya valisneria*), 3: mute swan (*Cygnus olor*), 4: black swan (*Cygnus atratus*), 5: hooded merganser (*Lophodytes cuculatus*), 6: common merganser (*Mergus merganser*), 7: northern shoveler (*Anas clypeata*), 8: Australian wood duck (*Chenonetta jubata*), 9: American wigeon (*Anas americana*), 10: black-bellied whistling-duck (*Dendrocygna autumnalis*), 11: plumed whistling-duck (*Dendrocygna eytoni*), 12: fulvous whistling-duck (*Dendrocygna bicolor),*13: white-faced whistling-duck (*Dendrocygna viduata*), 14: Egyptian goose (*Alopochen aegypticus*).

Table 3.2. Relationships between (log) body mass and (log) jaw muscle weights (r = Pearson correlation) in aquatic (Aq.) and terrestrial (Terr.) feeding anseriform species and non-anseriform (non-A.) species. Regression has the form y = a (slope) * log x + b (intercept).
c. slope = common slope, i.c. = independent contrasts, p^1 = probability that slopes are equal for the aquatic and terrestrial group, p^2 = probability that intercepts of the two groups are equal for the common slope.

		n	r*	slope	p^1	95% CI	intercept	Intercept common slope	p^2
Jaw muscle	Aq.	27	0.917	0.812		0.690-0.957	0.957	0.782	
mass	Terr.	18	0.839	1.087		0.818-1.446	-0.072	0.605	
(1-sided)	c. slope	45		0.873	0.072	0.751-1.014			0.000
	i.c.	45	0.840	0.901		0.730-1.080			
	non-A.	16	0.915	0.769		0.613-0.965	1.030		
Skull	Aq.	27	0.886	0.893		0.737-1.081	0.254	0.041	
adductors	Terr.	18	0.847	1.127		0.854-1.488	- 0.558	-0.045	
	c. slope	45		0.965	0.156	0.827-1.125	(0.005)		0.104
	i.c.	45	0.820	0.901		0.720-1.090			
	non-A	16	0.847	0.805		0.597-1.084	0.539		
Quadrate	Aq.	27	0.902	0.952		0.797-1.137	-0.501	-0.579	
adductors	Terr.	18	0.856	1.037		0.791-1.359	-0.834	-0.647	
	c. slope	45		0.978	0.582	0.848-1.128	(-0.603)		0.167
	i.c.	45	0.840	0.897		0.720-1.070			
	non-A	16	0.935	0.707		0.578-0.865	0.063		
Pterygoid	Aq.	27	0.888	0.868		0.722-1.044	0.024	-0.199	
muscles	Terr.	18	0.810	1.187		0.874-1.612	- 1.115	- 0.346	
	c. slope	45		0.943	0.082	0.800-1.111			0.009
	i.c.	45	0.810	0.886		0.690-1.080			
	non-A	16	0.914	0.763		0.607-0.958	0.546		
Protractor	Aq.	27	0.871	0.798		0.655-0.971	-0.115	- 0.345	
muscles	Terr.	18	0.772	1.142		0.820-1.591	-1.490	- 0.647	
	c. slope	45		0.875	0.064	0.731-1.047			0.000
	i.c.	45	0.750	1.149		0.850-1.450			
	non-A	16	0.935	0.855		0.698-1.047	- 0.551		
Depressor	Aq.	27	0.881	0.740		0.610-0.898	0.665	0.479	
muscles	Terr.	18	0.768	1.019		0.730-1.421	- 0.578	0.103	
	c. slope	45		0.803	0.093	0.673-0.957			0.000
	i.c.	45	0.770	0.907		0.680-1.130			
	non-A	16	0.961	0.797		0.680-0.933	0.135		

* all p = 0.000

Some species show large deviations from the muscle mass expected for their body size. In the aquatic feeding group *Anas platyrhynchos* and *Aythya valisneria* have very large opener muscles, while *Netta peposaca*, *Cygnus olor* and *C. atratus*, and the two *Merganser* species have relatively small jaw opener muscles. Surprisingly, the opener muscles of the northern shoveler are not very large but this species has relatively small adductor muscles, which gives it the highest ratio of jaw opener muscle mass / adductor muscle mass of all the species examined, while the other shoveler species studied (*A. rhynchotis*) did not show a high ratio. In the terrestrial grazing group *Anas americana*, *Chenonetta jubata,* most *Branta* and sheldgeese have relatively small jaw opener muscles, while most *Anse*r and especially the two grazing whistling duck species have relatively large jaw opener muscles compared to other grazing species. The jaw opener muscles in the two aquatic feeding whistling-ducks, however, are relatively larger than in the grazing whistling ducks.

To evaluate the difference between the two groups of anseriforms the data were compared to a sample of non-anseriform species with various foraging habits. The slope of the relationship between muscle group mass and body mass in the non-Anseriformes was very similar to the slope found for the anseriforms for all muscle groups. The intercepts for the opener muscles of the lower jaw (depressor) and of the upper jaw (protractors) of non-Anseriformes were statistically similar to those of the terrestrial feeding anseriforms and significantly smaller than for the aquatic feeding anseriforms (both $p = 0.000$). The pterygoid muscles, however, were much larger (2-3x for the common slope) in the non-anseriform group than in both the aquatic feeding group ($p = 0.002$) and the terrestrial grazing group ($p = 0.000$).
Although the adductor muscle groups in non-anseriforms tend to be higher than in the two anseriform groups no clear statistical difference was found.

Discussion

Main results

Our study strongly suggests that total jaw muscle mass in Anseriformes scales negative allometrically with body mass. A comparison between aquatic feeding species and terrestrial grazers shows that this relationship has the same slope (0.873, 95% CI 0.751-1.014) but different intercepts for the two groups. The jaw muscle mass is 1.5 times larger in aquatic feeders than in terrestrial grazers. The difference in total jaw muscle mass is the result of relatively large jaw opener muscles in aquatic feeders compared to terrestrial feeders. Compared to a sample of predominantly terrestrial feeding non-anseriform species, the size of the jaw openers of aquatic feeding wildfowl are larger as well, while those of terrestrial grazing anseriforms do not differ. The pterygoid muscles (upper jaw closers) are also larger in aquatic feeding anseriform species than in terrestrial grazing species, but the pterygoid muscles of both anseriform groups are smaller than in non-anseriform species.

In another study on the functional anatomy of the feeding apparatus of Anseriformes Goodman and Fisher (1962) found that the effective jaw opening and jaw closing force is higher and increases faster with body mass in straining species than in grasping species. They attributed this difference to large muscles for jaw opening and a combination of large muscles and long force arms for jaw closing. The presence of large jaw opener muscles in aquatic feeders compared to terrestrial grazers is confirmed by the present study, but the presence of large closer muscles is not. Adductor size varies widely in aquatic feeders and is not significantly different from that in equally large grazers. In the study by Goodman and Fisher sample size was small and their grasping group included not only species that spend part of their time grazing but also fish eating merganser species. The small sample size and heterogeneous combination of species may explain the different conclusion compared to the present study.

Scaling of jaw muscle mass

Data on jaw muscles in other groups of birds are very scarce. Van der Meij and Bout (2004) found positive allometric scaling of jaw muscle size with respect to body mass in seed-cracking finches (1.29; 95% CL, 1.09–1.50). They also calculated exponents for jaw muscle data from the literature and found that jaw muscle mass in a small sample of cormorant species also tends to scale positive allometrically. The exponent van der Meij and Bout calculated for the jaw muscle mass of 14 anseriform species reported by Goodman and Fisher (1962) was only 0.45 (95% CI 0.12–0.77). This is much lower than the value reported in this study (0.87). The difference between the two exponents is largely explained by the difference in regression technique used. In van der Meij and Bout (2004) the Goodman and Fisher data were fitted with a model I regression, which tends to underestimate the slope. For the same sample model II regression estimates a slope of 0.68 (95% CI 0.43–1.07).

The exponent for scaling of jaw muscle mass with respect to body mass in anseriforms may be related to the scaling of head size (see also van der Meij and Bout, 2004). Van der Leeuw (2002) found for 8 anatid species that head mass scales negatively allometric with body mass (0.7 ± 0.13). The weights of the organs contained within the cranium, the eyes and the brain, also scale negatively allometric (0.67) to body mass (Brooke et al., 1999; Schmidt-Nielsen, 1984). Based on this value, linear dimensions of the cranium are expected to scale with an exponent of 0.67/3 = 0.22 to body mass. As in finches, the cranium lengths of the anseriform species in the present study scaled with an exponent of 0.215 (95% CI 0.183 - 0.249, n = 44) to body mass (see chapter 4), similar to the expected value. Jaw muscle mass in anseriforms therefore seems to scale positively allometric to head size. Irrespective of the reference measure the slope of the relationship between jaw muscle mass and body/head size is significantly lower in anseriforms than in finches. Finches have approximately 4 times larger adductor muscles than anseriforms, but a similar head size relative to body mass. Apparently, overall cranium size is not limiting for jaw muscle size. In finches a large process, the processus zygomaticus, increases the area available for the insertion of muscle fibers. This process is absent in Anseriformes.

Terrestrial grazers have a higher-vaulted cranium than straining species (see also chapter 2) and relative skull height is often thought to increase the available area for the attachment of adductor muscle fibers posterior to the orbit (Goodman et al., 1962). Relative skull height has been suggested to improve bite capacity in other vertebrates as well (Claude et al., 2004; Herrel et al., 1999; Herrel et al., 2001; Herrel et al., 2004; Stayton, 2005; Van Cakenberghe et al., 2002). However, the present study shows that this relationship between skull height and muscle size or bite capacity may not be as straightforward, as it seems. Adductor size varies widely in aquatic feeders and is not significantly different from that in equally large grazers. In the grazer group, especially *Anser* and *Branta* species do have a high-vaulted cranium (chapter 2), but while most *Anser* species have larger adductors than expected for their body size, most *Branta* (and sheldgeese) species have smaller adductors than expected. The absence of a direct relationship between jaw muscle size and differences in cranial height is also illustrated by the size of the depressor muscles. While aquatic feeding species (e.g., *Anas*) have larger depressor (and adductor) muscles than terrestrial grazers, *Anas* species have a narrower and lower cranium than terrestrial grazing species (see chapter 2). Morphometric analysis has shown that a relatively high cranium is correlated with a more dorsal position of the eye and kinetic hinge. A high cranium may therefore be the consequence of selection on other traits than area for muscle attachment.

The higher effective closing force in strainers compared to grazers or graspers reported by Goodman and Fisher (1962) is even more unlikely when we consider bill length. Aquatic feeders have longer bills than terrestrial grazers (chapter 2 and chapter 4) and are therefore expected to have lower jaw closing force at the tip of the bill. Interestingly, terrestrial grazers increase their bite force compared to aquatic feeders through a short bill, not by a relatively large adductor muscle complex. Why this is so, is not clear. One possibility is that a short bill has the additional advantage of a shorter transport time for food.

Functional significance

It is tempting to relate the differences in jaw muscle size between the two trophic anseriform groups directly to the different physical characteristics of the environment in which the two groups forage. The opening and closing movements during feeding in water require a larger jaw opener force to overcome drag and to accelerate water, especially in straining species, which show fast repetitive movement cycles (Kooloos et al. 1989). In terrestrial foraging species these forces are much smaller, because the density of air is much lower. However, it not clear how the magnitude of drag force or the force to accelerate water compares to the forces produced by the jaw opening muscles of Anseriformes. In the mallard the upper and lower jaw open and close at a high frequency (20 Hz) but their measured rotation is small (6 and 3 degrees respectively; Kooloos, 1989). The drag F_d may be estimated as $0.5\ \rho\ A_w\ v^2\ Cd$, where ρ is the density of water, A_w the surface area, v the velocity of the movement and Cd is the drag coefficient. Cd is difficult to guess but would be 1 in the case of a flat plate moving perpendicular to the direction of movement. When both velocity and surface area (linear dimensions of the mandible 89 x 24 mm) are small Fd will be small too. The mass of water that has to be accelerated during

jaw opening may be a much larger component of the forces resisting jaw opening. In the mallard the depressor muscles are each capable of generating a maximum static force of approximately 60 N, but the opening force will decrease with jaw opening velocity.

However, the difference in force exerted by the environment is not the only difference between the two groups of anseriforms. The bill is 1.35 times longer in aquatic feeders than in terrestrial grazers (see chapter 2 (and chapter 4)). Bill height and width at the cranial hinge do not differ between the groups. The (angular) acceleration of the bills is determined by the moments exerted by a number of different forces (muscle forces, passive elastic forces from soft tissues and the bending zone of the upper jaw, pressure in the oral cavity, gravity, cf Van Wassenbergh et al. (2005) and by their moment of inertia. If the same angular acceleration of the bills were to be reached in species with similar cranial morphology, one would expect larger jaw muscles in species with larger bills. The shape of the upper bill may be approximated by a triangular prism with the rotation axis at the top corner (kinetic hinge). For such an object the moment of inertia is 1/6 ρhwl (h^2 + l^2), where l, h and w are the length, height and width of the upper bill and ρ is the density. The moment of inertia of the lower jaw may be approximated by that of a rectangular beam, which is simply two times the expression for the upper bill. As height and width do not differ between trophic groups the moment of inertia is proportional to l^3 for both bills. Drag forces are proportional to the surface area of the bill and (angular) velocity squared, but the moment from drag force increases even faster than the moment of inertia and is proportional to l^4 (Van Wassenbergh et al., 2005). For the upper bill this means that the moment of inertia is $(1.35)^3$ = 2.5 times larger in aquatic feeders than in similar sized terrestrial feeders. Given similar moments an aquatic feeder would also need 2.5 times larger protractor muscles for the quadrate and pterygoid to produce the same angular acceleration of the upper bill, assuming that muscle fibre length remains constant. The muscle data show that the protractor muscles are 2 times larger in aquatic feeders than in terrestrial feeders. This suggests that the relatively large protractor muscles in aquatic feeders are not an adaptation to the aquatic environment but are related to bill size as such.

For the opener muscles of the lower jaw the situation is slightly different. The mandible is 1.24 times longer in aquatic feeders than in terrestrial feeders (see chapter 4). An aquatic feeder would therefore require a $(1.24)^3$ = 1.9 times larger depressor muscle to produce the same angular acceleration of the lower jaw as a terrestrial feeder. The depressor muscle is estimated to be 2.4 times larger in aquatic feeders than in terrestrial feeders. The depressor in aquatic feeders is therefore somewhat larger than required to compensate for the increase in moment of inertia and may be used to overcome resisting forces.

Surprisingly, the size of the adductor muscles does not differ between the two trophic groups. The only closing muscle that seems to differ in size is the pterygoid muscle, which acts on both the upper and lower jaw and is 1.4 times larger in aquatic feeders. As for the upper bill opener, the relative increase in size of the pterygoid muscles seems too small to account for more than just the increase in moment of inertia of the bills. A relationship between pterygoid muscle size and aquatic feeding is also unlikely because non-

anseriform terrestrial species have larger pterygoid muscles than aquatic feeding anseriform species.

A proper assessment of the effect of the differences in drag, reaction force of displaced water and bill size for feeding movements requires biomechanical modelling of all the different forces that act on the bill. However, from the present data it would seem likely that aquatic feeding species are not able to produce angular accelerations as high as terrestrial feeding anseriforms. This may be true even when aquatic and terrestrial feeders are compared under the same (aquatic) conditions. The bill of terrestrial feeders is less wide at the tip than in aquatic feeders and will produce less resisting force than the bill of aquatic feeders, even when the bill is immersed equally far. Detailed kinematic data on jaw acceleration in anseriforms are not available, but data on a small number of straining geese and duck species suggest that this may be the case. Rough estimates on gape and straining frequency show that two geese species have low straining frequencies (12-13 Hz) but relatively large gapes compared to ducks and the mute swan. A number of ducks (mallard, wigeon, and tufted duck) use high straining frequencies (18-20 Hz), but have relatively small angular rotations of the bills. The mute swan has a much lower straining frequency (11 Hz) but also a relatively small gape compared to the geese. When angular rotation and frequency are used to estimate maximal acceleration for sinusoid movement of the bill accelerations in the two geese species are almost twice as high as in the ducks and swan. The northern shoveler has a relatively large bill but the jaw opener muscles are as large as expected for its body size and the jaw closers are smaller than expected from its size. The angular rotations of the bill during straining are similar to other duck species but its straining frequency is much lower (13 Hz). This species seems to illustrate that an increase in bill size may go at the expense of straining frequency. Such a relationship may reflect the decrease in net jaw opening force as bill size and the amount of water to be displaced increases.

Variation within trophic groups

For many species used in this study there is a considerable variation in food items taken, often depending on the season. Detailed data on food items taken over a year are often not available. Categorizing species as 'aquatic' or 'terrestrial' feeder therefore involves a considerable degree of arbitrariness, especially since different food items or foraging techniques may be associated with different forces regimes for the jaws. In the aquatic feeding group some of the examined species forage exclusively on small food items (seeds and/or small invertebrates) year round (*A. hottentota, A. clypeata*, *A. rhynchotis, A. formosa, A. bahamensis,* and *M. angustirostris*). Dabbling ducks feeding on the surface will experience resisting forces from the water especially on the lower bill when it is partly submerged, but on both bills when they forage by 'up-ending'. Species tend to use up-ending in steep ponds as found in Europe (Nudds et al., 2000). A number of species include parts of aquatic vegetation (*A. nyroca, T. cana*, *N. peposaca, N. rufina, D. viduata, D. bicolor*) and/or terrestrial vegetation (*T. ferruginea, A. platyrhynchos*, *A. specularis*), and some consume predominantly aquatic vegetation (*A. valisneria, C. olor, C. bewicki, C. atratus)*. Aquatic 'grazing' may in some respects be more like terrestrial grazing than filter-feeding. The velocity of jaw opening and jaw closing during foraging on aquatic plants may

be similar to the velocity for terrestrial grazing and lower than the high frequency movements during straining (18-20 Hz). Consequently resisting forces will be less. This may explain the relatively small depressor muscles found for *N. rufina* and the *Cygnus* species.

Several (diving) species add large invertebrates or even fish to their diet (*A. crecca*, *M. perspicillata*, *A. affinis, B. clangula, C. hyemalis, L. cucullatus, M. merganser, and T. pteneres*). Whether such species often experience large resisting forces is not clear and may partly depend on where the prey is swallowed, under water or at the surface. At least for a number of the species mentioned above it has been reported that food items may be swallowed underwater. Very large food items are taken to the surface (references in Austin et al., 1998; Eadie et al., 1995; Johnson, 1995; Mallory and Metz, 1999; Savard et al., 1998).

The small size of the depressor muscles of the two merganser species is considered to reflect the smaller drag forces experienced by the very narrow bills. In species that have to detach shellfish or hold struggling fish one may expect relatively large adductor muscles. *A. affinis* and *L. cucullatus* do have the largest adductors of the species examined. In other diving species adductor muscles are less prominent, but often larger than in many geese and sheldgeese.

Most species in the terrestrial grazing group predominantly use a single feeding method. The major ingredient of their diet consists of aerial parts of terrestrial vegetation. Within the geese, *Anser* species tend to have larger jaw opener muscles than *Branta* and sheldgeese species. According to literature data *Anser* geese forage not only on aerial plant parts, but also on underground parts (i.e. grubbing). Grubbing requires larger energy expenditure than grazing (Gauthier et al., 1984) and probably animals have to produce larger jaw opening forces as the bills push against the mud. In a study on snow goose feeding behaviour, it was found that grubbing juveniles had slightly heavier jaw muscles than did grazing juveniles (Jónsson, 2005). Four of the six *Anser* species studied are known to grub (references in Esselink et al., 1997; Mowbray et al., 2000; Petersen et al., 1994; http://www.birdskorea.org/Birds/Significant_Records/New_Birds/BK-NB-Bar-headed-Goose.shtml), which may explain their heavier muscles. For the bar-headed goose few data on food items are available, but the lesser-white fronted goose is known to forage exclusively on above-ground plant parts in spring (Markkola et al., 2003). A strong preference for above-ground plant parts may explain its lower jaw muscle sizes compared to the other *Anser* geese examined.

The three extant wigeon species are considered to be grazers. Of these three species the American wigeon feeds the least on terrestrial vegetation (Kear, 2005). However, this species is known to include terrestrial plants in its diet during winter, during migration and upon arrival on their breeding grounds (references in Mowbray (1999)). The size of the jaw opener muscles of this species is clearly different from the aquatic feeding group and similar to those of terrestrial grazers.
The two species of grazing whistling-ducks (*Dendrocygna eytoni* and *D. autumnalis*) have relatively large jaw opener muscles compared to other grazers and seem to fit the aquatic feeding group better than the terrestrial group. The assignment as terrestrial grazer was

based on Rylander and Bolen (1974) and references herein, James and Thompson (2001) and Kear (2005) but both species are also known to dabble (Kear, 2005). No data on the relative contribution of dabbling and grazing to energy intake are available for these species and it may be that *D. eytoni* and *D. autumnalis* are better characterized as aquatic feeders than as terrestrial feeders. Within the group of whistling-ducks however, the two grazing species have smaller jaw opener muscles than the two aquatic feeding species.

Despite the variation within trophic groups, we were able to show the presence of relatively large jaw opener muscles in aquatic feeders compared to terrestrial grazers. As the bill of aquatic feeders is also larger than in terrestrial feeders the difference in relative size of the jaw opener muscles cannot be simply explained as an adaptation to the large resisting forces in an aquatic environment. Longer and wider bills result in a larger moment of inertia. If angular acceleration and density of the environment remain the same, having a larger bill also requires larger jaw opener muscles. The difference in size of jaw opener muscles found is estimated to be approximately sufficient to compensate for the difference in bill size and there is no indication that muscle size increases to compensate for the larger resistance in an aquatic environment.

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Chapter 4

Morphology of the oral cavity in aquatic and terrestrial feeding Anseriform species

Summary

Anatidae (geese, swans and ducks) exploit many food resources ranging from filter-feeding small aquatic food items to terrestrial grazing. It is likely that feeding in different environments (aquatic versus terrestrial) on different types of food is associated with differences in feeding mechanism, which in turn may be linked to differences in the morphology of the oral cavity. In the mallard it has been shown that for high performance filter-feeding the 'under-tongue' transport mechanism for food items requires a bald roof of the oral cavity and a groove along the sides of the caudad part of the tongue (Zweers et al., 1977). The mechanism ensuring a high performance for grazing in the domestic goose requires caudally pointing spines on the palatal surface for efficient 'over-tongue' transport of food items (Van der Leeuw et al., 2003).

In this study we investigated whether the functional demands of aquatic feeding and terrestrial grazing has resulted in the evolution of similar morphologies of the oral cavity in different species. The morphology of the oral cavity within each trophic group resembles each other to a great extent. In most of the 19 aquatic species studied the roof of the oral cavity is bald and grooves are present along both sides of the caudad part of the tongue. In most of the 20 grazing anatids studied the roof of the oral cavity bears spines and grooves alongside the caudal part of the tongue are absent.
Several other oral structures are related to aquatic or terrestrial feeding as well: the dorsal row of mandibular lamellae are broad and sharp edged in most grazing species, but bladelike with a smooth dorsal rim in most aquatic feeding species, the depth of the rostral part of the maxilla is deeper in aquatic feeders than in terrestrial grazers, and the rostral part of the tongue is relatively larger in aquatic feeders than in terrestrial feeders.

In both the aquatic and terrestrial feeding group some species differ from the general oral morphology found. In most species that feed mainly on aquatic vegetation (e.g. swans) the grooves along the sides of the tongue are lacking. Such species ingest large pieces of food, which cannot be transported through the lingual grooves. As these species also possess sharp edged dorsal mandibular lamellae and palatal spines, it seems likely that these species use the 'over-tongue' transport mechanism as found in geese. In the terrestrial grazing group the oropharyngeal anatomy of the two grazing whistling-ducks and the wigeons is not consistent with the 'over-tongue' transport characteristics; and more similar to those of the 'under-tongue' transporting anatid species. Possibly terrestrial grazing is a recently acquired mode of foraging in whistling ducks. Wigeons are known to combine grazing with filter-feeding.

The association between oral morphology and grazing and filter-feeding suggests that 'over'- and 'under-tongue' transport mechanisms have developed more than once within the Anseriformes and that the transition from one mechanism into the other is relatively easy.

Introduction

Wildfowl (Anatidae) have diverged into specialized feeding niches ranging from piscivory to herbivory, and are often considered an example of adaptive radiation (Lack, 1971, 1974).
Differences in trophic morphologies between species are believed to affect the performance of feeding behaviour and to reduce competition for limited resources. Differences in the exploitation of resources linked to alternative morphologies directly or indirectly influences fitness upon which natural selection can act (Arnold, 1983), and may lead to divergent selection and adaptive radiation (Schluter, 2000a). However, often the exact relationship between trophic traits and recourse use is open to question (Arnold, 1983; Wainwright, 1991; Wake, 1992; Rubega, 2000).

Feeding in different environments (aquatic versus terrestrial) on different types of food is likely associated with differences in feeding mechanism, which in turn may be linked to differences in the morphology of the oral cavity. Extensive kinematical and X-ray analysis of an aquatic anatid feeder, the mallard (*Anas platyrhynchos*), and a terrestrial grazer, the domestic goose (*Anser anser domesticus*) has demonstrated that these species use different mechanisms to transport the same type of food through the oral cavity (Kooloos, 1986; Kooloos et al., 1989; Van der Leeuw et al.; 2003, Zweers et al., 1977). In filter-feeding mallards the rostral part of the tongue is pushed against the roof of the upper bill and functions as a piston, drawing in water and suspended food particles at the anterior part of the bill. Simultaneously, water behind the elevated anterior part of the tongue is expelled from the bill and food particles are retained between the rims of the bill (Gurd, 2005) and transported caudad along the sides of the tongue. This feeding mechanism is characterized as 'under-tongue' transport, because small food items pass through a groove between the elevated caudal part of the tongue, which prevents water from entering the oesophagus, and the wall of the oral cavity (Kooloos et al., 1989). The 'under-tongue' transport enables simultaneous collection and transport of food during a single movement cycle without the need to interrupt feeding to swallow food (Van der Leeuw et al., 2003).

Filter-feeding in the domestic goose, on the other hand, is typified by an 'over-tongue' transport of food particles. Seeds pass over the tongue cushion, instead of along the sides. As the tongue must be depressed to let food pass, this mechanism involves separate feeding cycles for collection and for transport of food particles. The difference in feeding mechanism between mallard and domestic goose seems to be related to their dominant food resource: filter-feeding small aquatic food items and terrestrial grazing respectively. During grazing relatively large parts of plants are collected, and as these parts are too large to pass along the side of the tongue, they are transported over the tongue. In the domestic goose series of for/backward movements of the tongue are used to transport the clipped vegetation through the oral cavity. Caudally pointing spines on the roof of the oral cavity retain the vegetation during rostrad movements of the elevated tongue (Van der Leeuw et al., 2003). Geese use this 'over-tongue' mechanism also to transport seeds during filter-feeding.

From the kinematical analysis of the feeding mechanisms, it may be concluded that the typical morphologies for optimal filter-feeding and grazing pose conflicting functional demands on oral morphology (Van der Leeuw et al., 2003). The typical morphology for filter-feeding is a bald inner surface of the upper bill, well developed cushion-like thickenings of the tongue, and a longitudinal groove on each lateral side of the posterior part of the tongue to allow for a continuous water flow. In grazing species there is no use for a lateral groove in the posterior part of the tongue or a thickening of the tongue to facilitate the continuous throughput of water. On the other hand, caudally pointing spines on the inner surface of the upper bill interfere with the piston function of the tongue during filter-feeding because the tongue cannot be properly pushed against the roof of the mouth, resulting in a 'leaky' pump. In the mallard such spines are absent and grass is transported through the beak by an inertial transport or 'catch-and-throw' mechanism, resulting in high losses of food items like grass (Van der Leeuw et al., 2003).

Although the kinematic analysis of food transport suggests that oral morphology is closely linked to feeding method only very few species have been extensively investigated. As kinematic analyses are very time consuming and can not be used to study a large number of species we investigated several morphological features of the tongue and oral cavity in a large number of aquatic feeding and grazing anseriform species to investigate whether oral morphology is consistently related to feeding habits. The morphological characters chosen are indicative of feeding mechanisms (e.g. presence grooves, spines) or expected to affect quantitative aspects of feeding mechanisms (e.g., volume of the oral cavity). Species were characterized as 'aquatic feeder' or 'terrestrial grazer' based on their main feeding habits reported in the literature. The aquatic feeding group not only includes species that feed on small food items by the 'under-tongue' transport mechanism, but also several species feeding on larger food items, which are transported over the tongue. All species have in common that at least part of the collection and transport of food items occurs with submerged bills. We specifically included swan species in our analyses, which are reported to forage on water plants and may be characterized as aquatic grazers.

Materials and Methods

The bill and tongue of 39 species of Anseriformes was investigated (table 4.1). Most birds were obtained dead from a commercial waterfowl farm, except for four individuals, which were sacrificed by administering an overdose of anaesthetic Nembutal (Sanofi Sante B.V., Maassluis, The Netherlands). Heads of mallards were obtained from a poulterer. Three dead Bewick's swans were generously made available to us by the NIOO, Nieuwersluis and dead greylag geese were obtained from Groningen University.

The oral cavity was dissected free and its general morphology was described according to the terminology of Kooloos (1986) and Baumel et al. (1993).
Presence or absence of features expected to be important for either the 'under-tongue' or 'over-tongue' transport mechanism was noted:

1) spines on the roof of the oral cavity,
2) grooves on the lateral sides of the lingual cushion (figure 4.1A: lg and figure 4.1B),
3) the presence of hairs on bulges (figure 4.1A: lb),
4) the presence of a lingual comb (figure 4.1A: lco), and
5) the form of the dorsal mandibular lamellae (figure 4.1C).

The following quantitative measurements on the head and oral cavity were made with needle pinned sliding callipers with an accuracy of 0.1 mm (for 1 to 6 see figures 4.2A and 4.2B, for 8 to 12 figure 4.1A)

1) length of the head, between the tip of the bill and the back of the head,
2) length of the bill along the rim to the rictus,
3) rostral width of the upper bill, at the caudal rim of the maxillar nail,
4) caudal width of the upper bill, at the frontonasal joint,
5) height of the bill at the frontonasal joint,
6) height of the bill at the level of the nail,
7) depth of maxilla at the level of the lingual bulges,
8) total lingual length, from tip to caudal end of cushion (just rostral from spines),
9) length of lingual tip, defined as the anterior part of the tongue with no lining projections (figure 4.1A: lt),
10) length of lingual bulges, i.e. thickened part of the tongue between tongue tip and scraper area (figure 4.1A: lb),
11) length of the part of the tongue lined with scrapers (figure 4.1A: ls),
12) length of most posterior part of tongue, caudad of scrapers (part of lingual cushion) (figure 4.1A),
13) density of lamellae of the maxilla, the dorsal mandibular row and the ventral/lateral mandibular row (if present): number of lamellae divided by the distance between the first and last lamella.

For a number of the species measured 2 or more individuals were available, but only the individual with the most complete data set was included in the analysis.
For several characters the data set was expanded with 9 species (*Anas clypeata, Aythya affinis, Aythya valisneria, Bucephala clangula, Clangula hyemalis, Melanitta perspicillata, Merganser cucullatus, Merganser merganser*) for which (average) data are available from Goodman and Fisher (1962).

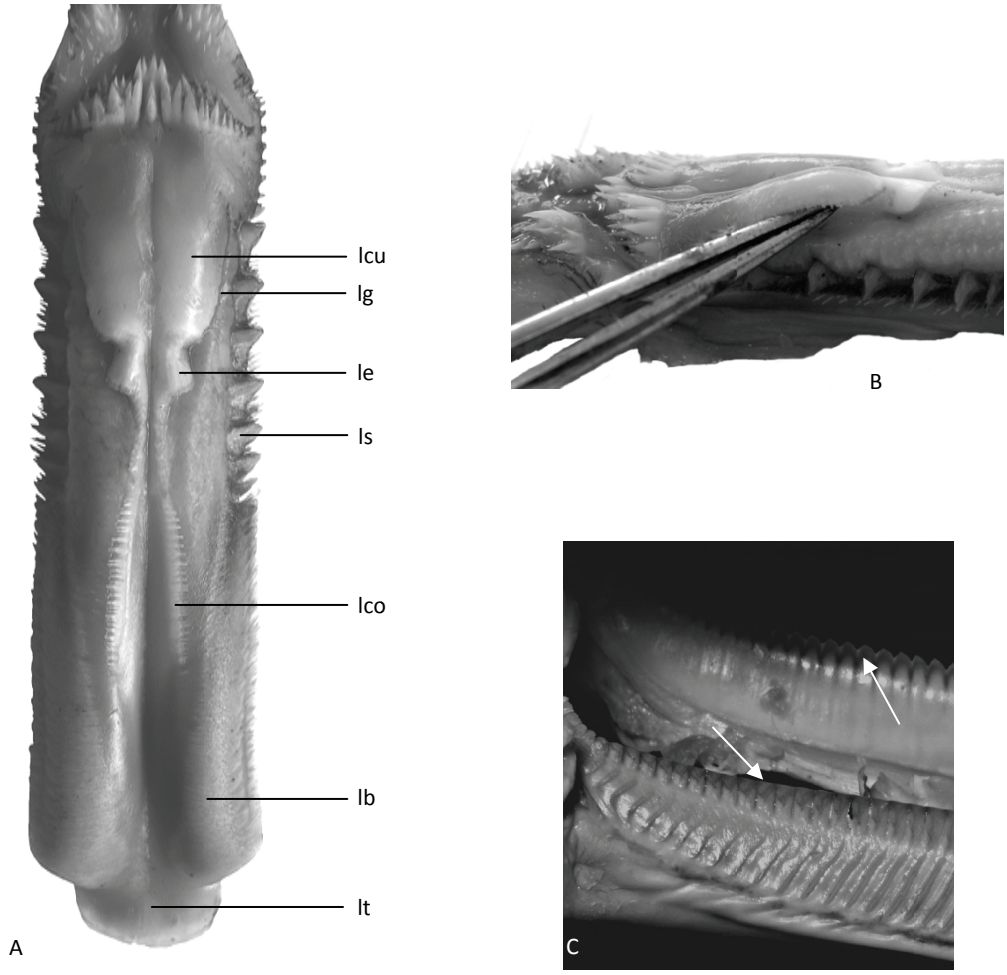


Figure 4.1. *A*. Dorsal view of tongue of the mallard. Note the large amount of hairs and area covered by the hairs on the bulges. *B*. Detail of the lingual groove, tongue tip to the right, *C*. Detail of mandibular lamellae next to the lingual cushion (tongue removed). Mandible slightly tilted, showing left and right rami. Beak tip to the right. Note the smooth rim of the dorsal row (arrows).

Abbreviations used in pictures (in alphabetical order)

bb:	bumps	lb:	lingual bulges
bcps:	caudally pointing spines	lco:	lingual comb
bml:	maxillary lamellae	lcu:	lingual cushion
bmr:	median ridge	le:	lingual ear
brps:	rostrally pointing spines	lg:	lingual groove
bsg:	shallow grooves	ls:	lingual scraper
btr:	transverse ridges	lt:	lingual tip

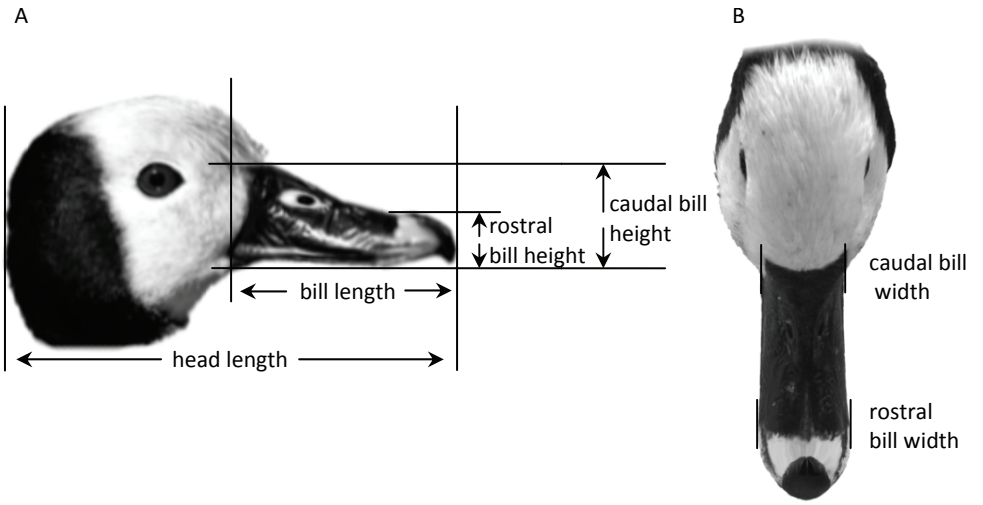


Figure 4.2. Lateral (*A*) and dorsal (*B*) view of head of white-faced whistling duck (*Dendrocygnus viduata*). Indicated are the external head dimensions measured.

Statistics

All data were log transformed to obtain normality. Basic statistical tests were performed in SPSS 12.0 (SPSS Inc. Chicago, IL, USA).
A linear relationship between two variables is often estimated using an ordinary least squares regression (model I approach). This technique minimizes the distance between the observed data points and the predicted line in the Y dimension only. As in biological studies often both y and x variables are measured with considerable error ordinary least squares regression tends to underestimate the slope of the relationship. Standardised major axis estimation (model II) minimizes residuals in both the x and y dimensions and is more appropriate to estimate the line-of-best-fit relating two variables. For the analysis of dimensions of tongue and bill therefore the standardized major axis routine (S)MATR (v1) (Falster et al., 2003), was used. This routine implements the algorithms developed by Warton and Weber (2002).

While standardised major axis regression assumes that data from different species are independent, species do of course share part of their evolutionary history and cannot be considered truly statistically independent beforehand (Felsenstein, 1985, 1988; Harvey and Pagel, 1991). We therefore also did an independent contrast analysis, which takes into account the statistical non-independence of species and allows testing for evolutionary correlations among traits. Independent contrasts were calculated with Compare v4.6b (Martins, 2004) with all branch lengths set to unit length, as has been recommended for clades that have undergone adaptive radiations through the occupation of diverse niches (Mooers et al., 1999). Our phylogenetic hypotheses were based on studies by Livezey (1991, 1995, 1996a, 1996b, 1997a) and Donne-Goussé et al. (2002).

Results

First a description of the common structures of bill and tongue within each trophic group is given, followed by an account of characteristic deviations from the general description for individual species. Finally, quantitative measurements are analysed and compared for both trophic groups.

Description oral cavity

Aquatic feeding species: the bill

The morphology of the oral cavity of the 19 aquatic feeding anseriform species studied resembles each other to a great extent. The inside of the upper bill is bald, except for several rostrally pointing spines on the median ridge at the level of the lingual cushion (figure 4.3: brps), and some short shallow grooves adjoining the maxillar lamellae medially (figure 4.3: bsg).

In aquatic feeding anseriforms the upper bill bears one row (figure 4.3: bml), and the lower bill two rows of lamellae, a dorsal and a lateral/ventral row (figure 4.1C). The dorsal side of the dorsal mandibular lamellae, facing the maxillar lamellae, is rounded and smooth, but the lamellae have a sharp edge on the lateral side (figure 4.1C).

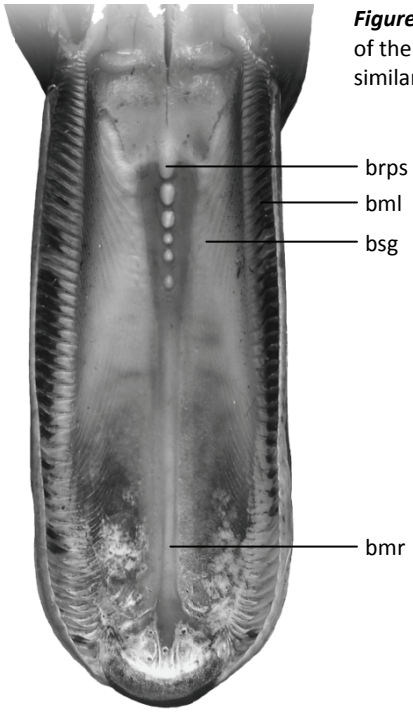


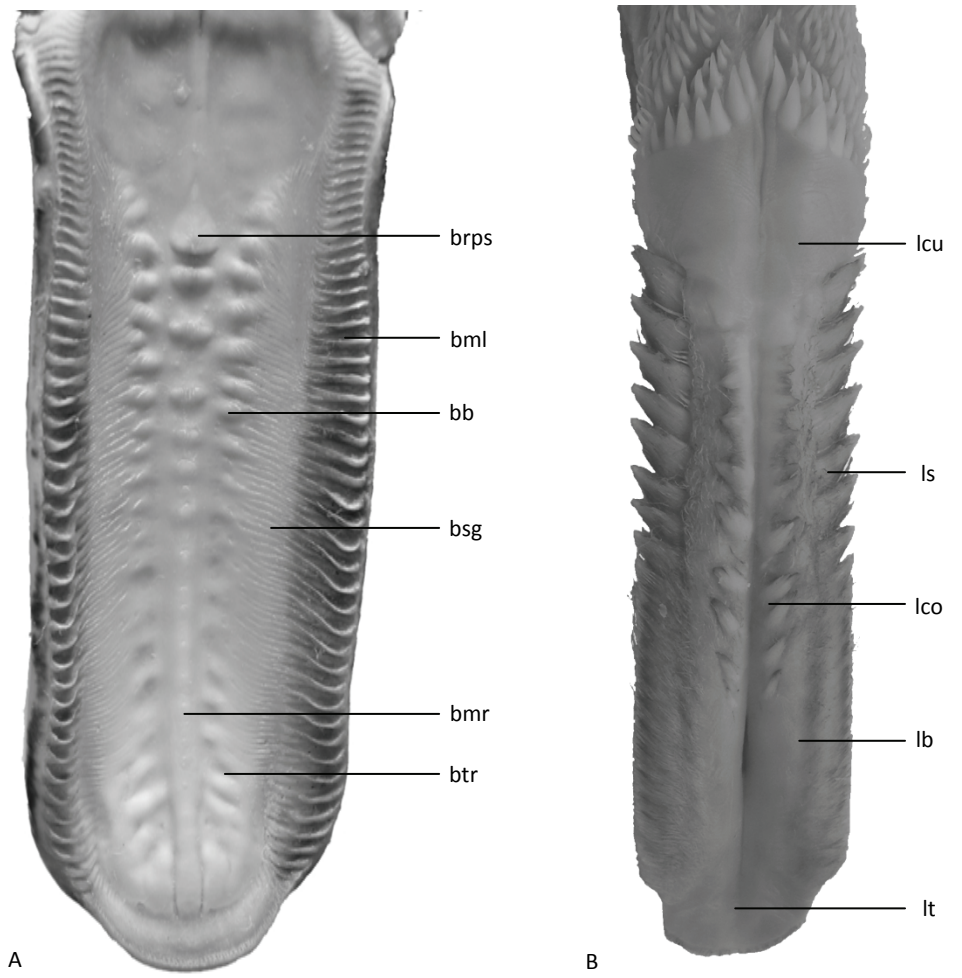
Figure 4.3. Ventral view of the upper bill of the mallard. Most of the other aquatic feeding anatid species studied have a similar bald inner surface (see text).

Aquatic feeding species: the tongue

The tongue can be divided into several parts based on anatomical structures. The most distal part of the tongue is formed by the lingual tip (figure 4.1A: lt), which in aquatic feeding anseriforms is distinct from the rest of the tongue because of its smaller width. Caudad to the lingual tip the tissue of the tongue forms two lingual bulges (figure 4.1A: lb). Left and right bulge are separated by a median groove. Dorso-laterally these bulges bear thin plates of closely bound keratinized 'hairs'. The next part of the tongue is characterized by small papillae on the lingual surface, while scrapers with tiny hairs in between border the tongue laterally (figure 4.1A: ls). The most caudal part of the tongue is formed by the tongue cushion (figure 4.1A: lcu).
In the median, just anterior of the lingual cushion are two small keratinised ear-like structures (figure 4.1A: le), which form the caudal end of the lingual comb. The lingual comb (figure 4.1A: lco) consists of two rows of small keratinized structures lining the median lingual groove. Starting at the two ear-like structures a longitudinal groove (figure 4.1A: lg and figure 4.1B) runs caudad on the lateral sides of the lingual cushion for two-third of its length, up to the most caudal scraper.

Aquatic feeding species: variation among species

Deviations from this general morphology of the oral cavity are found in several species. In the swan species studied, the palatal surface is not bald; caudally pointing papillae are present not just caudally but over the entire length of the median maxillary ridge (figure 4.4A: bmr). Rostrally these papillae are small (figure 4.4A: btr), but caudally they become much larger (figure 4.4A: bb).



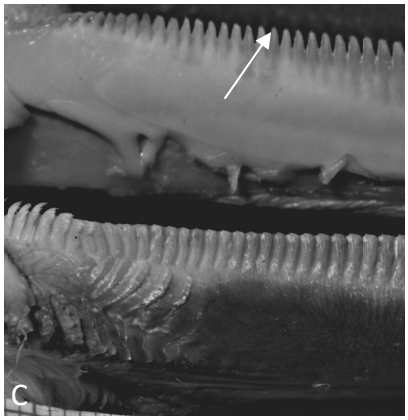
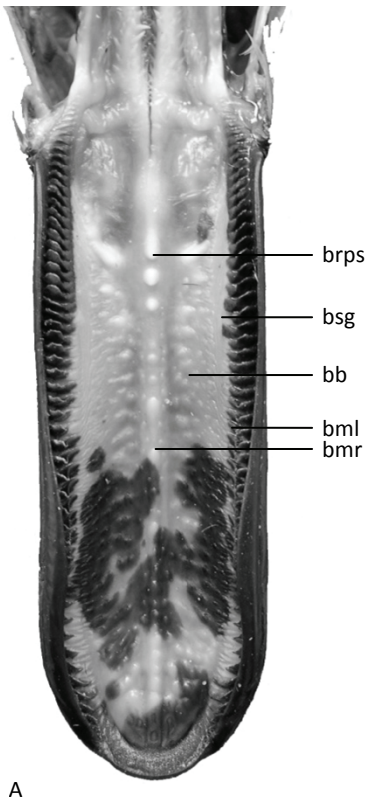


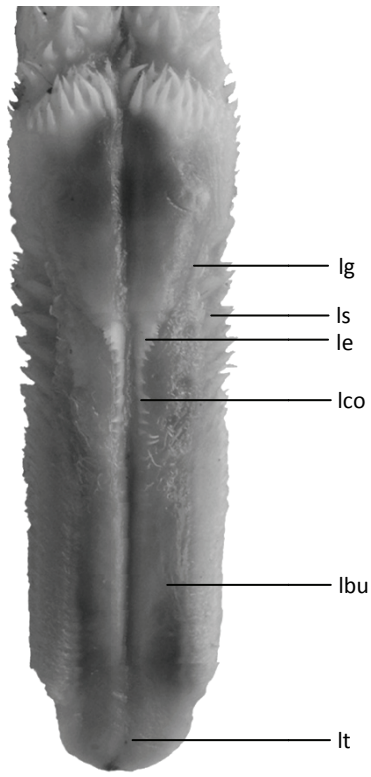
Figure 4.4. *A.* Ventral view of maxilla of upper bill of mute swan. Note that on the median ridge the spines are pointing caudally, *B*. Dorsal view of tongue. Note that the lingual grooves and lingual ears are absent and the hairs on the bulges cover only the lateral part (compare figure 4.1A). *C*. Detail of mandibular lamellae next to lingual cushion (tongue removed). Mandible slightly tilted, showing left and right rami. Note the sharp edge (arrow) of the dorsal row and the absence of lateral lamellae apart from the corner of the mouth. Beak tip to the right.

In some other aquatic feeding anatids small bumps (projections without a particular direction) are scattered on the inside of the upper bill, e.g. in the wood duck (*Aix sponsa*), the ferruginous duck (*Aythya nyroca*), the red-crested pochard (*Netta rufina*), the rosy-billed pochard (*Netta peposaca*; rostral part bill), the steamerduck (*Tachyeres pteneres*), the two shelduck species (many bumps) (figure 4.5A) and the swans (caudal part bill, figure 4.4A).
Grooves along the sides of the lingual cushion were absent in the red-crested pochard, the mute swan (figure 4.4B) and the black swan (but clearly present in Bewick's swan).
The lingual combs are absent in the wood duck or quite small and short in the steamerduck, the two shelducks (figure 4.5B), and filter-feeding whistling-ducks.
The edges of the dorsal row of mandibular lamellae are not smooth but sharp and more or less dorsally oriented in the three swan species (figure 4.4C), the steamerduck, the red-crested pochard and the wood duck.



A

Figure 4.5. *A*. Ventral view of upper bill of the ruddy shelduck (*Tadorna ferruginae*). Note the many small bumps and the caudally pointing spines on the median ridge.



B

Figure 4.5. *B.* Dorsal view of tongue of the cape shelduck (*Tadorna cana*). Note the smooth transition between lingual ears and lingual comb and the small size of the latter (compare figure 4.1A).

Terrestrial grazing species: the bill

The description of the structures in the oral cavity in grazing anseriforms is based on 20 species. On the inner lining of the upper bill many caudally pointing papillae are present, including the median ridge (figure 4.6A and figure 4.6B: bcps). In most grazers shallow grooves as found in a number of aquatic feeders are absent. In most species the maxilla and mandible have one row of lamellae; the lateral lamellae on the mandible are absent (figure 4.7A and 4.7B). The dorsal mandibular lamellae are triangular with a sharp dorsal edge (figure 4.7A and 4.7B).

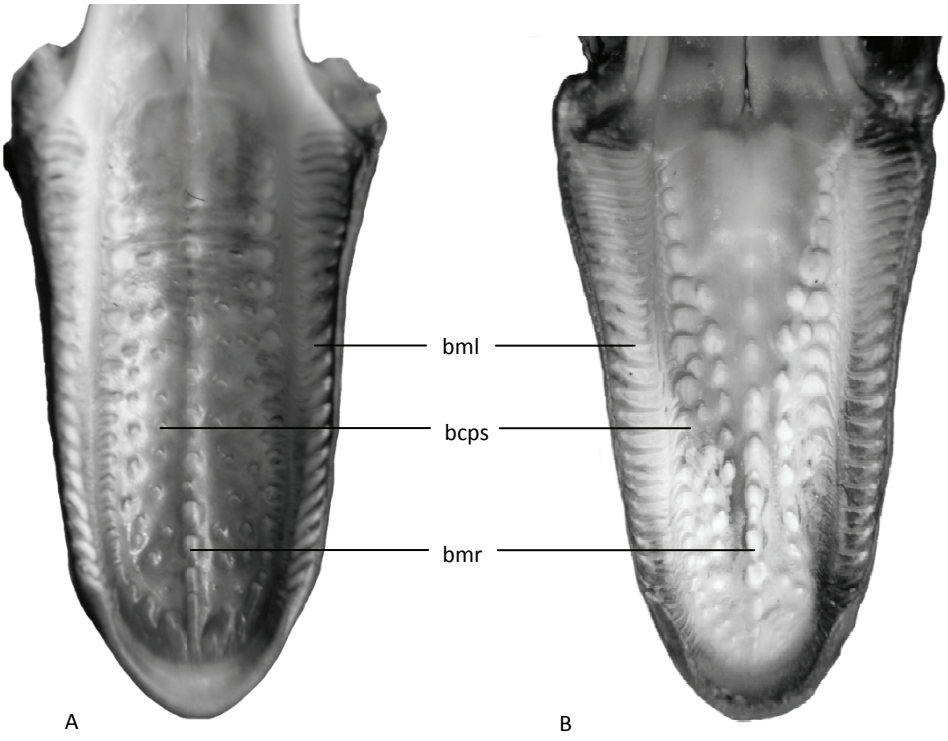


Figure 4.6. *A.* Upper bill of barnacle goose (*Branta leucopsis*). Note the large numbers of caudally pointing spines (bcps).

Figure 4.6. *B.* Upper bill of lesser white-fronted goose (*Anser erythropus*). The spines are stouter than in *Branta* (compare figure 4.6A).

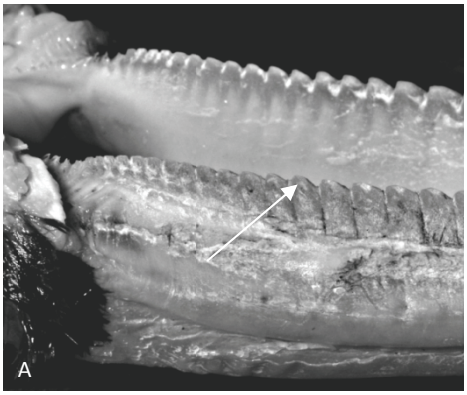


***Figure 4.7**. A.* Detail of mandibular lamellae next to lingual cushion level (tongue removed) of greylag goose (*Anser anser*). Mandible slightly tilted, showing left and right rami. The dorsal lamellae are triangular in shape and their base is oriented mediolaterally. The sharp edge is pointing upwards (arrow). Note the absence of lateral/ventral lamellae. Beak tip is to the right.

***Figure 4.7**. B.* Dorso-lateral view of mandibular lamellae of greylag goose. Showing are the right and left rami. See further caption figure 4.7A.

Terrestrial grazing species: the tongue

In most species there are no grooves along the sides of the tongue cushion. The tongue lacks well-developed lingual ears and comb and its surface is almost bald (figure 4.8A and 4.8B). In about half the species short hairs are only present next to the scrapers (e.g., *Anser*, *Branta* species). The anterior part of the tongue is rather flat instead of bulged as in filter-feeding ducks, and the tongue cushion is also less prominent and more difficult to delineate from the rest of the tongue. Small spines line the sides of the rostral part of the tongue, which are partly covered dorsally by a row of hairlike structures. Large scrapers line the sides of the caudal part of the tongue.

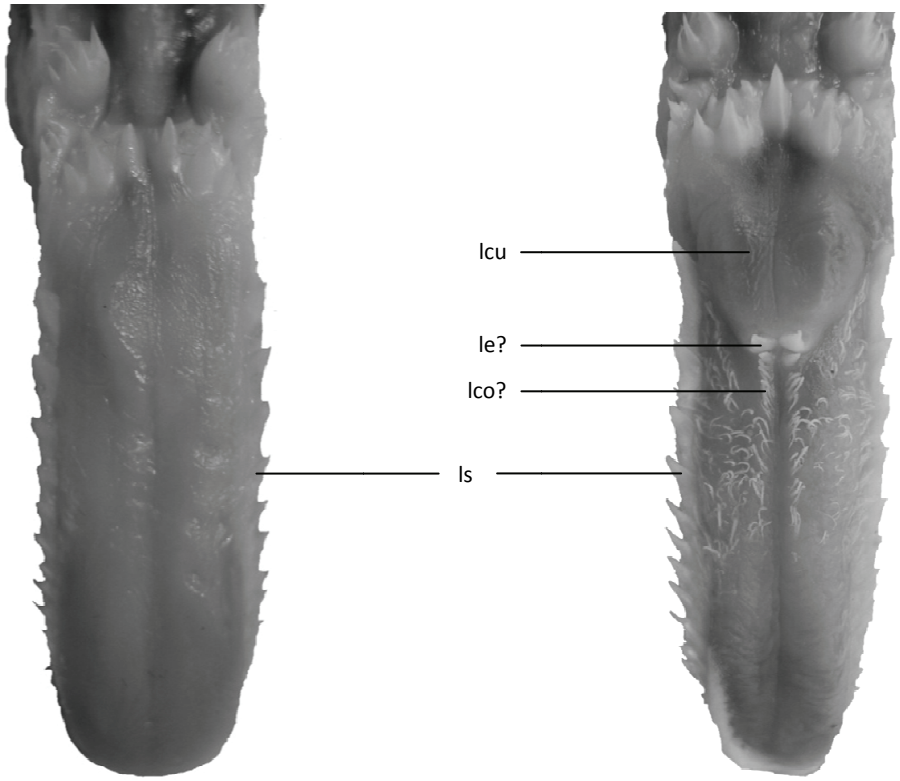


Figure 4.8. *A*. Dorsal view of tongue of barnacle goose. Note the flat hairless bulges and flat lingual cushion, and the absence of lingual ears and comb.

Figure 4.8. *B*. Dorsal view of tongue of lesser white-fronted goose. Note the flat hairless bulges. The lingual cushion is less prominent than in aquatic feeding anatids. Le and lco are thought to be homologous to lingual ears and comb respectively.

Terrestrial grazing species: variation among species

The morphology of the oropharynx of several grazing species departs more or less from the general description given above. In grazing whistling-duck species the inner surface of the upper bill is bold (*Dendrocygna eytoni*) or only few papillae are present caudally (*Dendrocygna autumnalis*) (figure 4.9: bb). In the two wigeon species the papillae on the roof of the oral cavity are small and bump-like and form transverse rows (figure 4.10: btr and bb). Both the whistling-duck species and the wigeon species possess longitudinal and transverse grooves (figure 4.9 and 4.10: bsg) in the upper bill.The mandible of the wigeon species, maned duck and all sheldgeese species studied has two series of mandibular lamellae instead of one as in the true geese.
In the maned duck, the ventral lamellae are relatively flat and do not cover the dorsal half of the mandible. In the wigeons, maned duck and especially the grazing whistling-ducks the dorsal mandibular lamellae are oriented less dorsal and more lateral than in the other grazing species, which makes the dorsal edges of the lamellae less sharp.

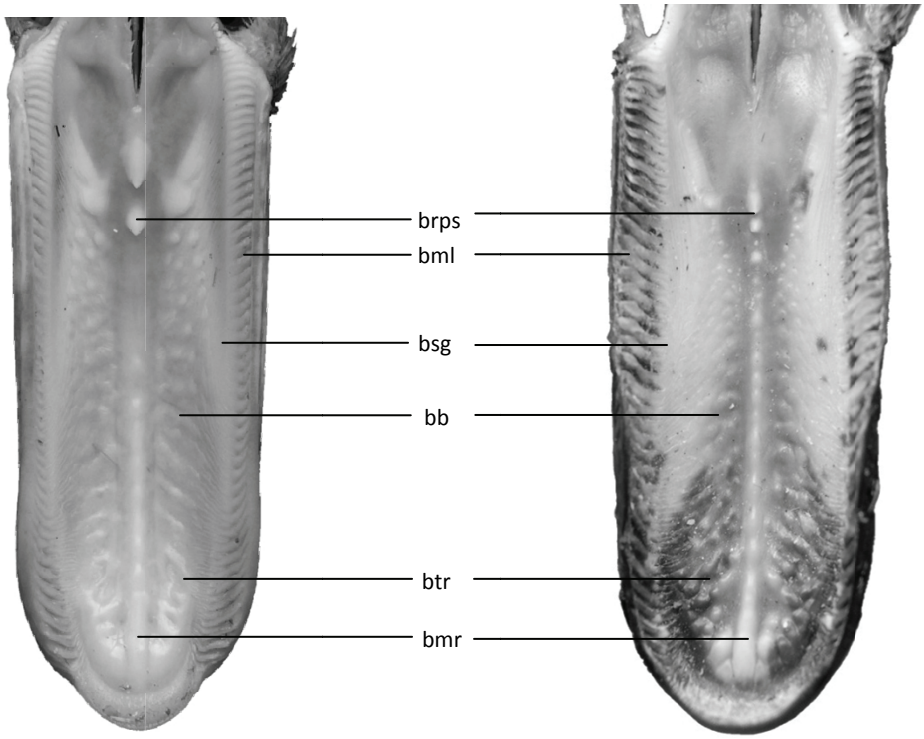


Figure 4.9. Upper bill of black-bellied whistling-duck (*Dendrocygna autumnalis*). Only a few small bumps and ridges are present on the inner side of the upper bill.

Figure 4.10. Upper bill of American wigeon (*Anas americana*). Note the many small bumps on the lining of the bill and the caudally pointing spines on the maxillary ridge. Similar in the other two extant wigeons.

Unlike most grazing species the two wigeon and two grazing whistling-duck species possess a prominent lingual cushion with a groove running along both sides (figure 4.11 and 4.12). Well-developed lingual ears and combs are only present in the wigeons (figure 4.12: le). In the whistling-ducks (figure 4.11), Canada goose (*Branta canadensis*), brent (*Branta bernicla*) goose and all six *Anser* species the rostral border of the lingual cushion is keratinized.
The black-bellied whistling duck and plumed whistling duck have lingual bulges with lateral scale-like structures (figure 4.11). In the two wigeon species the bulges of the tongue bear dorsally and laterally hair-like structures (figure 4.12: lb)

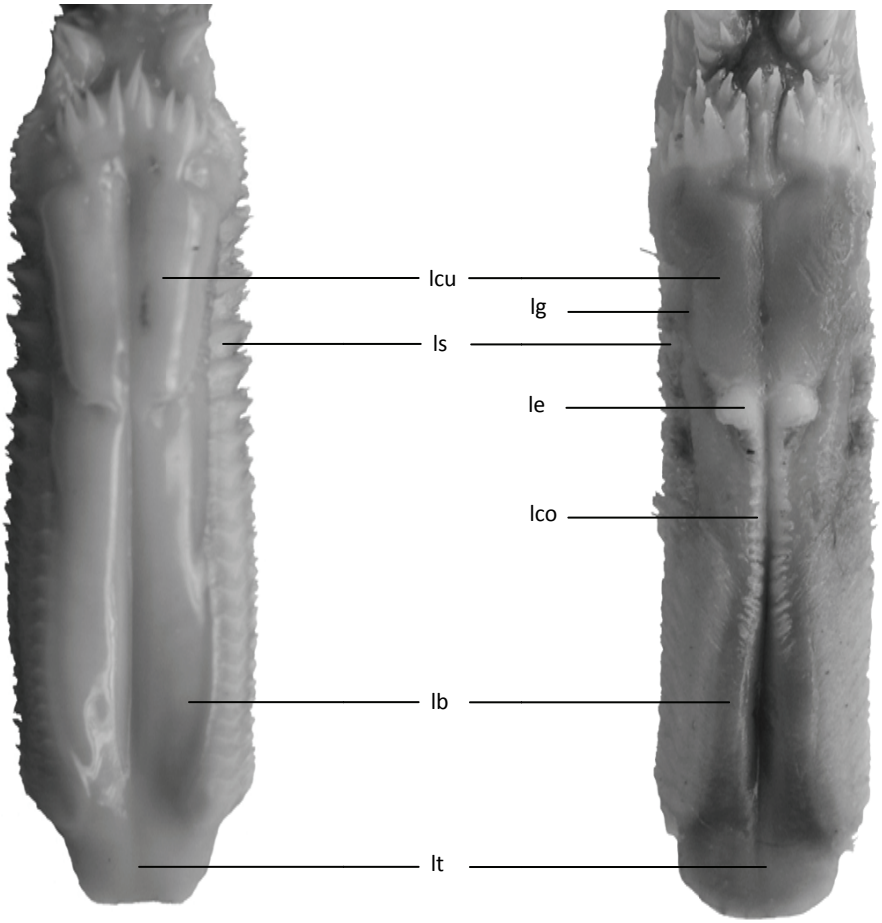


Figure 4.11. Dorsal view of tongue of black-bellied whistling-duck. Note the scale-like structures laterally on the bulges and the fringed edge of the lingual groove.

Figure 4.12. Dorsal view of tongue of American wigeon. The tongue resembles those of filter-feeding species to a large extent, and is similar to the tongue of the other two wigeons.

Quantitative analysis

Dimensions of the trophic apparatus are listed in table 4.1, presence, size, and number of structures of the tongue is given in table 4.2. Table 4.3 gives the quantitative relationships between bill or tongue dimensions and body mass. The calculated independent contrasts show that the effect of phylogeny on the model II regressions is very limited. The correlation coefficients and slopes calculated through independent contrasts are only slightly lower than for model II regression.

Quantitative analysis: the bill

Cranium length and bill length scale differently with body mass. Cranium length increases negative allometrically with body size (exponent 0.215), and is the same in aquatic feeders and terrestrial grazers. The bill scales isometrically with body size (exp. 0.339) in both trophic groups, but is 1.35 times longer in aquatic than in terrestrial feeders.

Measures for caudal and rostral bill height or width are all compatible with isometric scaling with respect to body mass, but intercepts may differ. Rostral bill width and the height of the bill at the level of the kinetic hinge are larger in aquatic feeders than in terrestrial grazers.

The height of the inside of the upper bill measured rostrally where the bulges operate differs between the two groups. The relationship between body size and height (curvature) of the inside of the upper bill is weak: there is no correlation in terrestrial grazers, and the correlation found for aquatic feeders ($r = 0.693$, $n = 19$) depends on the two largest swan species. However, on average the upper bill is 1.6 times deeper in aquatic feeders than in terrestrial grazers (aquatic feeders 11.1 mm (n = 19, CI 10.04-12.2), terrestrial feeders 6.8 mm (n = 20, CI 5.96-7.59)).

Table 4.1. Dimensions of head, bill and tongue of wildfowl species examined. Upper panel: aquatic feeder group, lower panel: terrestrial grazing group.

Species	Body mass (g)	Bill length (mm)	Bill width nail (mm)	Bill width joint (mm)	Bill height joint (mm)	Max. depth (mm)	Head length (mm)	# of max. lam.	# of dorsal mand. lam.	# of ventr. mand. lam.	# of palatal spines	Length lingual tip (mm)	Length bulges (mm)	Length bumps (mm)	Length posterior most part tongue (mm)
Aquatic feeders															
Fulvous whistling-duck (*Dendrocygna bicolor*)	600	58.96	20.99	19.13	25.37	1.35	101.44	60	110	53	0	5.25	26.86	11.8	5.51
White-faced whistling-duck (*D. viduata*)	480	54.31	19.20	17.70	25.20	1.30	94.27	60	117	55	0	5.65	20.29	12.91	4.14
Flightless steamer duck (*Tachyeres pteneres*)	2620	65.04	23.09	25.10	33.79	1.20	119.57	40	62	26	bumps	6.88	21.61	17.71	6.49
Ruddy shelduck (*Tadorna ferruginae*)	1460	56.53	18.35	18.69	26.22	1.00	104.41	44	116	54	bumps	5.49	18.74	11.75	6.40
Cape shelduck (*T. cana*)	1660	55.82	20.72	21.46	26.62	1.20	108.16	52	140	58	bumps	6.92	21.77	9.96	6.08
Spectacled duck (*Anas specularis*)	1134	60.67	19.94	20.19	25.90	1.25	111.10	44	69	46	0	5.14	23.72	12.71	5.38
Hottentot teal (*A. hottentota*)	200	38.00	14.48	12.66	14.79	0.85	71.45	51	107	59	0	3.17	15.90	7.82	3.20
Mallard (*A. platyrhynchos*)	1206	62.38	23.87	21.65	26.61	1.20	110.38	42	76	56	0	4.00	25.06	15.92	4.82
Australian shoveler (*A. rhynchotis*)	320	63.71	26.28	16.87	21.35	1.10	102.86	110	82	50	0	6.02	26.14	17.75	5.01

Species	Body mass (g)	Bill length (mm)	Bill width nail (mm)	Bill width joint (mm)	Bill height joint (mm)	Max. depth (mm)	Head length (mm)	# of max. lam.	# of dorsal mand. lam.	# of ventr. mand. lam.	# of palatal spines	Length lingual tip (mm)	Length bulges (mm)	Length bumps (mm)	Length posterior most part tongue (mm)
Baikal teal (*A. formosa)*	320	44.80	16.53	16.45	20.50	0.85	85.42	39	63	50	0	3.17	19.82	10.98	3.20
White-cheeked pintail (*A. bahamensis*)	440	50.34	17.06	16.53	25.33	1.00	89.34	48	93	63	0	3.73	19.45	11.19	3.60
Marbled teal (*Marmaronetta angustirostris*)	480	46.96	15.90	15.83	19.20	1.00	90.16	51	116	73	0	4.25	18.71	11.62	3.71
Ferruginous duck (*Aythya nyroca*)	520	39.13	15.23	17.19	21.90	1.00	78.68	32	45	37	0	2.78	17.15	6.17	4.35
Wood duck (*Aix sponsa*)	350	40.90	13.60	17.30	20.16	0.75	80.07	23	32	34	bumps	3.45	15.5	7.54	4.10
Red-crested pochard (*Netta rufina*)	780	55.61	18.32	25.58	22.76	0.80	102.00	34	57	22	bumps	5.26	19.01	11.76	4.84
Rosy-billed pochard (*N. peposaca*)	910	56.11	20.35	21.68	25.63	1.00	100.49	31	58	63	bumps	5.72	21.76	11.06	4.91
Mute swan (*Cygnus olor*)	6780	105.49	35.38	38.51	49.05	1.50	182.67	49	86	36	bumps	9.04	32.38	29.27	11.74
Bewick's swan (*C. bewickii*)	5100	84.31	30.72	30.66	42.16	1.50	147.32	38	62	28	bumps	9.08	29.56	14.36	13.05
Black swan (*C. atratus*)	4880	72.78	25.94	27.65	33.24	1.25	133.27	39	62	22	bumps	8.03	22.07	18.4	8.65

Species	Body mass (g)	Bill length (mm)	Bill width nail (mm)	Bill width joint (mm)	Bill height joint (mm)	Max. depth (mm)	Head length (mm)	# of max. lam.	# of dorsal mand. lam.	# of ventr. mand. lam.	# of palatal spines	Length lingual tip (mm)	Length bulges (mm)	Length bumps (mm)	Length posterior most part tongue (mm)
Terrestrial grazers															
Black-bellied whistling-duck (*Dendrocygna autumnalis*)	620	52.64	18.00	19.25	25.84	1.00	89.88	47	70	44	bumps	6.05	23.17	10.16	5.31
Plumed whistling-duck (*D. eytoni*)	780	47.10	18.25	18.90	24.54	0.90	84.51	45	75	38	0	6.85	18.97	8.21	4.34
Maned duck (*Chenonetta jubata*)	480	28.95	12.15	16.08	17.80	0.50	74.60	19	29	22	79	3.13	8.73	6.69	2.69
American wigeon (*Anas americana*)	740	42.59	14.52	16.15	19.52	0.80	87.38	36	66	34	35	4.70	15.15	11.18	3.43
Chiloe wigeon (*A. sibilatrix*)	440	43.27	16.31	18.80	19.42	0.90	86.68	33	60	31	35	3.08	14.06	8.76	4.88
Egyptian goose (*Alopochen aegypticus*)	1880	54.96	19.24	22.33	27.94	1.00	105.61	30	43	34	136	5.87	17.46	9.10	4.73
Orinoco goose (*Neochen jubatus*)	1350	44.65	16.95	18.90	22.82	0.90	92.93	31	50	36	101	6.74	12.13	7.75	4.95
Upland goose (*Chloephaga picta*)	1240	39.42	17.08	21.43	23.24	0.65	100.68	21	42	22	82	6.46	7.08	10.82	3.43
Ashy-headed goose (*C. poliocephala*)	720	33.60	13.94	16.90	21.25	0.65	85.97	22	36	25	67	4.99	5.96	9.53	3.54

Species	Body mass (g)	Bill length (mm)	Bill width nail (mm)	Bill width joint (mm)	Bill height joint (mm)	Max. depth (mm)	Head length (mm)	# of max. lam.	# of dorsal mand. lam.	# of ventr. mand. lam.	# of palatal spines	Length lingual tip (mm)	Length bulges (mm)	Length bumps (mm)	Length posterior most part tongue (mm)
Ruddy-headed goose (*C. rubidiceps*)	1700	31.87	12.90	17.08	19.05	0.50	84.29	21	35	23	61	5.15	6.20	6.34	2.35
Swan goose (*Anser cygnoides*)	2800	80.58	24.72	30.22	39.82	0.70	148.98	28	39	-	59	9.07	23.93	23.10	8.26
Greylag goose (*A. anser*)	4204	69.36	20.94	31.94	38.97	0.55	125.67	21	31	-	88	8.24	14.55	21.84	7.00
Lesser white-fronted goose (*A. erythropus*)	1640	39.70	15.60	22.63	24.58	0.60	87.61	24	42	-	62	3.45	12.27	8.91	4.65
Bar-headed goose (*A. indicus*)	1140	52.34	18.78	23.66	23.93	0.60	102.95	27	38	-	67	5.87	14.16	11.53	5.69
Emperor goose (*A. canagicus*)	1060	41.72	17.26	24.26	23.56	0.60	89.69	21	31	-	115	6.60	10.40	11.92	7.20
Snow goose (*A. caerulescens*)	3900	58.57	17.07	27.83	39.98	0.50	121.34	25	38	-	90	6.65	12.68	23.55	6.74
Brent goose (*Branta bernicla*)	1320	38.95	14.40	19.77	23.05	0.55	87.41	24	44	13	67	5.39	11.17	12.80	4.78
Barnacle goose (*B. leucopsis*)	1850	35.65	14.57	19.35	23.61	0.55	85.21	20	36	-	92	4.55	11.05	7.31	4.86
Canada goose (*B. canadensis*)	3480	57.20	19.61	27.29	32.10	0.60	119.06	34	41	-	120	5.02	20.61	15.46	6.67
Red-breasted goose (*B. ruficollis*)	920	27.58	14.38	18.08	21.16	0.50	73.27	13	31	-	47	3.00	7.37	6.47	3.80

Table 4.2. Summary of oropharyngeal features of anseriforms. Numbers indicate total number of species studied or number of species with specific features.

	Aquatic feeders			Terrestrial grazers					
	Filter-feeders[A] (n = 6)	Swans (n = 3)	Other[B] (n = 10)	Whistling ducks (n = 2)	Wigeons (n = 2)	Maned duck (n = 1)	Sheldgeese (n = 5)	Geese *Branta* (n = 4)	Geese *Anser* (n = 6)
Pronounced lingual bulges	Yes	Yes	Yes	Yes	Yes	No	No	No	No
Hairs on both dorsal and/or lateral side of lingual bulges	Yes	Yes	Yes scales: 2	No, scales instead	Yes	Yes	Yes	No	No
Papillae on lingual bathmat	Yes	No	No	No	Yes	No	No	No	No
Size of lingual scrapers[1]	Small: 4 Intermediate: 2	Large	Small: 2 Intermediate: 6 Large: 2	Large	Small: 1 Intermediate: 1	Intermediate	Small:2 Intermediate:2 Large: 1	Intermediate: 1 Large: 3	Intermediate: 2 Large: 4
Lingual comb with lingual ears	Yes	Yes	Yes: 4, No: 4, Small: 2	No	Yes	No	No	No	No
Longitudinal slits running from lingual ears on both sides of lingual cushion	Yes	No: 2 Small: 1	Yes: 9 No: 1	Yes	Yes	No	No	No	No
Spines on roof oral cavity	No	Yes	Small bumps: 7 No: 3	Small bumps: 1 No: 1	Small bumps	Yes	Yes	Yes	Yes
Dorsal edge of dorsal mandibular lamellae	Rounded	Sharp	Rounded Sharp: 3	Rounded	Rather sharp	Rather sharp	Sharp	Sharp	Sharp

A: *A. hottentota*, *A. rhynchotis*, *A. formosa, A. bahamensis*, *M. angustirostris*, *A. specularis,*

B: *A. nyroca*, *T. cana*, *T. ferruginea*, *N. peposaca*, *N. rufina*, *D. viduata*, *D. bicolor*, *A. platyrhynchos*, *T. pteneres*, *Aix sponsa,*

1: inverse relationship with amount of hairs in-between

Table 4.3. Relationships between (log) bill and (log) tongue dimensions and (log) body mass.
Aq: aquatic, Te: terrestrial, cs: common slope, ic: independent contrasts, r = Pearson correlation, p^1 = probability that slopes are equal for the aquatic and terrestrial group, p^2 = probability that intercepts of the two groups are equal for the common slope.

		n	r	slope	p^1	95% CI	intercept	intercept common slope	p^2
Cranium	Aq	28	0.906***	0.207		0.175-0.246	1.066	1.042	
Length	Te	20	0.773***	0.243		0.178-0.331	0.943	1.029	
-	cs	48		0.215	0.369	0.184-0.251			0.268
Body mass	ic	48	0.730***	0.190		0.140-0.240			
Bill length	Aq	28	0.744***	0.308		0.236-0.402	0.815	0.717	
-	Te	20	0.585**	0.423		0.286-0.626	0.328	0.583	
Body mass	cs	48		0.341	0.184	0.273-0.426			0.000
	ic	48	0.590***	0.250		0.148-0.344			
Bill width c	Aq	28	0.802***	0.318		0.250-0.403	0.340	0.349	
-	Te	20	0.800***	0.311		0.232-0.416	0.357	0.343	
Body mass	cs	48		0.315	0.901	0.263-0.377			0.792
	ic	48	0.590***	0.190		0.117-0.257			
Bill width r #1	Aq	26	0.694***	0.296		0.220-0.399	0.421	0.462	
-	Te	20	0.515*	0.261		0.173-0.394	0.408	0.339	
Body mass	cs	46		0.283	0.620	0.224-0.358			0.000
	ic	46	0.450**	0.150		0.061-0.241			
Bill height c	Aq	19	0.927***	0.270		0.223-0.327	0.606	0.531	
-	Te	20	0.819***	0.364		0.275-0.482	0.261	0.474	
Body mass	cs	39		0.296	0.079	0.251-0.349			0.003
	ic	39	0.770***	0.270		0.195-0.335			
Bill height r	Aq	19	0.822***	0.331		0.248-0.442	-0.053	-0.156	
-	Te	20	0.782***	0.410		0.302-0.555	-0.282	-0.146	
Body mass	cs	39		0.366	0.302	0.301-0.445			0.700
	ic	39	0.600***	0.250		0.141-0.361			

		n	r	slope	p[1]	95% CI	intercept	intercept common slope	p[2]
Bill depth	Aq	19	0.693***	0.198		0.138-0.284	-0.551		
-	Te	20	-0.347 ns	#2					
Body mass	cs								
	ic	39	0.140 ns						
Lamellar density	Aq	19	-0.777***	-0.321		-0.440/-0.234	1.905	2.011	
max.	Te	20	-0.739***	-0.400		-0.555/-0.288	2.144	2.008	
-	cs	39		-0.356	0.321	-0.441/-0.288			0.940
Body mass	ic	39	-0.680***	-0.290		-0.385/-0.187			
Dors. lamellar	Aq	19	-0.559*	-0.384		-0.580/-0.254	2.352	2.559	
density mand.	Te	20	-0.766***	-0.499		-0.682/-0.365	2.6641	2.524	
-	cs	39		-0.454	0.303	-0.579/-0.357			0.442
Body mass	ic	39	-0.500**	-0.250		-0.384/-.0111			
Vent. lamellar	Aq	19	-0.838***	-0.305		-0.402/-0.232	1.950	1.889	
density mand.	Te	11	0.083 ns					1.878	
-	cs	30		-0.284		-0.369/-0.219			0.186
Body mass	ic	30	-0.600***	-0.230		-0.336/-0.115			
Tongue length	Aq	19	0.988***	1.03		0.95-1.11	-0.149	-0.195	
-	Te	20	0.962***	1.14		1.00-1.30	-0.346	-0.205	
Bill length	cs	39		1.053	0.166	0.969-1.144			0.324
	ic	39	0.970***	1.060		0.973-1.153			
Tongue tip length	Aq	19	0.823***	0.347		0.260-0.462	-0.320	-0.431	
-	Te	20	0.533*	0.473		0.318-0.719	-0.766	-0.473	
Body mass	cs	39		0.384	0.200	0.299-0.488			0.249
	ic	39	0.410	0.190		0.059-0.319			
Tongue tip length	Aq	19	0.893***	1.40		1.11-1.75	-1.739	-1.585	
-	Te	20	0.726***	1.13		0.81-1.58	-1.137	-1.429	
Bill length	cs	39		1.308	0.292	1.081-1.585			0.000
	ic	39	0.670	0.800		0.515-1.075			

		n	r	slope	p[1]	95% CI	intercept	intercept common slope	p[2]
Length bulges #3	Aq	19	0.635**	0.194		0.132-0.983	0.755		
-	Te	20	0.228 ns	#3					
Body mass	cs	39							
	ic	39	0.390	0.200		0.048-0.348			
Length bulges	Aq	19	0.893***	0.783		0.623-0.983	-0.041		
-	Te	20	0.798***	1.476		1.100-1.981	-1.339		
Bill length	cs	39			0.002				
	ic	39	0.860***	1.120					
Length scraper	Aq	19	0.666**	0.347		0.239-0.505	0.062		
area	Te	20	0.652**	0.608		0.421-0.878	-0.869		
-	cs	39			0.036				
Body mass	ic	39	0.490**	0.300		0.126-0.466			
Length scraper	Aq	19	0.900***	1.40		1.12-1.75	-1.360	-1.386	
area	Te	20	0.819***	1.44		1.09-1.90	-1.341	-1.301	
-	cs	39		1.414	0.878	1.186-1.686			0.005
Bill length	ic	39	0.810***	1.240		0.954-1.534			
Length cushion	Aq	19	0.929***	0.382		0.316-0.461	-0.410	-0.462	
-	Te	20	0.540*	0.500		0.333-0.750	-0.884	-0.571	
Body mass	cs	39		0.400	0.255	0.320-0.498			0.002
	ic	39	0.350*	0.150		0.018-0.278			
Length cushion	Aq	19	0.887***	1.54		1.22-1.95	-1.975	-1.716	
-	Te	20	0.801***	1.18		0.88-1.58	-1.272	-1.617	
Bill length	cs	39		1.392	0.144	1.165-1.665			0.002
	ic	39	0.750***	0.810		0.576-1.036			

#1 without 2 merganser species

#2 aquatic feeders 11.1± 2.2 mm (n = 19) terrestrial feeders 6.8± 1.7 mm (n = 20) (df = 37; p = 0.000)

#3 aquatic feeders 21.9± 4.5 mm (n = 19) terrestrial feeders 13.6± 5.3 mm (n = 20) (df = 37; p = 0.000)

For all species the density of lamellae on the upper bill is lower (8.8 ± 2.8/cm; n = 39) than the density of the dorsal mandibular lamellae (15.5 ± 6.1/cm; n = 39) or the density of the ventral mandibular lamellae when present (11.3 ± 2.9/cm; n = 30). These densities differ significantly among each other (Wilcoxon Signed Ranks Test, all p = 0.000) and are correlated (r between 0.535-0.714; all p = 0.000). The interlamellar distance (i.e. inverse of lamellar density) of ventral mandibular and maxillary lamellae increases isometrically with body mass. The interlamellar distance of dorsal mandibular lamellae increases slightly positive allometrically. There are no differences in lamellar densities between aquatic feeders and terrestrial grazers (figure 4.13).

The average density of spines on the inside of the upper beak in terrestrial feeding anatids is 9.3 ± 4.7/cm^2 (n = 19). There is no clear correlation between spine density and body mass (r = -0.277, n = 19, p = 0.349). *Dendrocygnus eytoni* has no spines, while *Chenonetta jubata* has the highest density of all species examined (19.3/cm^2). Within the *Anser-Branta*-sheldgeese group the swan goose has a very low spine density (2.7/cm^2), which is even lower than that of the two wigeon species (approx. 5/cm^2).

Quantitative analysis: the tongue

The length of the tongue correlates highly with length of the bill (r = 0.982, p = 0.000, n = 39). The various parts into which the tongue can be divided have different relative dimensions in aquatic and terrestrial foragers (figure 4.14).

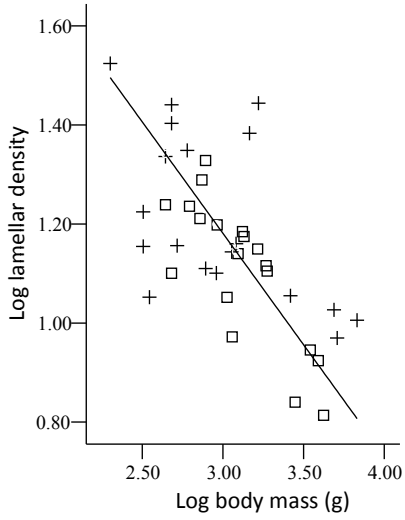


Figure 4.13. Log density of dorsal mandibular lamellae relative to log body mass. □: terrestrial grazing group, + : aquatic feeding group, line represents regression II fit between log body mass and log density lamellae.

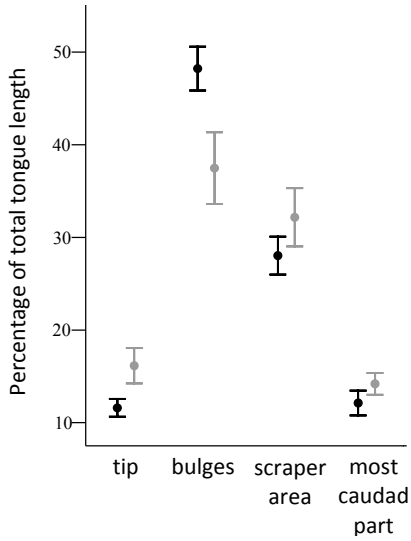


Figure 4.14. Relative lengths (% of total tongue length) of lingual elements (tip, bulges, scraper-area, and most caudad part of the tongue). Grey represents aquatic feeders, black terrestrial grazers.

The length of the tongue tip increases with body mass (exp. 0.382) and has the same size in both foraging groups. As bill and tongue are shorter in terrestrial feeders than in aquatic feeders the tip comprises a relatively larger part of the tongue in terrestrial feeders (16.2 vs. 11.6% of tongue length). The length of the bulges varies widely. In terrestrial feeders there is no correlation between length of the bulges and body mass (table 4.3). In aquatic feeders the length of the bulges is weakly correlated with body mass, but the significance of this correlation only depends on the values for the two largest swan species. On average the aquatic feeders (av. body mass 1592 g) have longer bulges than the terrestrial feeders (1633 g): 21.9 ± 4.5 mm (n = 19) versus 13.6 ± 5.3 mm (n = 20). Although one would expect terrestrial feeders to have shorter bulges because their beak is relatively shorter than in aquatic feeders, the bulges are also shorter relative to total tongue length: 37.5% compared to 48.2%. This situation is complicated by the fact that in aquatic feeders bulges become relatively shorter with increasing bill (or tongue) length (exp 0.783), while in terrestrial feeders bulges become relatively longer (exp 1.476) with increasing bill length (table 4.3). In large terrestrial grazers (geese) the difference in absolute length of the bulges compared to large aquatic feeders (swans) therefore becomes much smaller.

The relatively large bulges in aquatic feeders are associated with a relatively short scraper area behind the bulges, which is 0.82 times shorter than in terrestrial feeders. Note, however, that because the total bill/tongue length is longer, the absolute length of the scraper area in aquatic feeders is longer. The length of the most caudad part of the tongue is 1.3 times longer in aquatic feeders than in terrestrial feeders with similar body mass.

Discussion

Main results

We examined the oral morphology of a large number of anseriform species from several genera to check whether the typical morphological characters associated with different ways of transporting food through the oral cavity in mallard and domestic goose are consistently related to feeding habits. Although there is some variation in feeding habits within the trophic groups investigated most aquatic feeding birds have a bald roof of the oral cavity and a groove running along both sides of the lingual cushion, while in most grazing anatid species spines or papillae-like structures are present on the roof of the oral cavity. Most aquatic feeding species studied also have well developed lingual ears and lingual combs, which line both sides of the lingual median groove, and the tongue bears hair like structures and papillae. In grazing species the surface of the tongue is bald and the lingual ears and combs are very small or absent. All grazing species (and to a lesser extent the wigeons and whistling-ducks) have sharp edged dorsal mandibular lamellae, in contrast to most aquatic feeding species where the dorsal rim of the lamellae is smooth.

Previous descriptions of structures of the oral cavity of other aquatic feeding species are consistent with the general description of aquatic feeding species given in the present study, e.g. for the mallard (Berkhoudt, 1980; Zweers, 1974; Zweers et al., 1977) and the tufted duck (Kooloos et al., 1989). The oropharyngeal structures in the northern shoveler by Kooloos et al. (1989) are very similar to those described for the Australian shoveler in the present study. The descriptions of the oral cavity of the domestic and greater white-fronted goose, and the Eurasian wigeon (Van der Leeuw et al., 2003) are consistent with those of the *Anser* species and the two wigeon species in our study, respectively.

Quantitative measurements of the bill show that in aquatic feeding anatids the bill is relatively longer, deeper and rostrally wider than in grazing species. Similar results were found when scaling was based on the shape of the skull instead of body mass (chapter 2). Tongue dimensions show that on average, the absolute length of the lingual bulges is much larger in aquatic feeders than in terrestrial grazers. Relative to tongue length the bulges are also longer in aquatic feeding anseriforms than in grazing anseriforms. There is no difference in lamellar density between aquatic feeders and terrestrial grazers.

Functional significance

The association between oral morphology and feeding habits seems to be explained by the biomechanics of the feeding process.
In filter-feeding food and water are drawn into the bill through a piston-like function of the tongue. Kinematical analysis of high speed video and X-ray film recordings of filter-feeding (Zweers et al., 1977; Kooloos et al., 1989) has shown that in the mallard the intake of water and food at the bill tip occurs simultaneously with the expel of water and retention of food. The bill and tongue kinematics underlying this mechanism are complex. When the bill opens, the tongue is retracted while the rostral part of the tongue (lingual bulges) is kept elevated against the ventral side of the upper bill. These coordinated actions of tongue and bills draw water and food items into the anterior bill cavity. The amount of water that is sucked in per movement cycle depends on the size of the rostral compartment of the bill that is bordered by the bill tip at the front and the elevated bulges at the back. The depth, as well as the width of the bill and the enlarged rostral part of the tongue may therefore increase the pump capacity. When the bills start to close again the tongue protracts and the lingual bulges are depressed, forcing water and food items over the bulges to the back of the tongue. It has been hypothesized (Kooloos et al., 1989: figure 4.7) that the lingual combs and ears serve to divert food kernels coming from the lingual bulges to the sides of the tongue, where they are transported further caudad to the lingual cushion. The water that is transported backwards is prevented from entering the oesophagus by the elevated posterior part of the tongue (the lingual cushion), which remains elevated throughout successive pump-cycles. During the next movement cycle when the tongue retracts again the volume of the posterior bill cavity is reduced and water is forced out through the space between the lamellae. The movable upper and lower bill are set in such a way that the separation between upper and lower bill lamellae determines the lower limit on the size of the food retained (Kooloos et al., 1989; Gurd, 2005). To be able to continue filter-feeding food must be transported away from the filter area at the rims of the bill. Spines and scrapers at the side of the tongue, which move food

items through a groove along the side of the lingual cushion, mediate a further transport to the oesophagus. The function of the small spines bordering the rostral part of the tongue is unknown.

The process of food transport described above is called ‘‘under-tongue’ transport’. It enables filter-feeding ducks to continue feeding without the necessity to stop and swallow. This filter and transport mechanism requires a bold palate so that the tongue is able to seal off the different compartments of the oral cavity and to generate enough suction force, and structures to direct the food along the base of the tongue. The ‘under-tongue’ transport is typical for filter-feeding.

Grazing was studied by kinematical analysis of high speed video and X-ray film recordings of the domestic goose (Van der Leeuw et al., 2003). The sharp edge of the dorsal mandibular lamellae in grazing species may serve to pierce vegetation during the pulling phase of grazing. Clipped vegetation is transported to the lingual base through back-and forward movements of the tongue. Tongue movement cycles are timed differently with respect to opening and closing of the bills than in filter-feeding and food items are not diverted to the side of the bill but follow a more medial course over the tongue than in filter-feeders. During the transport of food items protraction of the elevated tongue coincides with bill opening, and when the tongue moves forward the food items are held in place by papillae on roof of the upper bill. The food is transported further backward during tongue retraction and depression when the bills are closed (‘over-tongue’ transport).

Some filter-feeders, like the mallard, are also able to graze. However, the way in which mallards transport grass through the bill to the oesophagus is completely different from the transport mechanism in the domestic goose. Due to its size and shape vegetation has to be transported over the lingual cushion, which is done in the same way as large food items are in many other avian species (Bramble and Wake, 1985; Zweers et al., 1994). During a fast head movement food is released from the bills and caught again, while the head is moved over the food item, a mechanism known as inertial transport or ‘catch-and-throw’.

Grazing species are also capable of filter-feeding; but food is transported over-the-tongue, as shown in the domestic goose (Van der Leeuw et al., 2003). To transport food over the lingual cushion to the oesophagus, the lingual cushion is depressed during tongue retraction, and elevated during the tongue protraction. This transport mechanism is very similar to the one used during grazing (Van der Leeuw et al., 2003). The use of inertial transport for clipped vegetation in the mallard and the ‘over-tongue’ transport during filter-feeding in geese is associated with low intake rates compared to ‘under-tongue’ transport for filter-feeding in the mallard and ‘over-tongue’ transport for grazing in geese, respectively (Van der Leeuw et al., 2003, chapter 5 en chapter 6).

Variation in morphology

Not all aquatic feeding anseriform birds use filter-feeding as their main method of foraging. Several species take food items such as molluscs, insects, or pieces of aquatic vegetation. Such food items are often too large to pass along the tongue cushion and for such food items 'over-tongue' transport may be expected. When both small and large food items are taken, possibly at different times of the year, combinations of oropharyngeal characters associated with 'over-' and 'under-tongue' transport are found. Three species from the aquatic feeder group, the mute and black swan, and the red-crested pochard, do not possess slits along the lingual cushion, as do the other members of the group. These three species also have diagonally running shallow ridges and small bumps on (part of) the roof of the oral cavity, and sharp edged dorsal mandibular lamellae. Swans and red-crested pochard all feed mainly on aquatic vegetation (Corti and Schlatter, 2002; Ciaranca et al., 1997; Kear, 2005) and may be characterized as 'aquatic grazers'. In two separate studies we demonstrated that the mute swan has indeed a significant lower (scaled) intake of suspended food particles than filter-feeding ducks (chapter 6), but the performance for terrestrial grazing in mute swans is equal to those of several grazing goose species (chapter 5). Although we did not examine the pathways of food kernels through the mouth large head movements, typical for the inertial transport mechanism used by the mallard to transport grass, were not observed in the grazing swans, suggesting the use of 'over-tongue' transport. Water expulsion during aquatic feeding may not necessarily be related to filter-feeding. Swans usually feed on pieces of aquatic plants and show large water expulsion during aquatic feeding. The water flow through the oropharynx is probably used to transport pieces of aquatic plants to the oesophagus, rather than to generate a water flow through the lamellae to filter out the food items. The shallow ridges and bumps on the roof of the oral cavity may play a similar role in the transport of pieces of water plants as the spines do in terrestrial grazers.

A number of species do have grooves at the base of the lingual cushion, but also possess small bumps or ridges on the roof of the oral cavity. These species include terrestrial or aquatic vegetation or other large food items in their diet, e.g., the ferruginous duck (a diving species, forages on molluscs and aquatic vegetation), the wood duck (terrestrial vegetation and acorns), the ruddy shelduck and cape shelduck (grass, seeds, algae, aquatic, plants, insect larva and crustaceans), and the steamerduck (feeds by diving in shallow kelp beds for marine molluscs and crustaceans). Note, however, that it is not always clear whether these species also take small food items that may be ingested through 'under-tongue' transport. The presence of bumps and ridges on the palatal surface may impair the performance of filter-feeding.

In the most recently evolved grazing species, the wigeons, the morphology of the oral cavity is less specialized than in other grazing species. The bumps on the roof of the oral cavity are smaller than in other grazing anatid species and restricted to the medial part of the oral cavity, while their lingual structures and dorsal mandibular lamellae are very similar to those of filter-feeding ducks. In the Eurasian wigeon such small bumps seem to enable this species to use the same mechanism for 'over-tongue' transport as found in the domestic goose (Van der Leeuw et al., 2003) without compromising the efficiency of filter-feeding. The filter-feeding performance of the Eurasian wigeon is very similar to the

performance of filter-feeding specialists (Van der Leeuw et al., 2003). Wigeons do not only take the green parts of terrestrial and aquatic plants but also feed on seeds, insect larvae and crustaceans (Mowbray, 1999). Although the types of transport mechanism used for grass and seeds or small animal items are not experimentally investigated is most likely that wigeons combine both an 'under-tongue' and 'over-tongue' transport mechanism for small insects or crustaceans and grazing, respectively. This may also be true for the wood duck, ferruginous duck, steamerduck and shelducks, which all possess a slit along the tongue cushion suggestive of 'under-tongue' transport. In these species the small bumps may aid in goose-like 'over-tongue' transport while foraging on terrestrial vegetation or rather large food-items. The features of the oral cavity of the two grazing whistling-ducks are not consistent with the 'over-tongue' transport characteristics; rather they are more similar to those of the 'under-tongue' transporting anatid species. Only one whistling-duck species has small bumps on the palatal surface. Possibly, grazing terrestrial vegetation is a recently acquired mode of foraging.

Evolution of feeding mechanisms in Anseriformes

Both filter-feeding (Lack, 1974; Olson and Feduccia, 1980) and feeding on aquatic plants (van der Leeuw et al., 2003) have been proposed as the ancestral feeding method for Anseriformes. The occurrence of lamellae-like structures and water expulsion during aquatic feeding are not necessarily related to filter-feeding. Geese use spines on the palatal surface for retention of food items during filter-feeding instead of their lamellae. The closely related swans feed mainly on pieces of aquatic vegetation, which are too large to be transported by the 'under-tongue' mechanism used by filter-feeding ducks. The water flow through the oral cavity is most likely used to transport pieces of plant material, rather than to generate a water flow through the lamellae to filter out food items (Van der Leeuw et al., 2003). In the Anserinae (geese and swans) lamellae may be used for grasping and cutting vegetation with the sharp edge of the lamellae, rather than for the retention of food particles during filter-feeding.
Van der Leeuw et al. (2003) suggested that feeding on aquatic plants by the 'over-tongue' transport mechanism as found in geese, has been derived from drinking movement patterns. In both geese and ducks drinking and filter-feeding mechanisms are similar. However, the tongue movements during drinking in a related galliform (chicken, (Heidweiller et al., 1992)) are similar to the movements of 'under-tongue' transporting species, and not like the 'over-tongue' mechanism applied by geese, as one would expect.

The earliest offshoots within the Anseriformes are the Anhimidae (screamers) (see figure 1 in 'general summary' chapter), which have chicken-like bills with vestigial (or ancestral) lamellae (Olson and Feduccia, 1980), and feed on aquatic plants (Naranjo, 1986). Observation of a terrestrial grazing screamer in a zoo (Avifauna, the Netherlands) hints at 'over-tongue' transport, as vegetation moved through a nearly closed bill with hardly any movements of the head. When transporting large food items most bird species use a thrust generated by back-and forward movements of the head ('catch-and-throw') to move food items over the tongue. This mechanism is considered to be the most general form of avian feeding behaviour (Zweers et al., 1994) and mallards use this 'catch-and-throw' mechanism to transport grass.

The next offshoot is the magpie goose (*Anseranas*), which filters food from water and can graze. It predominantly feeds on roots and bulbs of swamp plants (Davies, 1963; Marchant and Higgins, 1993). Unfortunately, no data is available on intraoral transport mechanism in this species.
Just before the split of Anatinae (duck-like birds) and Anserinae, the Dendrocygnidae (whistling-ducks) branch off. Only 2 of the eight species are known to graze, and the morphology of the oral characters in both foraging types is more similar to filter-feeding species than to terrestrial grazing anatids. As all morphological requirements for 'under-tongue' transport are present and virtually no grazing-related structures, it is most likely that these birds apply an 'under-tongue' mechanism in filter-feeding.

As both intraoral transport mechanisms seem to occur throughout the anseriforms (see figure 1 in 'general summary' chapter), indication of either mechanism as the ancestral feeding method is very difficult. Moreover, some of the aquatic feeding species possess structures similar to those of terrestrial feeding species in addition to structures related to an 'under-tongue' transport mechanism. These species are known to feed mainly on large aquatic food items, e.g. molluscs, large invertebrates or plant parts, and these species may be able to use both the 'under-tongue' and the 'over-tongue' transport mechanism. Wigeons, for instance, use both the 'under-tongue' transport mechanism for filter-feeding and the 'over-tongue' mechanism for the transport of grass and small seeds (Van der Leeuw et al., 2003).
Although it is sometimes believed that neuromotor patterns are conserved in evolution (Lauder, 1991) the different motor patterns underlying 'under'- and 'over'-tongue transport may be quite flexible. A comparison of the basic movement pattern of filter-feeding with those for filter-feeding or suction drinking in non-anseriforms (filter-feeding flamingos: Zweers et al. (1995); suction drinking pigeon: Zweers (1982); suction drinking estrildids: Heidweiller and Zweers (1990)), show a variety of movement patterns of tongue and bills. The basic difference between the drinking and filter-feeding mechanisms described seems to be the different timing between pro-and retraction of the tongue, and depression and elevation of the tongue. A second difference is the control of elevation and depression of the caudal part of the tongue or larynx independent of the other tongue movements, to seal off the pharynx/oesophagus. Changing the timing between different basic movements of bill and tongue may be a relatively easy way to change the transport mechanism of water or food through the oral cavity. As mentioned above the wigeon shows that movement patterns associated with 'over'-and 'under'-tongue transport may even be present within the same species (Van der Leeuw et al., 2003).

The association between oral morphology and grazing and filter-feeding suggests that 'over'- and 'under'-tongue transport mechanisms have developed more than once within the Anseriformes and that the transition from one mechanism into the other is relatively easy.

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Chapter 5

The grazing mechanism in geese and swans: how bite size, bite rate and amount of spill affect intake rate

Summary

In mammalian herbivores, the intake rate of grazing on a small spatial and temporal scale is determined by the product of bite size and bite rate (Spalinger and Hobbs, 1992). In this study we investigate how these components contribute to the intake rate in avian grazers. We performed grazing experiments with mute swans (*Cygnus olor*), Canada geese (*Branta canadensis*), lesser white-fronted geese (*Anser erythropus*) and barnacle geese (*Branta leucopsis*) on small, 8 cm tall turfs.

For all anatid species in our study intake rate increases proportionally with increasing bite size, but the increase is smaller as species are larger. Unlike in mammalian grazers, avian grazers loose significant amounts of severed vegetation during transport through the bill. The amount of grass lost increases with bite size. In both lesser white-fronted and barnacle geese no correlation between bite rate and bite size was found, but in Canada geese and mute swans bite size and bite rate show a negative correlation. As a consequence intake rate increases quickly at small bite sizes (*B. leucopsis* and *A. erythropus*), but at larger bite sizes the decrease in bite rate and the increase of food loss (*B. canadensis* and *C. olor*) start to balance the effect of increasing bite size, and intake rate levels off.

To determine the relative performance of grazing, we scaled intake rate to metabolic requirements, including data from grazing *Anas* species. Geese and swans have similar intake rates per metabolic weight. The barnacle goose, Eurasian wigeon (*Anas penelope*) and mallard (*Anas platyrhynchos*) show relatively lower intake rates. The morphology of the oral cavity may explain the relatively low intake rates in the *Anas* species, while grazing tips of leaves in barnacle geese may reflect selection for quality of food rather than quantity in this species.

Introduction

To cope with the low-energy content of grasses, grazing herbivores have to spend a considerable amount of time feeding. Intake rate, i.e. the quantity of food consumed per unit of time, determines the amount of time invested in feeding and the amount of time remaining for other activities that affect fitness.
To understand the mechanism determining intake rate in the field, several studies have focussed on a small temporal and spatial scale: intake rate over short periods of active grazing on food saturated patches. Assuming that on food saturated patches time to search for food items is negligible, intake rate is determined by the product of bite size (the amount of grass taken per bite) and bite rate (Gross et al., 1993a; 1993b; Laca et al., 1992; Parsons et al., 1994; Spalinger and Hobbs, 1992; Ungar and Noy-Meir, 1988). Hence, grazing animals may reduce time spent feeding by cropping larger bites (Gross et al., 1993a; Shipley et al., 1994; Spalinger et al., 1988; Spalinger and Hobbs, 1992), or alternatively by decreasing handling time, which is the time needed to crop and process a bite, thereby increasing bite rate. As processing time often depends on bite size, an increase in bite size leads to a decline in bite rate (Forbes, 1988; Hudson and Watkins, 1986; Laca et al., 1994; Prache, 1997; Wickstrom et al., 1984; Wilmshurst et al., 1999). Morphological properties of mammalian grazers have been related to the performance of intake rate (Andersen and Sæther, 1992; Demment and Greenwood, 1988; Gordon et al., 1996; Illius and Gordon, 1987). On both intra- (Illius et al., 1995) and interspecific level differences in body size and the size and shape of the feeding apparatus correspond to the size of a bite (Gong et al., 1996; Gordon et al., 1996; Illius and Gordon, 1987; Janis and Ehrhardt, 1988; Shipley et al., 1994) as well as to the rate of biting (Illius and Gordon, 1987).

Less detailed information is available on the mechanism controlling intake rate in grazing Anatidae (geese, swans and ducks). A number of field studies on herbivorous wildfowl have quantified intake rate (Durant et al., 2003; Hassall et al., 2001; Lang and Black, 2001; Prop, 1991; Riddington et al., 1997; Rowcliffe et al., 1999; Therkildsen and Madsen, 2000; Van der Wal et al., 1998). Similar to mammalian grazers intake rate in anseriform grazers is determined by variation in handling time (Mayhew and Houston, 1998; Owen, 1972; Sedinger and Raveling, 1986) and bite size (Black et al., 1992; Cope et al., 2005; Durant et al., 2003; Hupp et al., 1996; Stahl, 2001).
Size of the bill may be an important morphological character contributing to intake rate in anatid grazers. For bite rate, a negative relation with bill length was observed for several goose species (Owen, 1980, but see Durant et al., 2003). Durant et al. (2003) found that bite size is the main determinant of intake rate, and bite size appears to be positively related with bill size on both interspecific and intraspecific (Cope et al., 2005) level.

Grazing as feeding mechanism seems to have evolved several times within the anatid clade; of which some *Anas* species represent the most recent example (wigeon spp., Donne-Goussé et al., 2002; Livezey, 1991, 1997a). Swans (*Cygnus*) are closer related to the true geese (*Anser* and *Branta*) than the dabbling ducks (Brush, 1976; Donne-Goussé et al., 2002; Livezey, 1996b, 1997a; Sorenson et al., 1999; Sraml et al., 1996). Like geese, swans are herbivorous, although most species secure their food from aquatic plants, which may

require a somewhat different feeding technique then grazing on land. In aviculture, however, all species are able to sustain on swards. Up to now, intake rate of grazing in swans has not been studied.

The time since divergence and degree of adaptation seem not only to be reflected in skull features related to grazing (chapter 2), but also in the morphology of the oropharynx, i.e. the morphology of the tongue and lining of the bills (Van der Leeuw et al., 2003 and chapter 4). The oropharyngeal morphology of geese is particularly characterized by the presence of spines on the roof of the mouth. These spines are believed to play an important role in the retention of vegetation during the transport of food through the mouth. Species lacking such spines (*Anas*) use a different transport mechanism to transport food, which results in the loss of a large proportion of the cropped leaves (Van der Leeuw et al., 2003). Such morphological differences are therefore expected to affect handling time and indirectly intake rate.

As feeding mechanisms are important in understanding the foraging and population ecology of anseriforms (Pettifor et al., 2000), this study aims to broaden our understanding of the mechanism of grazing and its underlying factors in herbivorous Anatidae. We compared the intake rate of selected species of *Anser*, *Branta* and *Cygnus* by examining bite size, amount of leaves lost during food transport, and bite rate over short periods of active grazing. Observed differences were related to the morphology of the lining of the upper bill.

Materials and Methods

Experimental set-up

Grazing experiments were performed with four mute swan, two barnacle geese, two lesser white-fronted geese, and two large Canada geese, all purchased from a local trader. Three sets of trials were conducted, the first in August 2004, the second between April and June 2005 and the third between June and August 2005. In the first set two mute swans were used and in the second set the barnacle geese and the lesser white-fronted geese were examined.
The trials took place in an inside aviary with flowing water and ad libitum food (mixture of commercially available cereals and pellets). Both training and experimental sessions were conducted within an enclosure inside the aviary, allowing individual birds to be tested. The remaining two mute swans and the Canada geese were individually tested in an enclosure in an outside aviary also with flowing water and ad libitum food. Immediately prior to the experiments, the birds were trained for several weeks (1-3) to eat from small turfs. After the training sessions the actual measurements of intake rate were performed. The turfs were cut from larger sods purchased from a garden centre. The sods were put outside and allowed to grow until use (max. 20 cm). The sods were dominated by *Poa* spp. and *Lolium perenne* with a small proportion of *Festuca rubra*.

The afternoon preceding a trial, four turfs were prepared from the large sod and put inside. The turfs were secured to trays measuring 40x 15 cm (600cm^2), inflorescences were cut to ground level, and the remaining grass was cut to 8 cm measured with a ruler. The evening before a trial, food was removed from the aviaries. Trials started the following day between 08:00 h and 09:00 h. Five minutes before a trial a bird was gently guided to the enclosure and allowed to settle down. The animal was allowed to graze for 30 to 40 bites, or, to minimize depletion effects on intake, a trial was ended as soon as bites were taken from an area previously grazed.
A trial lasted about 5 minutes, after which spilled grass leaves were collected.
About ten trials per bird were conducted at a rate of one trial a day for the smaller geese (barnacle en lesser-white fronted geese), while the remaining birds were offered a turf twice a day. Trials usually finished before 12:00, after which food was returned to the birds.

Measurements

To characterize the turfs offered, leave density was measured for each sod. An area of 89.92 cm2 was clipped to trial height and then cut to ground level. The cut vegetation was sorted in green and dead material, weighed and the green material was then dried at about 54°C to constant weight. The mean density of fresh green leaves was 667.26 g/m^2 and ranged between 1064.28 g/m^2 and 474.87 g/m^2. Throughout the experiments leave density of the sods remained constant ($F_{3,23} = 2.23$, $p = 0.112$).

To assess the amount of grass removed after grazing, each turf was weighed to the nearest 0.1 g before and after each trial. To account for evaporative weight loss, prior to each trial the turf was weighed and placed in the experimental set up (fenced off for the bird) for 5 minutes and then re-weighed. The evaporative weight loss was subtracted from the total weight loss during the trial to derive the biomass removed from the turf by the feeding bird.
Intake was then calculated as the biomass removed minus the weight of the grass leaves lost during grazing.
Bite depth was calculated by measuring the difference between sward height at the start of the experiment and the height of the area grazed.

During each trial a video-camera recorded the activity of the grazing bird. Frame by frame replay of these recordings were used to verify the counted bites, to determine the rate of biting and to calculate the duration of cropping and transport per bite. The average bite size (fresh weight per bite in g) of a trial was calculated by dividing biomass removed by the number of bites observed from the video during that trial. Intake rate was determined as intake divided by total time of grazing, corrected for excessive bite durations. Bites that took much longer to ingest than the average of the trial were mostly due to the tearing loose of tillers with the roots still attached, and were excluded from time related calculations.

Statistical analyses

Data were ln-transformed and analysed with SPSS 12.0 and the standardized major axis routine (S)MATR (v1, Falster et al. (2003), which implements the algorithms developed by Warton and Weber (2002).
To assess differences between species in intake rate, bite size, amount of loss per bite and bite rate nested ANOVA procedures were used. Species were considered as fixed effect and individuals were random variables nested within species. When F-values proved to be significant ($p < 0.05$), post-hoc tests were performed. The Games-Howell method was used when variances were not equal.

Results

Intake rate

In table 5.1 intake rate and the factors underlying intake rate are listed per individual. Intake rate differs significantly between species ($F_{3, 6.06} = 16.97$, $p = 0.0024$) and between individuals ($F_{6, 124} = 10.871$, $p = 0.0000$). The statistical significance of individual variation is completely due to the low intake rate for mute swan #2 and the high intake rate for mute swan #3. All other individuals do not differ within the same species. Post hoc tests show that each species differs from all other species (all $p < 0.000$). In the mute swan intake rate is roughly twice as high as in the Canada geese, except for individual #2, and in Canada geese intake rate more than doubles the intake rate in barnacle geese. The lesser white-fronted geese have an intake rate intermediate of those in Canada and barnacle geese.

Bite size

Bite size (i.e. amount of grass removed per bite) is largest in the mute swan, and subsequently smaller in Canada goose, lesser white-fronted goose and barnacle goose (table 5.1). Species differ significantly in bite size ($F_{3, 6.05} = 60.90$, $p < 0.0001$). As for intake rate the difference between individuals ($F_{6, 124} = 13.955$, $p = 0.0000$) is the result of the variability in the mute swan data. Removing mute swan #1 and #2 or swan #3 and #4 from the analysis makes the variation of individuals within species not significant. Post hoc tests show that each species differs from all other species (all $p < 0.000$).
In all four anatid species measured, a clear positive relationship is found between intake rate and bite size (figure 5.1). On the individual level this correlation is always significant except for two of the four mute swans. A model II regression shows that the slopes are not significantly different among individuals ($p = 0.1489$) and that the data are consistent with a single common slope (1.09 95% CI 0.96-1.23) for all birds (figure 5.1, table 5.2). For this common slope y-intercepts differ significantly ($F_{9, 124} = 146.281$, $p = 0.000$). Lesser white-fronted and barnacle geese have similar intercepts, but ln intake rate for the same

bite size is lower in the two Canada geese (p = 0.000). The mute swans have lower intake rates relative to their bite size than all other species (p = 0.000).

Table 5.1. Averages with standard deviation between brackets of intake rate and the determinants of intake rate per individual of anatid species studied.
Intake rate = (bite size- amount of lost leaves per bite) * bite rate.

Individual	Intake rate (mg min^{-1})	Bite size (mg)	Loss per bite (mg)	Loss per bite (%)	Bite rate (min^{-1})	n
Cygnus olor #1	14051.07 (2751.41)	492.66 (111.20)	159.85 (53.93)	32.23 (7.57)	42.42 (7.95)	24
Cygnus olor #2	6933.09 (1353.99)	388.71 (69.27)	164.21 (41.13)	42.35 (7.25)	31.18 (2.95)	9
Cygnus olor #3	18135.35 (3854.37)	922.58 (239.47)	179.49 (47.54)	20.32 (6.27)	26.02 (7.35)	13
Cygnus olor #4	12548.18 (5472.23)	765.97 (249.02)	199.52 (63.77)	27.95 (10.88)	22.62 (4.94)	13
Branta canadensis #1	6676.43 (1553.32)	153.94 (37.05)	10.73 (6.15)	6.93 (3.45)	47.00 (5.12)	12
Branta canadensis #2	7011.12 (1125.26)	149.64 (29.36)	8.73 (3.49)	6.11 (3.04)	50.58 (6.71)	15
Anser erythropus #1	4877.93 (1620.02)	63.15 (8.18)	2.15 (1.61)	3.34 (2.41)	78.62 (18.55)	13
Anser erythropus #2	4238.28 (1482.51)	65.65 (19.20)	4.07 (3.44)	6.13 (4.54)	68.24 (8.08)	13
Branta leucopsis #1	2518.45 (1024.43)	37.60 (13.85)	3.23 (2.40)	8.18 (5.64)	72.47 (7.29)	12
Branta leucopsis #2	2584.03 (637.96)	37.12 (7.16)	3.35 (1.73)	9.06 (4.64)	76.78 (12.61)	10

Table 5.2. Pearson correlation-coefficient and SMA results on ln-transformed bite size and intake rate. Ln intake rate = slope * ln bite size + intercept.

Species	Pearson's r	slope	Lower CI	Upper CI	Intercept	Intercept slope = 1.09	n
Cygnus olor	0.630 **	1.011	0.824	1.240	3.004	2.533	59
Branta canadensis	0.826 **	0.910	0.723	1.146	4.266	3.394	27
Anser erythropus	0.858 **	1.327	1.053	1.671	2.836	3.835	26
Branta leucopsis	0.919 **	1.125	0.937	1.350	3.765	3.908	22

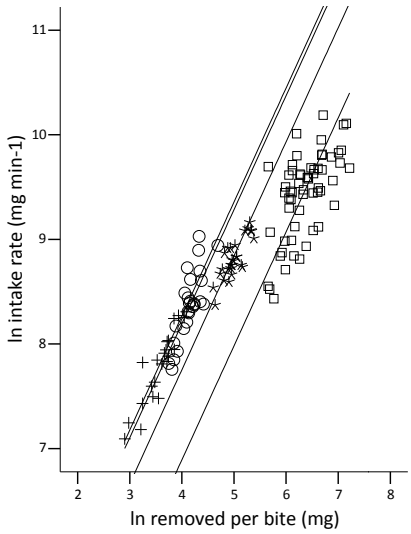

Figure 5.1. Amount of grass removed per bite (mg) against intake rate (mg min^{-1}), both ln transformed. Lines represent a model II regression with common slope but different intercepts (except for *A. erythropus* and *B. leucopsis*). Legend: □: *Cygnus olor*, *: *Branta canadensis*, ○: *Anser erythropus*, +: *Branta leucopsis*.

Bite depth

Bite size may be determined by beak width or beak length (table 5.3) and bite depth. The remaining lengths of the initially 8 cm tall leaves after a bite clearly differ between mute swan and the three goose species used in this study (figure 5.2; Kruskal Wallis $\chi^2 = 128.61$, df = 3, $p < 0.001$). The mute swan clearly has the largest bite depth (Mann-Whitney U-tests all $p < 0.001$). Canada and lesser white-fronted geese clip similar lengths (Mann-Whitney U test $p = 0.19$), but both bite slightly deeper than the barnacle goose (Mann-Whitney U test, both $p < 0.001$).

Table 5.3. Average body mass, length of the bill (gape) and width at rostral part of the bill of the individuals used in this study. Numbers in brackets indicate standard deviations.

Species		Body size (kg)	Bill length (mm)	Bill width (mm)
Cygnus olor	(n = 4)	9.22 (1.13)	105.25 (14.06)	35.45 (0.90)
Branta Canadensis	(n = 2)	3.88 (0.82)	63.81 (2.13)	22.05 (0.28)
Anser erythropus	(n = 2)	2.07 (0.11)	39.50 (0.57)	15.69 (0.01)
Branta leucopsis	(n = 2)	2.14 (0.17)	36.43 (0.40)	16.45 (0.92)

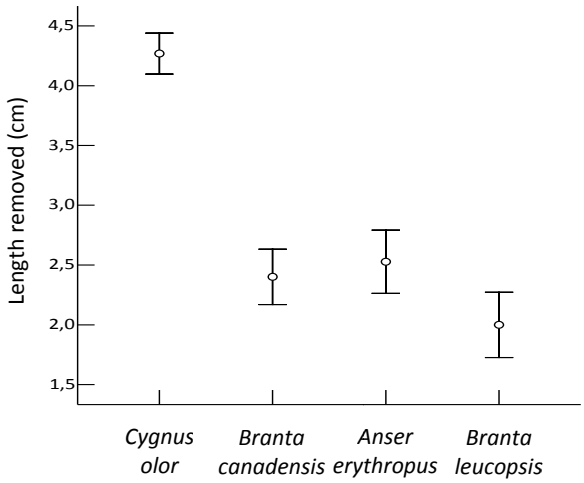

Figure 5.2. Average and 2 times the standard error of bite size, expressed as the length of the initially 8 cm tall leaves removed, specified per species.

Loss after clipping

Spilling of severed leaves during transport through the mouth occurs in all four species. A nested ANOVA on the ln transformed weight of grass leaves lost shows that species differ in amount of food lost during food transport ($F_{3, 6.48} = 459.15$, $p < 0.001$) but there is no significant difference between individuals ($F_{6, 124} = 1.45$, $p = 0.202$). Post hoc tests show that mute swans loose the most (all $p < 0.001$), and that Canada geese loose more grass than lesser white-fronted geese ($p < 0.000$) and barnacle geese ($p < 0.000$), which do not differ among each other ($p < 0.993$).
The amount of grass leaves spilled as a percentage of the amount clipped is highest in the mute swan, which looses about 30% of the amount clipped, ranging from 20% for individual #3 to 42% for individual #2. The three goose species spill much less; 6.4 % in Canada geese, 4.7 % in lesser white-fronted geese and 8.6 % in barnacle geese (table 5.1). These data suggest a progressive increase in the amount of food lost during transport with increasing bite size across species, which may also be present within species or individuals. However, the relationship between bite size and food loss is weak at both the individual and species level (table 5.4). The amount of grass lost varies widely and the range of bite sizes within a species is limited.
However, in a number of animals the correlation is significant and all other correlations are positive and sometimes close to $p = 0.05$. A model II regression shows that the slopes are not significantly different among individuals ($p = 0.1230$) and that the data are consistent with a single common slope (1.71, 95% CI 1.444-2.029) for all birds.

Slopes vary for individuals within species, and although the slope for mute swans tends to be lower than for other species (table 5.4), the slopes for most individuals of the mute swan are not different from that of individuals of other species. For the common slope y-intercepts differ significantly ($F_{9, 124} = 22.970$, $p = 0.000$). As for the slopes, the differences

in y-intercept do not show a consistent pattern across species but represent individual variation.
The y-intercept of the mute swan is low but individual swans show y-intercepts that are very similar to the intercept for Canada geese or lesser white-fronted geese.
We therefore conclude that the loss of grass during food transport only depends on bite size, and that loss increases exponentially (exponent 1.71) with bite size. This relationship seems similar for individual birds and across species. Note that the relationship between average bite size and average loss per species (n = 4) has a similar slope as for the individual birds (ln loss = 1.49 * ln bite size – 4.64; r = 0.957; p = 0.043).

The progressive loss of grass with increasing bite size only partly explains the decrease in intake rate with increasing bite size (see before). An analysis of net bite size (bite size minus loss) shows that again the slopes of the ln transformed data are not significantly different among individuals (p = 0.1010) and that for the common slope (1.036, 95% CI 0.936-1.147) y-intercepts still differ significantly ($F_{9,124}$ = 91.612, p = 0.000). However, the difference in increase in intake rate with bite size between species has become smaller. In mute swans intake rate increases 4 times slower with increasing bite size than in barnacle geese, but only 2.4 times slower with net bite size.

Table 5.4. Pearson correlation-coefficient and SMA results on ln-transformed bite size and food loss. Ln loss = slope * ln bite size + intercept.

Species	Pearson's r	slope	Lower CI	Upper CI	Intercept	Intercept slope = 1.71	n
Cygnus olor	0.479 ***	0.808	0.642	1.018	-0.036	-5.810	59
Branta canadensis	0.213	2.105	1.421	3.119	-8.258	(-6.296)	27
Anser erythropus	0.368	2.785	1.900	4.082	-10.304	(-4.625)	26
Branta leucopsis	0.604 **	1.720	1.196	2.474	-4.824	-4.798	22

Bite rate and handling time

As the decrease in intake rate with increasing bite size (and body size) is only partly explained by the progressive loss of grass with increasing bite size, the remaining variation must (by definition) be the consequence of a reduced bite rate. Again the relationship between bite size and bite rate is weak at the individual level, but there is a clear decrease in bite rate with bite size across species (table 5.1; ln transformed data: r = -0.984, n = 4, p = 0.016, ln bite rate = -0.336 * ln bite size + 5.571 95% CI slope: -0.566 /-0.199). Larger species take relatively larger bites but at a relatively lower rate than small species. At the individual level this relationship is less clear.

As none of the individuals of lesser white-fronted and barnacle geese show a correlation between bite size and bite rate, the data of the mute swan and Canada geese were analysed separately (table 5.5). Among these 6 individuals there was no significant difference in slope for the relationship between ln bite rate versus ln bite size (p = 0.0635, common slope -0.778, 95% CI -0.650 / -0.930) but the two species differ in intercept (p = 0.000). Bite rate drops faster with bite size in mute swans than in Canada geese (figure 5.3).

Table 5.5. *Pearson correlation-coefficient and SMA results on ln-transformed bite size and bite rate. Ln bite rate = slope * ln bite size + intercept.*

Species	Pearson's r	slope	Lower CI	Upper CI	Intercept	Intercept slope = -0.778	n
Cygnus olor	0.653 ***	-0.855	-1.044	-0.700	8.879	8.390	59
Branta canadensis	0.470 **	-0.582	-0.831	-0.408	6.794	7.776	27
Anser erythropus	0.319	0.876	0.593	1.292	0.651	(7.463)	26
Branta leucopsis	0.179	0.429	0.275	0.669	2.768	(7.083)	22

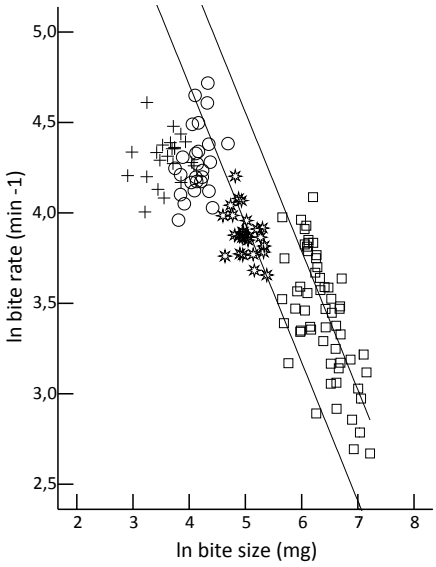

Figure 5.3. Bite rate (min^{-1}) against amount of grass removed per bite (mg), both ln transformed. Lines represent the model II regression with common slope for *Cygnus olor* and *Branta canadensis*. No correlation between bite size and bite rate was found either in *Anser erythropus* or in *Branta leucopsis*.
Legend: □: *Cygnus olor*, *: *Branta canadensis*, ○: *Anser erythropus*, +: *Branta leucopsis*.

The inverse relationship between bite size and bite rate, which seems to exist across species and at least partly within species, and individuals within species, may be the result of a an increase in the time needed to transport an increasing amount of food to the oesophagus, but also from an increase in time invested in cropping (i.e. time to sever a bite).
A nested ANOVA shows that species (and individuals) clearly differ in cropping time ($F_{3, 6.023} = 17.500$, $p = 0.002$), but transport time is just above significance level ($F_{3, 6023} = 4.473$, $p = 0.056$). In post hoc tests both variables follow the same pattern across species: the duration of cropping a bite from an 8 cm turf of grass and transporting the food collected was longest in the mute swan (table 5.6). Lesser white-fronted and barnacle geese spent the least time to apprehend and transport a bite of grass, while Canada geese showed intermediate values that are significantly different from mute swans and the two smaller geese species.

Table 5.6. Averages with standard deviations between brackets of handling time split into cropping time and transport time per anatid species studied.

Species	Cropping time per bite (s)	Transporting time per bite (s)	n
Cygnus olor	1.08 ± 0.40	0.98 ± 0.39	59
Branta canadensis	0.46 ± 0.10	0.79 ± 0.12	29
Anser erythropus	0.35 ± 0.08	0.50 ± 0.11	26
Branta leucopsis	0.34 ± 0.07	0.49 ± 0.08	22

Discussion

Variation in foraging performance between species emerges from situations where some species are better than others at handling and consuming food items (Caldow et al., 1999; Stillman et al., 2000). Grazing anatid species spend most of the time available for foraging on the foraging site, where searching time is minimized and processing food items may be optimised. Quantifying the underlying processes of their grazing mechanism over short periods of active grazing as in the present study may thus be a proper approach to field situations.

Intake rate

Our experiments showed that grazing intake rates on sods of 8 cm height differ considerably between anatid species. Mute swans ingest twice as much per unit of time, except for one out of the four individuals tested, than individuals of Canada geese. In turn, intake rate in Canada geese is about twice as high compared to barnacle geese. Lesser white-fronted geese have an intake rate intermediate of those of Canada and barnacle geese.

Comparable data from literature for the anatid species, grass species and sward height used in this study is scarce and only available for the barnacle goose (Durant et al., 2003; Prop and Black, 1998). In the study by Prop et al. (1998) grass density was very low, and therefore difficult to compare with our experiment. Durant et al. (2003) based their findings on dry weight of grass leaves. Assuming a water content of 83% of fresh weight, based on the ratio found in the present study (x = 83.0, s.d. = 1.9, n = 25) barnacle geese in the study of Durant et al. (2003) had an intake rate of about 1735 mg fresh weight per minute on 8 cm tall swards, which is considerably lower than the 2550 mg per minute found in the present study. This difference is unlikely to be due either to our estimate for water content, as Naujeck and Hill (2003)) estimated a water content of grasses of 72%, and Van der Graaf et al. (2006) found a conversion factor of 46% for *Festuca rubra,* or to differences in sward density between the present study and those reported in Durant et al. (2003). It may well be that the indirect determination of intake through the estimation of digestion results in an underestimation of the true intake rate. Only for the barnacle goose data on digestibility are available (Prop and Black, 1998; Prop et al., 2005; Prop and Vulink, 1992), which show that the digestibility of 14% as estimated by Durant et al. (2003) is 2.9 times too low. Correcting for this inconsistency, barnacle geese in the previous mentioned study had an intake rate of 2763 mg, very close to our own estimate.

To account for species-specific features of intake rate, we examined the mechanics of intake rate by relating bite size, amount of food lost during transport through the bill and bite rate to intake rate as well as to each other. For all anatid species in our study, intake rate increases proportionally with increasing amount of grass removed from the turf per bite. The rate at which intake rate increases with bite size, however, differs among the species. Intake rate increases much faster in the two smaller goose species than in the larger Canada goose, and intake rate is lowest in the mute swan. This proportional increase implies a complex relationship between bite size, bite rate and amount of food lost. The differences in rate of increase in intake rate with bite size are partly explained by a progressive loss of food during transport through the bill and partly by a decrease in bite rate with increasing bite size (see below).

Bite size

Like mammalian herbivores, which show a positive relationship between bite size and the size of the mouth (Gordon et al., 1996), the anatids in our study show an increase in bite size with increasing size of the bill (or body size). A similar relationship was found for the anatid species in the study of Durant et al. (2003). Only a few studies are available to compare bite sizes. Based on the conversion rate of 83% for fresh to dry matter the barnacle geese in the study of Durant et al. (2003) ingest about 22 mg fresh weight per bite on grass of 8 cm, but correcting for their low estimate of digestibility (see above) yields bite sizes of 31 mg. Cope et al. (2005) found an average bite size for barnacle geese on 8 cm tall turfs of 32 mg. Both values are very close to the bite size determined in our study (34 mg). Interestingly, lesser white-fronted geese have similar bill dimensions as barnacle geese, but do take larger bites. One possible explanation for the small bite size of barnacle geese on taller swards is that these birds have difficulty grasping the long leaves (Hassall et al., 2001; Van der Wal et al., 1998), called the ‘spaghetti effect’ by R. Drent

(pers. com., see also Bignal, 1984; Van der Graaf, 2006). However, the bite size of lesser white-fronted geese does not seem to be affected by this 'spaghetti-effect'. A second possibility is that the barnacle goose is not able to produce the forces required to take larger bites, either because they can not generate the force to break the grass during the pulling movement of the head or because they are unable to keep the bite clamped between the bills during the pull. Note that in the barnacle geese bite size does not increase when sward height increases above 8 cm (Cope et al., 2005; Durant et al., 2003; Lang and Black, 2001; Van der Graaf et al., 2006). Another observation that may indicate the limiting effect of bite or pulling force on bite size is the increase in cropping time with bite size. In the mutes swans and Canada geese cropping time of individual birds (constant bill dimensions and sward characteristics) increases almost proportional with bite size (exponent 0.948, 95% CI 0.787/1.142). Our video-recordings showed that mute swans often uses more than one pull to remove the grasped leaves, resulting in longer cropping times.
A third explanation for the difference in bite size between lesser white-fronted and barnacle geese is that the latter select for the high quality parts of the forage (see bite depth below).

Loss of food during transport

After cropping a bite food has to be transported down the length of the bill to the oesophagus. Transport time seems to increase with bill length (body size) across species, but the effect is not very strong. The differences in transport time between species are very close to the level for significance $p = 0.05$. Grass is transported through the bill by alternating forward and backward movements of the tongue (Van der Leeuw et al., 2003). Although experimental data are not available, it seems likely that with increasing linear dimensions of bill and tongue, the transport movements also become larger, and that it takes as much time to transport an amount of food along a short bill as it takes to transport the same amount of food along a long bill. However, with increasing body size several variables increase in magnitude, including bite size. The relationship between bite size and amount of food lost is very similar across species and within individuals. These data suggest that the amount of food lost before swallowing only depends on bite size and the mechanics of food transport through the bill.

Van der Leeuw et al. (2003) suggested that the morphology of the interior of the mouth plays an important role in the efficient transport of severed vegetation. The presence of papillae on the roof of the mouth may determine the amount of vegetation that can be transported efficiently. In geese, these papillae retain food items when the tongue moves forward again, after a backward movement to transport food in the direction of the oesophagus. In the mallard (*Anas platyrhynchos*) such papillae are absent. This species employs a completely different transport mechanism during grazing, in which food is released after a jerky backward movement of the head and caught again during the forward movement of the head with open bills (inertial transport, (Bramble and Wake, 1985) or 'catch-and-throw' mechanism (Kripp, 1933)). In most grazing anatid species many short papillae are present (chapter 4) and form a rough inner lining of the mouth. However, as bite size increases the number of leaves of grass that make direct contact

with the roof of the mouth during food transport (instead of other leaves) may decrease, resulting in longer transport times and a larger loss of food. In spite of the papillae on the inner lining of the upper bill, all three goose species examined spilt some of the leaves during transport, but losses were less than 10%. Whether grazing in field conditions in goose species involves loss as well is unknown. Mute swans spill on average about 30% of the amount of food severed per bite, but the percentage food lost varies among individuals (20%-42%). Compared to geese, the mute swan has relatively few papillae in the caudal part of the mouth and low transverse ridges instead of papillae in the rostral part of the mouth. This makes the roof of the mouth less rough than in geese, but apparently the papillae and ridges are sufficient to transport clipped grass leaves with the tongue and to avoid the energetically expensive inertial transport mechanism of the mallard. We did not observe the characteristic head and jaw movements of the 'catch and throw'-mechanism in the mute swans. However, the absence of papillae in the anterior part of the bill and the small amount of papillae in the posterior half may contribute to the relatively large and variable food losses found in mute swans. Under field conditions grazing mute (Sears, 1989) and Bewick's swans (Rees in Sears 1989) were also observed to drop a large proportion of the vegetation cropped.

Large losses during the transport of grass were also reported for the mallard. The inertial or 'catch-and-throw' transport mechanism, which is normally employed by the mallard to transport large food items, is also used for the transport of grass. Following a 'throw' large amounts of grass are not caught within the bills and are lost for ingestion. A loss of 40 percent of the amount of grass clipped on tall turfs was found by Van der Leeuw et al. (2003). Note that such losses are relatively high compared to the losses reported in the present study. Mallards take 125 mg of grass per bite. From the relationship between bite size and food loss found in our study (ln loss = 1.71 * bite size – 5.743), one would expect a loss of 12 percent in the mallard instead of 40%. The absence of papillae on the roof of the mouth in this species is believed to be characteristic for straining species (Van der Leeuw et al., 2003; Zweers et al., 1977). During straining the tongue is pressed against the roof of the mouth and used as a piston to generate a waterflow through the beak. The different mechanisms for feeding suggest that there is a trade-off between straining and grazing. A bold palate results in an inefficient inertial transport mechanism for grass, while a rough palate may limit the performance of straining because the tongue does not properly fit the roof of the mouth, creating a 'leaky' pump.

Bite rate

Food intake rate not only depends on bite size but also on bite rate. Our data suggest a negative relationship between bite size and bite rate, but this relationship seems to differ between species.
Across species the large bite sizes taken by the mute swans are collected at a relatively low frequency (33 bites/min), while barnacle geese collect much smaller bites at a high frequency (74 bites/min). Bite rates of barnacle geese in other studies on swards of comparable height are similar to the rate found in our study (Durant et al. (2003): 89/min; Lang and Black (2001): 70-90/min, Van der Graaf et al. (2006): 60/min on a narrow leaved grass species). In lesser white-fronted and barnacle geese no correlation between bite

rate and bite size was found. In Canada geese and the mute swans bite size and bite rate show a negative correlation. In these two species bite rate drops much faster with increasing bite size (exponent -0.778) then one would expect from the same relationship across species (exponent -0.336). The fast decrease in bite rate with bite size within species does have consequences for intake rate. While intake rate increases quickly at small bite sizes, the decrease in bite rate at large bite sizes starts to balance the increase in bite size, and intake rate levels off (figure 5.4). This may explain the increase in variation of bite size with increasing body size and average bite size (e.g., mute swan). Intake rate changes much less at large bite sizes than at small bite sizes. For the two smaller goose species in our study variation in bite size would result in relatively large changes in intake rate. A more accurate control of bite size, close to its maximum, may be of more importance in these species. An accurate control of bite size while the variation in instantaneous bite rate remains constant for all species would explain the absence of a correlation between bite rate and bite size in the two smallest species.

When the relationship between bite rate and bite size for Canada geese and mute swan is also applied to lesser white-fronted and barnacle goose data, the results show that bite rate becomes higher for the same bite size as species get larger. This is consistent with what one would expect for species of varying body size. As larger species are able to generate more force than smaller species to crop a bite of the same size, cropping time should go down, and bite rate should go up.

The force required to sever a bite is not considered to constrain intake rate in large mammalian grazers. Therefore, cropping time is assumed to be independent of bite size and transport time is proportional to bite size in the mechanistic model describing intake rates in these animals (Spalinger and Hobbs, 1992). These assumptions may not hold for all grazing anatid species. In mute swans cropping time and transporting time are positively related to bite size. In small geese, like in the Spalinger-Hobbs model, cropping time seems to be independent of bite size, although individual birds may show the same relationship as found in the mute swans.

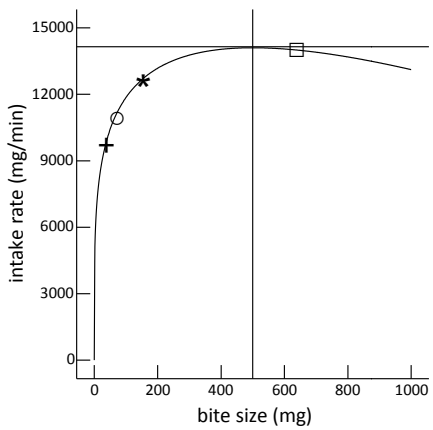

Figure 5.4. Intake rate as function of bite size, calculated from bite rate and bite size minus food loss as found in *Mute swan*. Lines indicate maximal intake rate and corresponding bite size. Average bite sizes per species are indicated by symbols. Small changes in bite size in *B. leucopsis* and *A. erythropus* results in large changes in intake rate. In *B. canadensis*, and in particular in *C. olor* a change in bite size affects intake rate very little. Legend: □: *Cygnus olor*, *: *Branta canadensis*, ○: *Anser erythropus*, +: *Branta leucopsis*.

Bite depth and daily energy requirements

Larger bite sizes may be the result of larger bite depth and/or severing more leaves per bite. We did not find a clear relationship between bite depth and bill (or body) size. Although bite depth roughly increases with body size across species, it varies relatively little among the three goose species, and only mute swans take a clearly larger part of the grass leaves. On the other hand lesser white-fronted geese seem to clip a larger proportion of the length of the grass leaves than barnacle geese, which have a similar body mass. The small bite depth of the barnacle geese is very similar to values reported by Lang et al. ,2001 and Therkildsen and Madsen, 1999. These differences in bite depth may be related to the amount of force required to severe a bite, but also to food quality and foraging strategy.

Daily food intake is limited by either the short-term rate of intake or the turn-over rate in the gut, and quality of the food is of primary importance. Protein/nutrient content decreases from the top to the base of a sward (Delagarde et al.; 2000, Duru, 2003; Summers and Critchley, 1990), while fibre content increases towards the base of the sward (Delagarde et al., 2000). In addition, several studies have shown that quality of the sward declines with increasing sward height (e.g. Bos et al., 2005; Durant et al., 2004; Hassall et al., 2001; Summers and Critchley, 1990). Not only does high fibre content increases tensile strength of leafs, requiring a greater effort for severance, it also causes a decline in digestibility. As digestibility is positively related to length of the digestive system and thus to body mass (Bruinzeel et al., 1997), large Anatidae are less susceptible to the quality of vegetable food (e.g. Allport, 1991) than small species. For the large mute swan quality of food may be of less importance than for the three smaller goose species, enabling them to ingest about 75% of the length of 8 cm tall sods.
Barnacle geese are the smallest anatid species in this study and they exploit only the superficial layer of natural swards, which contain the least fibre and the most nutrients (Aerts et al., 1996; Durant et al., 2004; Loonen and Bos, 2003; Prins and Ydenberg, 1985; Van der Graaf, 2006). Lesser white-fronted geese are similar in body mass to barnacle geese, but clip a larger proportion of the length of the grass leafs compared to barnacle geese. Apart from mechanical differences in the head-neck apparatus in the barnacle geese discussed above, this difference in short-term rate of food intake may reflect long-term foraging strategies. While plant biomass may constrain short-term intake rate, turn-over rate may constrain intake on the long-term. It is assumed that animals strive to maximize the long-term rate of energy intake (Stephen and Krebs, 1986), and that turn over rate in the gut constrains long-term intake. The two extremes are represented by energy maximizers on the one hand and time-minimizers on the other hand, which only forage long enough to obtain energy requirements and thereby free time to devote to other activities contributing to an increase in fitness. Although this theory is based on ungulate foraging, in geese this phenomenon has been observed as well during the breeding season, where individual geese consistently follow one of the two strategies (Prop, 2004). In addition, geese are shown to be able to prolong retention times, which enable them to feed on low digestible food in summer (Prins et al., 1981; Prop et al., 2005; Prop and Vulink, 1992) and thereby revert their foraging strategy from energy-maximizers to time-minimizers. In our study, barnacle geese may behave like energy-maximizers,

while lesser white-fronted geese have adopted a time-minimizing strategy, taking in grass of lower quality (longer part of the leaves).

To determine whether anatid species differ in performance, we scaled intake rate to the metabolic requirements per kilogram bodymass ($M^{0.75}$). The results obtained in the present study as well as findings in two other studies (Durant et al., 2003; Van der Leeuw et al., 2003) are given in table 5.7 (data from Durant et al. (2003) are adjusted for a too low digestibility estimate, see above). Mute swans, Canada geese, greylag geese (*Anser anser*), lesser white-fronted geese and greater white-fronted geese *(Anser albifrons*) have similar intake rates per metabolic weight. Barnacle geese, Eurasian wigeons (*Anas penelope*) and the mallard form a second group with much lower intake rates per metabolic weight. The intake rate per metabolic weight is lowest in the mallard.

The differences in intake rate between wigeon and mallard seem to be due to differences in both bite size (wigeon: 26 mg, mallard: 125 mg) and in transport mechanism, reflected in amount of food loss (wigeon: 1%, mallard: 40%) and bite rate (wigeon: 37/min, mallard: 17/min). Although cropping takes longer in the mallard (1.385 s, wigeon: 0.99 s), the difference in transport time contributes most to the difference in bite rate between the mallard and the wigeon (2.144 s and 0.632 respectively) (Van der Leeuw et al., 2003). The mallard has a smooth surface on the inner lining of the upper bill, while wigeons have small papillae on the median ridge and on the roof immediately lateral from the median ridge (Kooloos et al., 1989; Van der Leeuw et al., 2003; chapter 4.). These small papillae enable wigeon to adopt the transport mechanism of geese, using the papillae to retain food during forward movements of the tongue.
Although wigeon and barnacle geese seem to obtain less energy per metabolic weight, selecting the most nutritive parts of plants (see above) or extending daily foraging time (Cope et al., 2003; Ebbinge et al., 1975; Madsen, 1998) may counterbalance this apparent difference in intake. In the mallard, intake rate of grazing may just be too low to meet its energetic needs, and grazing may be only employed to fulfil certain nutrient needs.

Table 5.7. Average body weight, intake rate, and intake rate scaled to metabolic weight of several anatid species (ranked according to body weight) from the present and other studies.
Body weights are measured (present study) or given by the respective authors.

Species	Body weight (kg)	Intake rate (mg min^{-1})	Intake rate / Metabolic weight ($M^{0.75}$)	Reference
Cygnus olor	9.22	13534.1	2557.9	This study
Branta canadensis	3.88	6862.4	2482.3	This study
Anser anser	3.50	5859.2	2289.8	Durant et al. (2003)
Anser albifrons	2.69	5675.9	2702.2	Unpublished student report
Anser erythropus	2.07	4558.1	2641.2	This study
Branta leucopsis	2.14	2548.3	1440.2	This study
Branta leucopsis	2.00	2762.7	1642.7	Durant et al. (2003)
Anas platyrhynchos	0.963	1273.0	1309.5	Van der Leeuw et al. (2003)
Anas penelope	0.534	1000.0	1600.8	Van der Leeuw et al. (2003)
Anas penelope	0.620	1016.9	1455.4	Durant et al.(2003)

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Chapter 6

Filter-feeding performance in wildfowl (Anatidae)

Summary

Wildfowl (Anatidae) exploit many different food sources. The relationship between bill morphology and the exploitation of food resources is poorly understood. In particular, foraging in different physical environments (aquatic versus terrestrial) may be expected to require different ways of handling food items. In a previous study (chapter 5) we have shown that specialized grazing wildfowl have a higher performance for grazing than aquatic feeding species. Morphological and biomechanical analysis of feeding in geese and ducks suggest that the presence of spines on the inner surface of the upper beak, which are necessary for the effective intra-oral transport of vegetation, is incompatible with the piston function of the tongue during filter-feeding, resulting in a trade-off between grazing and filter-feeding. To demonstrate that high grazing performance is associated with low filter-feeding performance we investigated filter-feeding of two goose species and the mute swan and compared the results to previous results on ducks.

Filter-feeding performance is determined by the percentage of food-items retained as well as by the amount of water and suspended food particles pumped through the bill. Filter-feeding ducks, the goose species and the mute swan are all able to retain more than 95% of the millet seeds drawn in at the tip of the bill. On the other hand, the volume of water per straining cycle relative to body size is larger and the straining frequency is higher in ducks than in grazing wildfowl. Differences in relative bill size only explain part of the difference in volume taken in per movement cycle. The major cause for the difference in performance seems to be related to the different mechanisms used. Duck species use their elevated tongue in a piston-like way to generate a flow of water through the bill and filtered out food particles are transported simultaneously alongside the tongue to the lingual base. In grazing geese the tongue is not elevated during filter-feeding, which results in a less efficient intake of water, and seeds are retained and transported over the tongue in the same way as vegetation during grazing.

The results on filter-feeding performance in the present study in combination with the results on grazing performance clearly indicate a functional trade-off between filter-feeding and grazing in wildfowl.

Introduction

Differences in trophic morphologies among species are believed to reduce competition for limited resources. At the population level differences in the exploitation of resources linked to alternative morphologies may lead to divergent selection and adaptive radiation (Schluter, 2000b). While it is difficult to relate differences in feeding performance to measures of fitness, often the exact relationship between trophic traits and recourse use is also open to question (Arnold, 1983; Wake, 1992; Wainwright, 1991; Irschick, 2002; Rubega, 2000).
For divergent selection to operate morphological adaptations that offer an advantage in the exploitation of one resource should decrease feeding performance (and ultimately fitness) on alternative resources (Schluter, 2000a). However, it is not always apparent how such a trade-off might occur.

Lack (1971, 1974) suggested that differences in bill morphology among filter-feeding ducks might lead to partitioning of resources by selectively sieving different sized food particles from the water, by means of the comb-like lamellae on the margins of the bill. Some studies have documented interspecific differences in the size of food items ingested by ducks (Nummi, 1993; Nudds and Bowlby, 1984; Guillemain et al., 2002) and related this selective uptake to interspecific variation in interlamellar spacing. Other studies did not find such a relationship (Nummi and Väänänen, 2001) or found that bill size and shape were more important than lamellar density (Lagerquist and Ankney, 1989).
A mechanical analysis of the jaw apparatus and filter-feeding process (Zweers et al., 1977; Kooloos et al., 1989) showed that ducks can move the upper and lower bill in such a way that the separation between upper and lower bill lamellae during filter-feeding is larger than interlamellar distance. With such an adjustable filter ducks are able to set a lower limit on the size of the food retained, largely independent of mean interlamellar distance (Gurd, 2006). However, this flexible filter mechanism alone does not cause a trade-off in foraging performance, which is necessary for resource partitioning to evolve.
When ducks are able to set the lower limit of the range of food items that can be retained there is no clear benefit for a wide interlamellar spacing. On the other hand the amount of water pumped through the bill per movement cycle decreases with increasing lamellar separation (i.e. the distance between lamellae on the maxilla and mandible) but does not directly depend on interlamellar spacing (i.e. the distance between the lamellae within a row) (Kooloos et al., 1989; Gurd, 2005).

The relationship between morphology and particle retention is further complicated by the fact that terrestrial grazers like geese, and aquatic grazers like swans feeding on submerged plants are also able to ‘filter-feed’. Although geese and swans do possess lamellae these are apparently not used to retain food items. While, as in dabbling ducks, geese and swans generate a water flow through the bill, X-ray analysis (Van der Leeuw et al., 2003) in geese has shown that food particles pass to the oesophagus squeezed between the tongue and palate and are not transported along the margins of the bill. This way of transporting seeds collected during filter-feeding is very similar to the transport of grass. Although it may proof difficult to demonstrate differences in feeding performance

among dabbling ducks, one would expect a clear trade-off in feeding performance between such diverse trophic groups as anseriform grazers and filter-feeding ducks.

Two morphological traits seem to be closely linked to filter-feeding (Zweers et al., 1977; Kooloos et al., 1989; Van der Leeuw et al., 2003). First, a bald inner surface of the upper bill enables the tongue to act as a piston within the slightly opened beak and to generate a one-way flow of water from the anterior of the bill to the posterior. Second, a slit on the lateral sides of the posterior part of the tongue is thought to allow food items diverted to the margins of the bill to pass to the oesophagus and enables a continuous throughput of water and small food items.
These two characters are clearly different in grazing species. Instead of a bald surface grazers have many caudally pointing papillae on the inside of the upper bill, which retain clipped vegetation that is carried backwards over the tongue with a series of rostro-caudal tongue movements during grazing. The lateral lingual slits that allow the transport of small food items to the oesophagus during filter-feeding are absent in grazing species (see also chapter 4).

In a previous study we showed that grazing performance measured as intake rate scaled to metabolic weight is higher in grazing geese and mute swans than in 2 duck species. The morphological and biomechanical analysis of feeding in geese and ducks suggest that the over-tongue transport of grass is incompatible with the piston function of the tongue during filter-feeding and that a trade-off between grazing and filter-feeding performance will exist. We hypothesize that both goose species and the mute swan will perform less well during filter-feeding than duck species. In the present study, we therefore asses the performance of filter-feeding in two goose species and the mute swan, and compare the results with previous work on filter-feeding anatinids (Kooloos et al., 1989).

Materials and Methods

Experimental set-up

Filter-feeding trials were conducted with three mute swans (*Cygnus olor*), two barnacle geese (*Branta leucopsis*) and two lesser white-fronted geese (*Anser erythropus*), all purchased from a local trader.
Two mute swans and the lesser white-fronted and barnacle geese were tested in an indoors aviary where birds had continuous access to a small pond. The third mute swan was held in an outdoors aviary and trials were conducted under otherwise similar conditions. When not engaged in filter-feeding trials, ad libitum food (mixture of grains and waterfowl pellets) was available.
Both training and experimental trials were performed within an enclosure inside the aviary, allowing birds to be tested individually. Immediately prior to the experiments, the birds were trained for 1-3 weeks to get accustomed to filter-feed from a small tray.

The evening before a trial, food was removed from the aviaries. Trials started the following day between 08:00 h and 09:00 h. About five minutes before a trial a bird was gently guided to the enclosure and allowed to settle down. The animal was allowed to filter-feed from the tray until it raised its head, after which it was guided out of the enclosure. Birds were very fast in removing the seeds from the water, on average less than 5 seconds were needed to empty the tray. About fifteen trials per bird were conducted at a rate of one to three trials a day. Trials usually finished before the afternoon, after which food was returned to the birds.

To be able to compare filter-feeding performance as measured in the present study with data on duck species collected by Kooloos et al. (1989) we used the same tray and set-up. This tray was specifically designed to measure the amount of seeds retained by the bird and the amount of water expelled along the sides of the bill. The tray consists of four parts (figure 6.1). Part 1a and 1b serve as storage for water and food. A bird was allowed to strain only from part 1b. Expelled water flows down a slope (2) carrying lost seeds along with it, and is collected into a tray (3).

During each feeding trial high-speed video-recordings (50 fr/s) from a lateral view were made. To avoid blurring of the video-recordings as a result of large head movements, part 1b could be mechanically adjusted to minimize the movement space for the bill tips. During the training sessions of the geese we determined the water level at which continuous filter-feeding was performed. This level forced the birds to forage by filter-feeding instead of pecking, while at the same time scooping out water was prevented. For the broader-billed swans a simple rectangular tray was used in which small plates could be adjusted to secure a similar position of the bill as in the goose trials. A plastic sheet was placed underneath the tray to collect expelled water and seeds. From video-recordings of the geese, the relative length of the bill that was inserted into the water was determined and adjustments to the tray of the swans were made to achieve a similar water level.

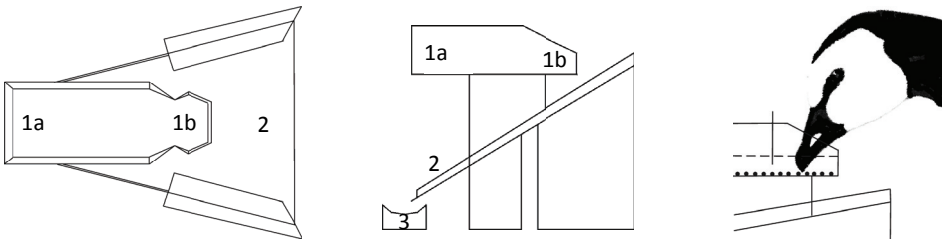

Figure 6.1. Schematic drawing of upper and side-view of experimental tray used in the goose filter-feeding experiments. 1a: reservoir, 1b: part where birds immerse bill tip, 2: slope along which expelled water (and seeds) roll down to 3: collection tray. Part 1b can be reduced in size by a mechanical adaptor.

Measurements

As in the filter-feeding experiments of Kooloos et al. (1989), 1 gram (dry weight) of millet seeds was suspended in 70 ml water for the goose trials. In the swan trials a similar concentration of millet seeds was offered in 200 ml water. Immediately following a feeding trial the expelled water from the collection tray was weighed. Spilled drops outside the tray were wiped with a tissue of known weight and their weight was determined by reweighing the tissue.
Seeds lost during filter-feeding were collected and counted. The seeds remaining in the feeding tray were filtered from the water and the amount of water that remained was determined. The seeds were left to dry at room temperature overnight and then weighed.

Frame by frame replay of video recordings were used to count the number of beak openings and closings and the exact duration of a feeding trial. Several measures were used to characterise filter-feeding performance:

1) the amount of water pumped through the beak measured as millilitre per second and per cycle (pump-performance),
2) the amount of water swallowed, expressed as percentage per cycle,
3) the amount of seeds retained by the filter relative to the amount of seeds that entered the mouth, expressed as percentage (filter-performance), and
4) the amount of seeds filtered measured as gram per second and per cycle (seed intake).

Statistical analyses

To assess differences between species in filter-feeding performance, the amount of water and seeds entering the bill per second and per pumping cycle were used as input for nested ANOVA procedures (SPSS 12.0). Species were considered as fixed effect and individuals were random variables nested within species. When F-values proved to be significant ($p < 0.05$), post-hoc tests were performed to attribute differences to specific species. When data were not normally distributed, or had unequal variances (tested with Levene's test) values were ln-transformed and subsequently analysed. The Games-Howell test was used when variances were still not equal.

Results

Pump performance

The amount of water that is expelled at the caudal rims of the bills during a series of cyclic straining movements may be expressed as the amount of water pumped per unit of time or per movement cycle. Values for volume per cycle for the goose and swan species are given in table 6.1, together with literature data on duck species. Volume per unit of time can be estimated by multiplying the frequency with the volume per cycle. The volume of water pumped through the bill per cycle is 5 times larger in mute swans than in the two goose species. The difference between the two goose species is small: the lesser white-fronted geese pumps just slightly more water per cycle than the barnacle geese. A nested ANOVA shows that species differ significantly more than individuals within a species ($F_{2,4.042} = 72.713$, $p = 0.001$). Post-hoc tests (Bonferroni) show that all species differ significantly from each other (all $p < 0.01$).

As there is a large difference in body size between the two goose species and mute swans, we scaled volume pumped per cycle to body size (table 6.1). After accounting for body size the differences in the amount of water pumped through per cycle have become much smaller, and are no longer significant ($F_{4.042,\ 2} = 1.778$, $p = 0.279$).

The frequency with which the bill opens and closes (11-14 Hz) is relatively constant within species (table 6.1). Individuals within species do not differ in straining frequency ($F_{4,92} = 1.382$, $p = 0.246$), but the small differences in frequency among species are significantly different from each other ($F_{2,4.152} = 92.493$, $p < 0.001$).
As the differences in frequency among species are small the volume of water pumped through the bill per second (water pumped per cycle x frequency) is also significant ($F_{2,4.05} = 70.785$, $p = 0.001$), and all species differ among each other.

The small amounts of water lost during each trial are considered to have been swallowed by the birds (table 6.1). There is no significant difference in the percentage of water swallowed ($F_{4.01,\ 2} = 0.339$, $p = 0.73$) among species.

Table 6.1. Parameters of filter-feeding performance expressed as averages with standard deviations.

	N[+]	Body mass (kg)[#]	Gape (mm)	Freq. (Hz)	Vol. per cycle (ml)	Vol. per cycle relative to body weight (ml/kg)	Percentage of water swallowed (%)	Filter perfor-mance (%)	No. seeds per ml	Seeds per cycle and body weight (mg/kg)	Rate of seed ingestion (mg/s)	Seeds ingested per metabolic weight and unit of time ($mg/kg^{0.75}.s$)
Lesser white-fronted goose	43	2.07	12.0 ± 1.0 (n = 6)	13.5 ±0.6	0.26 ±0.06	0.13 ± 0.03	8.41 ± 3.64	99.7 ±1.4	9.7 ±2.9	7.6 ± 2.0	211.9 ± 53.4	122.2 ± 31.0
Barnacle goose	30	2.14	14.6 ± 1.7 (n = 12)	12.4 ±0.4	0.22 ±0.04	0.10 ± 0.02	10.10 ± 3.84	99.9 ± 0.3	13.5 ±3.8	8.8 ± 2.2	233.2 ± 56.5	131.8 ± 31.9
Mute swan	26	8.67	18.4 ± 0.7 (n = 7)	11.2 ±0.5	1.24 ±0.28	0.14 ± 0.03	9.25 ± 5.77	99.4 ± 0.9	6.4 ±2.3	5.6 ± 1.9	543.9 ± 178.2	107.65 ± 35.3
Literature data*												
Mallard		1.04	5.3 ± 1.5	18.0	0.58 ± 0.13 (n = 49)	0.57 ± 0.13		95.2 ± 3.3 (n = 36)	5.4 ±1.9	8.9[$] ± 2.3 (n = 49)	167 ± 43.6 (n = 49)	162.5 ± 42.3 (n = 49)
Wigeon	13	0.63	?	22.0	0.42 ± 0.11	0.66 ± 0.17	5.41 ± 1.82 (n = 14)	98.3 ± 2.1 (n = 14)	6.1 ± ??			
Tufted duck		0.77	5.0	20.0	0.60 ± 0.27 (n = 34)	0.77 ± 0.35		96.4 ± 3.0 (n = 22)	7.2 ±3.4	15.2[$] ± 5.7 (n = 34)	233 ± 87.2 (n = 34)	283.5 ± 106.1 (n = 34)
Northern shoveler		0.64	5.5 ± 1.0	13.0	0.63 ± 0.21 (n = 51)	0.99 ± 0.33		92.0 ± 5.9 (n = 33)	5.1 ±2.3	15.1[$] ± 7.1 (n = 51)	125 ± 59.3 (n = 51)	175 ± 82.9 (n = 51)

+: number of trials, #: weight of birds from literature, *: Kooloos et al. 1989, van der Leeuw et al. 2003, $: seed mass (3.07 mg, av. diam. = 1.8 mm) estimated from reported diameter range and density calculated from data (6.4 mg; av diam = 2.3 mm).

Filter performance and seed intake

The filter performance, i.e., the amount of millet seeds retained as percentage of the amount of millet seeds sucked in, is very high for all species. Less than 1% is lost along with the water expelled (table 6.1). The amounts of seed retained per cycle and per second are listed in table 6.1. Per cycle swans draw in about 3 times more millet seeds than the two goose species. However, a nested ANOVA showed that this difference between the mute swan and the two goose species is not significant ($F_{2,4.011} = 5.516$, $p = 0.071$). This is due to relatively large variation among individuals, which differ significantly within species ($F_{4,92} = 18.174$, $p < 0.001$).

To account for the effect of body mass we scaled the amount of seeds ingested per second to metabolic weight ($M^{0.75}$). Clearly, the differences between species only become smaller and are not significant ($F_{4.012,\ 2} = 0.518$, $p = 0.631$). As the differences in straining frequency are small the results for the amount of seeds per second are very similar to the results for the amount of seeds per cycle.

Discussion

In the present study we assess the performance of filter-feeding in three non-specialized filter-feeders, the lesser white-fronted goose, the barnacle goose and the mute swan, and compare the results with previous studies in duck species. The data show that non-specialized filter-feeders are able to retain seeds with a diameter of 2.3 ± 0.2 mm with the same high efficiency as dabbling ducks. While a filter-feeding specialist like the northern shoveler (*Anas clypeata*) retains 90-100% of the seeds (Kooloos et al., 1989), the goose species and mute swan scored over 99% on the same seed in our study. In ducks the efficiency with which food items are retained depends on the size of the food item and on interlamellar distance. The smallest food items are retained by species with the smallest interlamellar distance (Kooloos et al., 1989; Mott, 1994; Guillemain et al., 2002; Figuerola et al., 2003). The mallard (*Anas platyrhynchos*) and tufted duck (*Aythya fuligula*) are able to retain approximately 60% of seeds with a diameter of 0.7 – 1.2 mm (Kooloos et al., 1989). The white-fronted goose (*Anser albifrons*) is unable to retain food items smaller than 1.2 mm and expel water from the bill at the same time. Such small food items are swallowed together with 74% of the water entering the bill (Van der Leeuw et al., 2003). The sizes of seeds most commonly exploited by filter-feeding duck species in the field (Taylor, 1978; Dirschl, 1969; Euliss and Harris, 1987; Gammonley and Heitmeyer, 1990; Gruenhagen and Fredrickson, 1990; Afton et al., 1991; Marchant and Higgins, 1993; Nummi, 1993; Baldwin and Lovvorn, 1994; Rogers and Korschgen, 1996; Petrie, 1996; Tréca, 1986; Silveira, 1998; Green et al., 2002; Guillemain et al., 2002) are in the range of 1 to 5 mm and thus very similar to the size range geese are able to retain effectively. Although no data is available on geese foraging on seeds in water it is highly unlikely that they would not consume these seeds when available (Sedinger, pers. comm.).

The mechanism

The high efficiency with which relatively large food items are retained is remarkable because a mechanical analysis of the jaw apparatus and filter-feeding process (Zweers et al., 1977; Kooloos et al., 1989; Van der Leeuw et al., 2003) suggests that ducks and geese use very different techniques to retain seeds. Kinematical analysis of high speed video and X-ray film recordings of filter-feeding show that in geese seeds are transported over the tongue (see below) and than swallowed, while in the mallard and wigeon (*Anas penelope*) food follows a path through the oral cavity to the rims of the bill where seeds are retained and, during straining, transported alongside the tongue to the oesophagus. This difference in the way food is transported is associated with differences in tongue movement during bill opening and closing.
Although tongue movements are difficult to analyse kinematical studies (Kooloos et al., 1989; Zweers et al., 1977) suggest the following scenario for filter-feeding. When the bill opens, the tongue is retracted while part of the tongue (lingual bulges) is elevated against the ventral side of the upper bill. In this position the lingual bulges divide the oral cavity into an anterior and a posterior section. The coordinated action of tongue and bills draws water and food items into the anterior bill cavity. When the bills start to close again the tongue protracts and the lingual bulges are depressed, forcing water and food items over the bulges to the back of the tongue. The water that is transported backwards is prevented from entering the oesophagus by the elevated posterior part of the tongue (the so-called 'lingual cushion'), which remains elevated throughout successive pump-cycles. During the next movement cycle when the tongue retracts again the volume of the posterior bill cavity is reduced and water is forced out through the space between the lamellae (figure 6.2).

Ducks, as most birds, have a movable upper jaw and are able to move the upper and lower bill in such a way that the separation between upper and lower bill lamellae during filter-feeding is greater than interlamellar distance (figure 6.3). With this adjustable filter ducks are able to set a lower limit on the size of the food retained that is larger than interlamellar distance (Gurd, 2006).
To be able to continue filter-feeding food must be transported away from the filter area at the rims of the bill. A further transport to the oesophagus is mediated by spines and scrapers lining the tongue, which move food items through a groove along the side of the lingual cushion. This enables filter-feeding ducks to continue feeding without the necessity to stop and swallow.

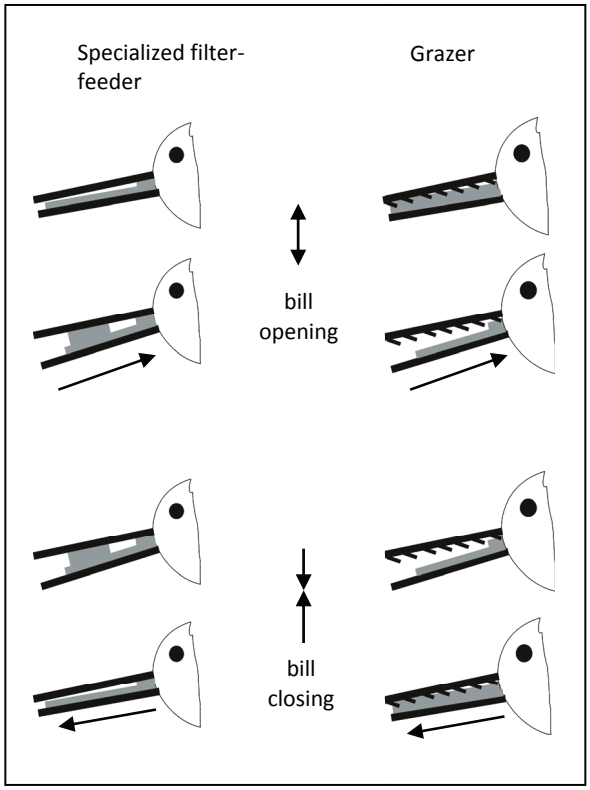

Figure 6.2. Schematic representation of movement cycles of tongue and bills of the filter-feeding mechanisms of specialized filter-feeding (left) and grazing (right) wildfowl species. Upper figures: opening of the bill, lower figures: closing of the bill (indicated by arrows in between species). Arrows underneath bills indicate direction of movement of the tongues.

Filter-feeding species: opening of the bill coincides with elevation of the lingual bulges (rostral part of the tongue) and elevated lingual cushion (caudal part of the tongue) and retraction of the tongue. Water and food are drawn into the bill, and water from a previous cycle (in between the bulges and cushion) is expelled. During closing the lingual bulges are depressed and the tongue protracts, moving underneath the water and food items.

Grazing species: during opening the tongue retracts with depressed bulges but elevated cushion. Water and food enter the oral cavity and food items from a previous cycle are carried backwards on top of the lingual surface. During closing of the bills, the tongue protracts with elevated bulges and cushion. Food items on top of the lingual surface are retained by the caudally directed spines on the ceiling of the oral cavity. As the cushion remains elevated, several collection cycles are followed by transport cycles, in which the cushion is depressed and food items swallowed.

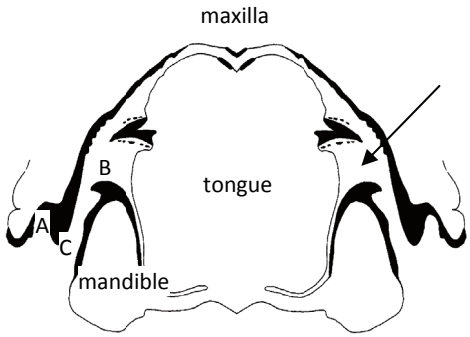

Figure 6.3. Cross-section of bills and tongue of the mallard at the level where food items are filtered from the water flow. Indicated are the maxillary lamellae (A), the dorsal mandibular lamellae (B), and the ventral mandibular lamellae (C). Keratin elements are indicated by black areas. Food items are retained between the inner surface of the upper bill and the dorsal mandibular lamellae (arrow). Modified after Kooloos et al. (1989).

Although the exact mechanism of filter-feeding in the two goose species used in this study and the mute swan has not been studied, the presence of spines on the inner surface of the upper beak and the absence of a lingual groove suggests that they use a mechanism similar to the one described for the domestic goose (*Anser anser*; Van der Leeuw et al., 2003). The mechanism of filter-feeding in the domestic goose is different from the filter-feeding mechanism in ducks. Instead of a continuous process, filter-feeding in the domestic goose typically has two separate phases, a collection phase and a transport phase.
During the collection phase, opening of the bill occurs simultaneously with a large retraction of the tongue, but in contrast to the mallard the bulges are depressed. Water and food items enter the bill and at the same time the large lingual retraction causes the expulsion of water from the preceding movement cycle at the rims of the bill. As in ducks, the elevated lingual cushion may serve to prevent water from running into the oesophagus. During closing of the bills, the tongue protracts and the lingual bulges are elevated, while water and food items are transported over the tongue. Food items are not diverted to the side of the bill but follow a more medial course over the lingual bulges and are retained by pressing them against the spines on the inside of the upper bill.
During the transport phase, there is a shift in phase between the movement cycles of the bill and tongue. During the transport phase protraction of the elevated tongue coincides with bill opening, and when the tongue moves forward the food items are held in place by spines on the upper bill. The food is transported further backward during tongue retraction and depression when the bills are closed. To transport food over the lingual cushion to the oesophagus, the lingual cushion is depressed during tongue retraction, and elevated during the tongue protraction (figure 6.2). This transport mechanism is identical to the one used during grazing (Van der Leeuw et al., 2003).

Water lost

Part of the water provided to the birds is not recovered after the trial. Some of this water may represent a true loss. In most trials some drops of water were vigorously shaken of the bill and lost for collection after the end of a filter-feeding trial. Also measurement errors due to weighing very small amounts of water may accumulate over a trial. Alternatively, a significant amount of water may have been swallowed by the birds. Performance experiments on filter-feeding in an ontogenetic series of the domestic goose shows that only after 4 weeks of age the adult filter-feeding mechanism starts operating. Up to this age goslings still swallow 83% of the water along with the food particles (Van der Leeuw et al., 2003). It is not clear whether the total amount of water not recovered in the present experiments is actually ingested, but the only duck species for which data is available seems to ingest less water than the geese and swan (table 6.1). This may be related to the use of the 'under-tongue' transport mechanism in straining ducks.

Cycle volume and bill size

The amount of water pumped through the bill per movement cycle or unit of time by the lesser white-fronted goose and barnacle goose is very similar, but much lower than in the mute swan. However, the mute swan is 4 times larger than the goose species.

After accounting for the size difference by scaling water intake per pump cycle to body weight pump performance is very similar in geese and swan. A comparison with previous studies on the greater white-fronted goose (Van der Leeuw et al., 2003) and three anatid species (Kooloos et al., 1989) shows that, scaled to body size, goose species and the mute swan have a much lower pump performance than both specialized (*Anas clypeata*) and non-specialized (*Anas penelope*) filter-feeding ducks (figure 6.4 and table 6.1). The absolute volume pumped per cycle in the mute swan is only 2.1 times larger than in the mallard.

It has been demonstrated that geese and swans have relatively shorter and narrower bills than filter-feeding *Anas* species (chapter 2), and therefore a relatively smaller pumped volume per cycle may be expected. However, it is unlikely that this difference in bill volume is large enough to explain the large difference in pump performance between the geese and swan, and smaller ducks. A rough comparison between the outer volume of the closed bill of a mallard and a mute swan indicates that the bill of a mute swan is only 60 % of the size expected for its body size. Geometric scaling would predict an 8.67 (weight mute swan) / 1.04 (weight mallard) = 8.33 larger bill volume for the mute swan, while the measured bill volume is only 65/13 ml = 5 times larger. The measured difference in pumped volume per cycle is however lower than the expected 60 % reduction from bill volume. Measured intake of mute swan divided by the expected intake of mute swans based on geometric scaling with respect to the mallard (table 6.1) equals 1.24 /(8.33 * 0.58) = 26% of the expected cycle-volume.

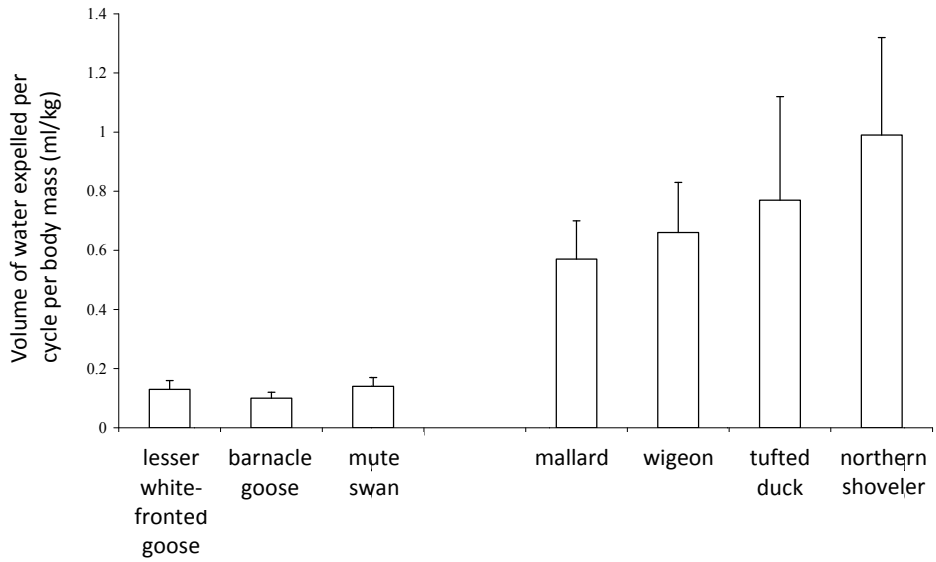

Figure 6.4. Volume of water expelled per movement cycle of the bill scaled geometrically for two goose species and the mute swan. Figures from literature data for ducks are depicted at the right-side.

The difference in volume per cycle that remains after accounting for the difference in relative bill size may be due to either a relatively smaller opening of the bill (gape), or a difference in the extent to which the bill is immersed. The cycle volumes of the ducks in the study of Kooloos et al. (1989) may underestimate the true pump-capacity (Gurd, 2005). Values of cycle volumes obtained from a biomechanical model of the bill and oral cavity were higher than those measured experimentally. This is probably the result of the experimental set up. To be able to capture expelled water and seeds, the birds were allowed to submerge only the most rostral part of their bills (approximately one third of total bill length). Under natural conditions ducks may feed with at least half of their bill submerged, and at a more acute angle to the water surface. In this position cycle volume may depend less on suction force and become larger than in the experimental set up used. As the geese and swans in the present study were tested in a similar situation as the ducks in the study of Kooloos et al. (1989) an underestimate of cycle volume does not affect the comparison among the species.

Alternatively, geese and swans may use relatively smaller gapes during filter-feeding, which reduces the volume of the oral cavity. However, a rough estimate of gape from video recordings suggests the opposite (table 6.1). When the gape of the mallard is geometrically scaled up to the size of the geese and swan species (ratio of body weights to the power 1/3 times gape) the gapes measured in geese and the mute swans are almost twice as large as expected. Note that this comparison assumes geometrical scaling of bill length, while in fact the bills of geese and mute swan are relatively shorter. However, relatively short bills only further reduce the expected gape.

Pump capacity and transport mechanism

We believe that the difference in cycle volume between duck species on the one hand, and geese and swan species on the other hand is most likely related to different transport mechanisms and morphological adaptation of the upper bill used to filter-feed or graze. Large pieces of vegetation (grass, waterplants), but also large seeds (Kooloos, 1986), can not be transported along the tongue cushion but must be transported over the tongue cushion in both straining ducks and grazing geese. In geese and mute swans the inside of the upper bill bears spine-like structures to facilitate transport of pieces of vegetation. By elevating the tongue, while the tongue is protracted and the bills are closing, food items are pressed against the roof of the mouth and retained by the spines. Compared to the tongue movement in straining ducks the elevation-depression movement of the tongue is shifted with respect to the rostro-caudal movement of the tongue and the opening-closing movement of the bill. In straining species the tongue is elevated during retraction and depressed during protraction. In geese the presence of spines prevents an elevated tongue from properly acting as a piston during straining, even when the duck-straining type of tongue movement is used. Elevation of the tongue during retraction would result in a ‘leaky’ pump with a reduced pump capacity. In ducks, the inside of the upper bill is bald and food items are not trapped between the tongue and upper bill, allowing the tongue to operate as a closed valve-system (Zweers et al., 1977).

A further disadvantage of eating large food items may be that for large food items a continuous throughput of food to the oesophagus is not possible. The video-images of the filter-feeding experiments in geese and mute swan clearly show that food is collected during a series of movements with immersed bill, after which the head is lifted from the water and a further series of bill movements is used to transport the food over the tongue cushion. During the collection phase the number of seeds on the tongue is seen to increase, and sometimes seeds are observed to drop back into the water again. Ingestion of a particular amount of seeds may therefore take longer in Anserinae species than in ducks.

Straining frequency

One way to compensate for a decrease in pump-capacity is to increase the frequency of bill movements, and to increase the amount of water passing through the bill per unit of time. Straining frequencies vary little within individuals and species (present study; Kooloos et al., 1989), and are largely independent of food size (Kooloos et al., 1989). In contrast to expectation, the geese and mute swans in the present study show lower frequencies than most ducks. Although the data are limited, there appears to be a relationship between the size of the bill and straining frequency, especially in ducks. The northern shoveler has a bill that is almost twice as large as that of the wigeon, and its straining frequency is almost half that of the wigeon. Such a relationship may result from the forces that are generated by the bill movements through the water during filter-feeding. The flow of water along the bill (drag) and the displacement of water resist jaw opening. Drag forces are proportional to both area of the bill and velocity squared; the reaction force of the water is proportional to the displaced mass and to its acceleration. An increase in bill size will increase both forces and may therefore be at the expense of filter-feeding frequency. Interestingly, grazing Anseriformes have relatively small jaw opener muscles compared to non-grazing species (chapter 3), which may further limit filter-feeding frequency.

Intake

A comparison of seed intake per straining cycle shows that the goose species take in more seeds per ml water pumped through the bill than the mute swan and ducks. This is probably an effect of an uneven distribution and delivery of seeds that are drawn in from the supply tray during the experiment**.**
The comparison of relative intake rate (mg/cycle.kg) is further biased by the fact that the millet used in our experiments was larger than used for the duck species (2.3 versus 1.8 mm). Although the difference in size contributes to an overestimation of intake rate in the anserine birds compared to ducks, duck species still have a higher intake rate when scaled to (metabolic) body mass.

Filter-feeding versus grazing

In a previous study we showed that grazing performance measured as intake rate scaled to metabolic weight is higher in grazing geese and mute swans than in two duck species. The morphological and biomechanical analysis of feeding in geese and ducks suggest that the presence of spines on the inner surface of the upper beak, which are necessary for the effective intra-oral transport of vegetation, is incompatible with the piston function of the tongue during filter-feeding, resulting in a trade-off between grazing and filter-feeding performance. As may be expected from the biomechanical analysis the performance of filter-feeding, measured as the amount of water and suspended food items drawn in relative to (metabolic) body size, is higher in duck species than in specialized grazers (geese and mute swan).

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General Summary

The role of food selection in the evolution of wildfowl

Wildfowl are a diverse group of birds, which populate every continent except Antarctica. Wildfowl species are all closely related and belong to four different families that constitute the order Anseriformes (see figure 1). The three screamers (*Chauna chaviara, Chauna torquata* and *Anhima cornuta*) of the family Anhimidae are considered to possess the most ancestral features. The magpie goose (*Anseranas semipalmata*) is the sole member of the family Anseranatidae. This species is considered to represent an evolutionary link between the Anhimidae and the Anatidae (Brush, 1976; Delacour, 1954; Johnsgard, 1961; Johnsgard, 1978; Livezey, 1986, 1997a, 1997b; Madsen et al., 1988; Olson and Feduccia, 1980; Woolfenden, 1961). Whistling-ducks (Dendrocygnidae) form the third family (Sibley and Monroe, 1990, 1993), although some authorities place them within the Anatidae, as sistergroup of the ducks, geese and swans (Donne-Goussé et al., 2002; Livezey, 1997a). The Anatidae family is divided into two subfamilies: the Anserinae and the Anatinae. True or northern geese (*Anser* en *Branta*) and swans (*Cygnus*) form the Anserinae. The Anatinae comprises all true ducks (about 30 genera, among others the genus *Anas*) and the Tadornini. The Tadornini are the sheldgeese (*Cyanochen*, *Alopochen*, and *Chloephaga*) and the ducks from the genera *Tadorna* and *Casarca*. The Tadornini form the sistergroup of the other Anatinae and are considered to be intermediate between the true geese and the true ducks (Delacour and Mayr, 1945; Donne-Goussé et al., 2002; Johnsgard, 1965; Johnsgard, 1978; Livezey, 1986).
Although the earliest fossils date back to the Palaeocene (65 mya) phylogenetic analyses indicate that the Anseriformes originated in the late Cretaceous, about 80 million years ago (Livezey, 1997b; Olson and Feduccia, 1980; Sibley and Monroe, 1990, 1993).

The diversity of waterfowl is reflected by the multitude of food items taken. Not only do species differ in food type, but within species the food type taken depends on habitat, season, age and sex. Even differences among individuals within a species may occur (reviews in Baldassarre and Bolen (1984) and Krapu and Reinecke (1992)).

Most wildfowl are dependent on waterbodies for feeding. However, some species may feed at great distances from water. The feeding techniques wildfowl apply to gather food are linked to the foraging habitat and the food type preferred (reviews in Kear (2005) and Krapu and Reinecke (1992)). The two most frequently used methods are filter-feeding and grazing. Filter-feeding involves pumping of water and suspended food particles through the beak. Water is expelled and invertebrates, seeds, and/or parts of vegetation are seized. Filter-feeding is applied both at the water surface (called dabbling) or at a larger depth by up-ending or even during diving (e.g. review in Kear (2005)). Grazing is typically used on land to feed on leafy plant parts, but may also be employed when foraging on aquatic vegetation.

Screamers forage mainly on the aboveground parts of aquatic plants while wading, although subterranean parts are taken as well. Also included in their diet are both above- and belowground parts of terrestrial vegetation (review in Kear (2005)). The magpie goose mainly forages on tubers of swamp plants, although it is also observed to graze and dabble (Marchant and Higgins, 1993). Whistling-ducks are primarily vegetarian. Most species filter-feed on seeds and tubers (Petrie, 2005; Petrie and Petrie, 1988), while two species are considered to be terrestrial grazers (review in Kear (2005)).

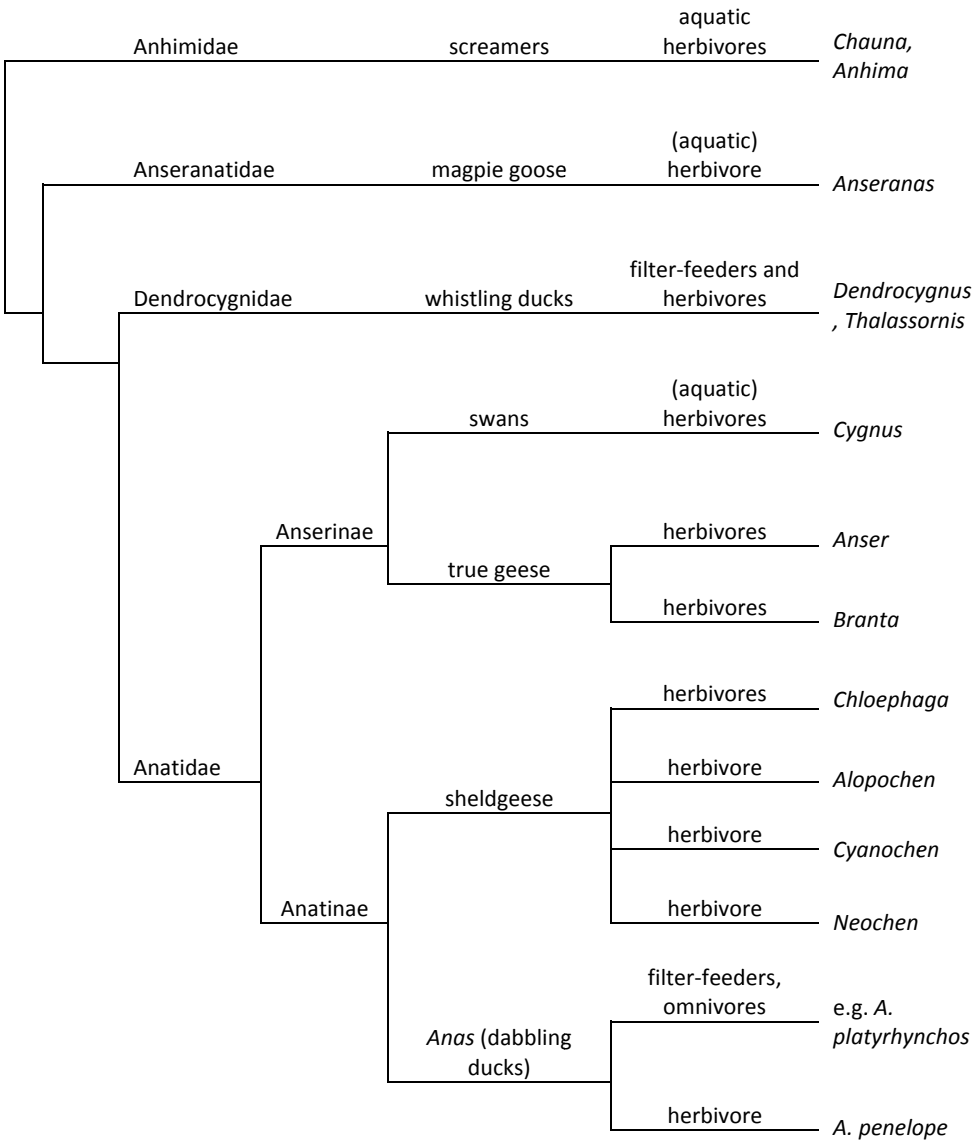


Figure 1. Overview of the anseriform order supplemented with trophic characterizations. All extant families are indicated, but for convenience of comparison most of the duck genera (Anatinae) are omitted. Phyologeny compiled from Brush (1976), Delacour and Mayr (1945), Delacour (1954), Donne-Goussé et al. (2002), Johnsgard (1961, 1965), Johnsgard (1978), Livezey (1986, 1997a, 1997b), Madsen et al. (1988), Olson and Feduccia (1980), Sibley and Monroe (1990, 1993), Woolfenden (1961).

A striking distinction in the occurrence of feeding method is present within the Anatidae. Filter-feeding as principal feeding method is applied only by species of the Anatinae, while the Anserinae mainly feed by grazing. The geese are terrestrial grazers while swans forage on aquatic vegetation, but may include terrestrial vegetation in their diet (Bollinger and King, 2002; Brazil, 2003; Chisholm and Spray, 2002; Earnst, 2002; Earnst and Rothe, 2004; Gillham, 1956; Grant et al., 1994; Owen and Kear, 1972). Some anatinid species may also be characterized as terrestrial grazers: the three wigeon species (*Anas penelope*, *A. sibilatrix* en *A. americana*), the sheldgeese and the maned duck (*Chenonetta jubata*) (review in Kear (2005)).
A minority of wildfowl species preys on fish and/or large aquatic invertebrates. Aquatic grazing or feeding on large aquatic prey does not seem to be compatible with filter-feeding on small food items, as few wildfowl species, if any, combine these feeding methods.
The large variety of species may be the consequence of the occupation of similar niches in different parts of the world. For example, the sheldgeese form the South-American grazing counterparts of the northern geese and species within the duck communities occupy similar niches in the new world and the old world (Delacour, 1964; Nudds et al., 1994).

Adaptive radiation

The many species of wildfowl and their diversity in feeding methods and habitat use are believed to represent an example of adaptive radiation. Adaptive radiation is the evolutionary process that involves the divergence of a single ancestral species into a group of species, each adapted to exploit a different environment (Benkman, 2003; Grant, 1986; Lovette et al., 2002; Schluter, 2001; Schluter, 2000a). For divergent selection to occur, there must be trade-offs in the ability of species to exploit different resources (Doebeli, 1996; Taper and Case, 1992). Performance trade-offs create variation in fitness between phenotypes (Arnold, 1983; Emerson and Arnold, 1989; Lande, 1979) because adaptations to the preferred resource come at the cost of reduced performance when exploiting a less preferred resource. In order to determine resource use a mechanistic understanding of how phenotypes interact with different environments is necessary (Moermond, 1986; Wainwright, 1996).

Conflicting functional demands on the feeding-apparatus

Anseriform birds feed either on land or in water, the exploitation of both feeding environments by the same species is rare. Since foraging in water will pose different functional demands on the feeding apparatus than feeding on land, it may be expected that these two environments will lead to different, possibly opposing, adaptations of the feeding apparatus. Some support for this suggestion comes from studies on the mechanism with which food is gathered and transported through the oral cavity by the mallard (*Anas platyrhynchos*; Kooloos et al., 1989; Zweers et al., 1977) and domestic goose (*Anser anser domesticus*; Van der Leeuw et al., 2003). Filter-feeding in ducks is based on a so-called ‘under-tongue’ transport mechanism in which the rostral part of the tongue is

used as a piston to draw water and suspended food items into the bill. Simultaneously, water is expelled caudally, while food particles are retained by the rims of the bill. Food items are transported through grooves along the sides of the caudal part of the tongue, which is held against the roof of the oral cavity to avoid the ingestion of water. This way of collecting and transporting food through the oral cavity is limited to relatively small food items, up to the size of a pea (Kooloos and Zweers, 1991). For (terrestrial) feeding on large food items and grazing the mallard applies an inertial transport mechanism ('catch-and-throw'). This mechanism involves anterior-posterior jerks of the head accompanied by jaw opening so that the food item is disengaged from the jaws and moves backwards by inertia (Gans, 1969). Simultaneous anterior movement of the head increases the extent of the posterior movement of the food item with respect to the pharynx.

The mechanism underlying both grazing and pecking in the domestic goose is fundamentally different from both the inertial transport mechanism and the 'under-tongue' transport used by the mallard. A different coordination of tongue and bill movements enables the domestic goose to transport clipped vegetation or seeds over the tongue ('over-tongue' transport mechanism), instead of along the sides of the tongue. During retraction of the depressed tongue food items are carried caudad. During subsequent protraction the tongue is elevated and food items are retained behind small caudally pointing spines on the inner surface of the maxilla. Occasionally, geese obtain food items from the water by filter-feeding, and they then use the same 'over-tongue' mechanism used for vegetation instead of the 'under-tongue' mechanism seen in dabbling ducks.

The contradictory functional demand for a bald palatal surface associated with the 'under-tongue' transport mechanism and a palatal surface covered with spines related to the 'over-tongue' mechanism may result in limitations of wildfowl to apply both mechanisms equally efficient.

Research aims

Knowledge of the relationship between head morphology and feeding performance is limited. Whether the diversity of wildfowl is the result of an adaptive radiation of the feeding apparatus is not clear: a trade-off between different ways of foraging has never been demonstrated. This thesis aims to increase our understanding of the functional trade-off between grazing and filter-feeding in wildfowl. This will be assessed by measuring the performance (intake rate) of both grazing (chapter 5) and filter-feeding (chapter 6). When intake rate for both filter-feeding and grazing are maximized, but a maximal intake rate for both feeding methods is not possible, conflicting adaptations in the trophic morphology may be expected. For instance, a large volume per pumping movement of the bill enhances filter-feeding capacity. Therefore, a long (and broad) bill will enable filter-feeding ducks to achieve a high performance. However, during grazing muscle force must be effectively transferred to the tip of the bill to maximize the amount of vegetation severed per bite, and requires a short bill. High performance for filter-feeding *and* grazing results therefore in conflicting demands on bill length. The relationship between these and other conflicting functional demands and differences in

the structures of the jaws, tongue and muscle apparatus are investigated by making a detailed comparative analysis of
1. the shape of the skull of aquatic and terrestrial feeding wildfowl species (chapter 2),
2. the size of the five functional jaw muscle groups in both trophic groups (chapter 3) and
3. the morphology of bill and tongue (chapter 4).
Below, for each chapter a summary is given of the methods used and of the results.

Form of the skull

In this chapter a comparison of the shape of the skulls between specialized filter-feeding and grazing anatid species is made using a geometric morphometric analysis. This analysis is based on the coordinates of homologue features (landmarks), like the tip of the bill or joints between bones. After correction for size significant differences in the positions of many characteristic skull landmarks are found. However, the shape differences between aquatic and grazing species are in many instances small.

Clear relationships with feeding method were apparent for some of the larger differences. To reduce the large number of variables (3 coordinates of 33 landmarks) and to gain insight into the relationship between variables a principal component analysis is applied to the scaled coordinates. This analysis indicates that at least three independent factors affect the shape of the skull. The first component describes co-variation in height of the skull, the position of the orbit and of the craniofacial hinge and the lengths of palatine and pterygoid. A number of these characteristics are related to force transfer. Static 2D force modelling indicates that the more caudad position of the craniofacial hinge in grazers may result in the resistance of a larger external force applied to the tip of the bill. In addition, the more caudad position of this hinge correlates with an increase in width. A wider craniofacial hinge enhances the ability to resist forces generated during grazing without interfering with maxillary movement as would thickening of this bony connection. Using the same 2D-model the relative differences in pterygoid and palatine suggest a decrease in the reaction forces in the jugal –and palatine connection with the maxilla in grazers. However, more realistic modelling requires measured values for pulling and bite forces.

Other covarying variables are less clearly related to foraging method. The position of the orbit increases with skull height, however the importance of skull height for foraging method is obscure. Grazing anseriforms have a relatively higher skull than filter-feeders, a feature that may be interpreted as a way to increase maximal muscle force by increasing the available space for the attachment of muscle fibres. However, muscle size (chapter 3) does not show a relationship with skull height.

The second principal component describes co-variation of the length, width and angle of the maxilla, the width of the cranium, the position of the occipital condyle and again the position of the craniofacial hinge. Specialized filter-feeding species have relatively larger and straighter bills with an expanded tip, a more rostral position of the occipital condyle and a smaller neurocranium. For efficient filter-feeding a large pump capacity is required and this typically involves a long and broad bill. Grazing species have relatively shorter (up to 60%), tapering and more downward pointing bills and a wide cranium. Efficient grazing

benefits from a short narrow bill for an efficient transfer of forces, decreasing the work arm of the pulling forces up to 30%. This short work arm has much larger effect than the modelled effect of relative position of craniofacial hinge.
The effect of the angle between the bill and cranium is not evident, although static force modelling in finches has shown that a more ventrally directed beak increases bite force (van der Meij, 2004). A relative wider cranium is also proved to be a good predictor for bite force in Darwin's finches (Herrel et al., 2005b).

In the third principal component the shape at the back of the skull and width and rostro-caudal position of the craniofacial connection covary. This component shows an allometric effect. No clear relationship with feeding method is apparent for the shape differences at the back of the head. As grazers are larger than specialized filter-feeders the former have a wider craniofacial hinge. As noted before, a wider craniofacial hinge enhances the ability to resist reaction forces generated during grazing without interfering with maxillary movement as would thickening of this bony connection.

Comparing differences in skull shape among terrestrial grazing species from different genera suggests that the degree of adaptation to grazing reflects evolutionary history. Recent taxa like the wigeons and sheldgeese show only modifications in bill dimensions, while the more ancestral taxa, *Anser* and *Branta*, show large differences in cranial shape as well.

Jaw musculature

In addition to differences in skull shape the muscles moving the feeding apparatus may show adaptations related to the foraging method as well. Aquatic feeding anseriforms have a larger bill surface area (chapter 2 and 4) and the frequency of the cyclical bill openings and closings are higher compared to terrestrial grazing species (20 Hz in filter-feeding in specialized filter-feeders (Kooloos et al., 1989) vs. max. 2 Hz in grazing in grazers (Durant et al., 2003). The high frequency of bill movements of the submerged bill may generate considerable reaction forces in these species. On the other hand in grazing anseriforms a forceful closure of the bill is necessary to hold vegetation firmly in the bill so that when the head and neck are drawn backwards, the grass will snap off, rather than be pulled out of the bill. Furthermore, the backward movement of the head will result in forces that elevate the upper bill, which is moveable with respect to the neurocranium.

In chapter 3 the size of the 5 functional groups of jaw muscles of 45 anseriform species is determined. These 45 anatid species were categorized as either aquatic or terrestrial feeding based on literature data.
Although in both trophic groups total jaw muscle mass scales with the same exponent and negatively allometric with respect to body mass, total jaw muscle mass is 1.5 times higher in aquatic feeding species. Not all jaw muscle groups contribute equally to this relative difference. The depressors of the mandibula and the openers of the maxilla are approximately 2 times larger, and the pterygoid muscles (closers of the mandibula and the maxilla) on average 1.4 times larger in aquatic feeding species than in grazing species.

The two remaining jaw-closing muscle groups do not contribute to the difference in total jaw muscle mass.

The larger depressor muscles of aquatic feeding species do not seem to be related to the larger reaction forces experienced during feeding with submerged bill. Since aquatic feeding species have larger bills moving the bills will involve larger moments of inertia, independent of foraging environment. Calculations show that the difference in size of the jaw opener muscles is approximately sufficient to compensate for the difference in bill size. Similarly, the relatively large pterygoid muscle of aquatic feeders does not seem to be related to the feeding environment. The pterygoid muscles of both trophic anseriform groups are smaller than the pterygoid muscles of a sample of predominantly terrestrially feeding birds.

There is no obvious relationship between shape of the skull and muscle mass. The relative larger area for adductor muscle attachment available through a higher-vaulted cranium in grazing species is not accompanied by relatively larger adductor muscles. Similarly, the increase in space between the eye and the palatines and pterygoids available through a relatively dorsal position of the eye, is not associated with an increase in pterygoid muscles. On the contrary, the pterygoid muscles are relatively smaller in terrestrial grazing anseriforms. A similar situation applies to the depressor muscles. Filter-feeding species have relatively narrower and lower crania, but have relatively larger depressor muscles.

Although the differences in jaw muscles masses are significant between trophic groups, there is a considerable variation of food items in the aquatic feeding group. About one-fifth of these species may feed predominantly on small food items. About half of the aquatic feeding species adds parts of aquatic plants to their diet, and some species forage predominantly on aquatic vegetation. Feeding on aquatic vegetation may resemble terrestrial grazing. Support for this idea comes from the similarity of the skulls of swans to those of terrestrial feeding anatids and it may explain the smaller depressor muscles in these four species. Relative large adductor muscles, even larger than those of many (sheld)geese, are found in aquatic species foraging on fish and shellfish. Detaching shellfish or holding struggling fish may involve forces on the jaws larger than those experienced during filter-feeding or grazing.

In the terrestrial grazing group a distinction can be made between species feeding only on aerial parts of vegetation (*Branta*, sheldgeese, wigeon and maned duck), and those feeding on belowground plant parts as well (*Anser*). Grubbing in wet soil to expose these subterranean parts involves powerful jaw openings (gaping-action) to push the soil particles aside (Glazener, 1946). This way of feeding may explain the often relatively larger jaw opener muscles in *Anser* species compared to the other grazing species.

Morphology of the oral cavity

Specific adaptations of the structures of the tongue and oral cavity seem to be related to pumping of water and transport of grazed vegetation, respectively. Kinematic analyses of the mallard and domestic goose have shown that drawing in water and suspended food

particles and the ‘under-tongue’ transport mechanism of food items are associated with a bald palatal roof and a longitudinal groove along both sides of the most caudal thickened part of the tongue (tongue cushion). The bald palatal surface serves the piston-action of the tongue, while the grooves alongside the tongue cushion enables continuous throughput of food without interference of separate swallowing actions. In the domestic goose lingual grooves are absent, and spines cover the palatal surface. These spines retain severed vegetation during forward movements of the tongue on which food items are carried caudad. In this chapter the oral morphology of anseriform species is studied to investigate whether the functional requirements of aquatic versus terrestrial foraging has resulted in similar morphologies within trophic groups.

The species studied are divided in two trophic groups based on literature data. One group comprises the terrestrial grazing species; in the other group aquatic feeding species are assembled. In the latter group food items taken are diverse and prey size differs accordingly.
Most of the 19 aquatic feeding anatid species studied possess the intraoral elements required for the ‘under-tongue’ transport mechanism: a bald maxillar roof, a thickened rostral part of the tongue and a groove running along both sides of the caudal part of the tongue (the so called tongue-cushion). In contrast, in most of the 20 species of grazers the maxillar roof bears spines and the lingual grooves are lacking.

Other features of oral structures are related to the feeding method as well. In general, the dorsal row of mandibular lamellae is broad with a sharp dorsal edge in most grazing species. The lamellae are bladelike and with a smooth dorsal side in most aquatic feeding species. The sharp dorsal edge may serve to sever grass leaves. Aquatic feeding species have a 1.6 times deeper maxilla increasing the volume. The relative size of the rostral part of the tongue is larger in aquatic feeders enhancing piston action of tongue.

In both trophic groups deviations of the typical morphology occur. In the aquatic feeding group some of the birds that feed mainly on aquatic vegetation lack the grooves along the sides of the tongue, but do have sharp edged dorsal mandibular lamellae and papillae on the palatal surface. These features are typical of the ‘over-tongue’ transport mechanism as found in terrestrial feeding species.
Small maxillar papillae are also found in some other aquatic feeding species that do have lingual grooves. These species take large food items, and as large items cannot be transported through the grooves alongside the tongue the palatal papillae may enable the ‘over-tongue’ transport mechanism instead of the inefficient ‘catch-and-throw’ mechanism. Whether these birds apply the ‘over-tongue’ transport mechanism is unknown.
A combination of morphological characters related to both oral transport mechanisms are also found in the wigeons, which in our study are classified as grazers. In the Eurasian wigeon it has been experimentally shown that both transport mechanisms are applied by the same species: ‘over-tongue’ transport in grazing and ‘under-tongue’ transport in filter-feeding (Van der Leeuw et al., 2003).

Performance of grazing and filter-feeding

The oral morphologies associated with the 'over-tongue' and the 'under-tongue' transport mechanism are functionally incompatible. The presence of spines on the palatal roof, required for 'over-tongue' transport of grass or large food items, are incompatible with an efficient piston action of the tongue. The presence of spines prevents the elevated tongue from properly acting as a piston during straining, resulting in a 'leaky' pump with a reduced pump capacity. In addition, the absence of lingual grooves, associated with taking large food items, will prevent the use of the 'under-tongue' mechanism to transport food items. On the other hand most aquatic feeding species lack spines on the palatal roof and will thus not be able to transport food by the 'over-tongue' mechanism. It may be expected that this incompatibility limits the ability of anseriforms to apply both intraoral transport mechanisms as efficiently. In the next two chapters the performance of both grazing and filter-feeding is measured to check whether the expected trade-off exists.

The grazing performance of three species of terrestrial grazing geese (lesser white-fronted goose (*Anser erythropus)*, barnacle goose (*Branta leucopsis)*, and Canada goose (*B. canadensis*)) and one species of aquatic grazing swans, the mute swan (*Cygnus olor)*, is determined in chapter 5. The amount of grass ingested by individual birds grazing from a small turf of grass during a short period of time is very precisely measured. Intake rate is used as measure for performance and is determined by the product of bite rate, and the size of the bite cropped minus the amount lost during transport.
Intake rate in all four species increases proportionally with increasing bite size, however the increase in intake rate is smaller as species are larger. Large species with large bills take larger bites, but also loose relatively more grass leaves and have a lower bite rate. Intake rate increases quickly at small bite sizes, but at larger bite sizes the decrease in bite rate and the increase of food loss start to balance the effect of increasing bite size, and intake rate levels off or even declines.

Comparisons of grazing performance among species are based on the intake rate relative to metabolic requirements. The intake rates in two of the three species of goose and the mute swan are similar, and did not differ from scaled intake rates in goose species reported in the literature (Durant et al., 2003; Van der Leeuw et al., 2003). All four species probably applied the 'over-tongue' transport mechanism during grazing. Although no kinematical analyses are performed, this statement is supported by the facts that large head movements and wide gapes typical of the inertial transport mechanism are not observed and all the morphological prerequisites for 'over-tongue' transport are present. The lower intake rate of barnacle geese, which is also found in other studies (Cope et al., 2005; Durant et al., 2003), may reflect differences in long-term foraging strategy rather than differences in the mechanics of grazing.

Relative grazing performance in wigeon and especially mallard (Van der Leeuw et al., 2003) is lower than in the geese and the swan. The low intake rate of the wigeon is caused by small bite sizes and low bite rates. In the mallard the effect of a low bite rate is reinforced by a relatively high loss of grass during food transport. These suboptimal performances seem to be due the specific morphology of their oral cavity. A small number of papillae on the maxillar median ridge and immediately adjacent to this ridge enable

wigeon to adopt the 'over-tongue' transport mechanism used by geese, although one leaf of grass is transported at a time resulting in small bite size and long transport times and thus lower bite rate. In the mallard the roof of the oral cavity is completely bald and this species has to use the inertial transport mechanism for large food items, which explains the relatively high food loss and the low bite rate.

In chapter 6, the performance of filter-feeding is assessed in two goose species, the lesser white-fronted and barnacle goose, and in the mute swan. Filter-feeding performance is determined by the percentage of food-items retained as well as by the amount of water and suspended food particles pumped through the bill. The goose species and the mute swan are all able to retain more than 95% of the millet seeds drawn in at the tip of the bill. Similar values were found in several other aquatic feeding species (Kooloos et al., 1989). It is remarkable that retention of seeds behind palatal spines is as efficient as retention of seeds by the intervention of the lamellae on the edges of the bills. Possibly, retention of food items by palatal spines does not allow for selective straining of different sized items as demonstrated in filter-feeders.

In aquatic feeding species the volume of water per straining cycle relative to body size is much larger and the straining frequency is higher than in the geese and the swan. Consequently, relative intake rate is higher in the filter-feeders than in geese or mute swans. Differences in relative bill size only explain part of the difference in volume taken in per movement cycle. The major cause for the difference in performance seems to be related to the different mechanisms used. The tongue and bill movements of geese during 'over-tongue' transport are similar to the tongue and bill movements during the transport of severed vegetation and different from the coordination of movements in filter-feeding duck species. In geese, the tongue is not positioned against the palatal roof during bill opening and food and water are more or less scooped up. After water has been taken in the tongue moves forward and is pressed against the maxillar roof where food items are retained by the spines. This is in contrast to the movements in filter-feeding ducks, where the tongue makes a forward movement with a depressed tongue. As a consequence, the movements associated with the 'over-tongue' transport mechanism are less efficient in drawing in water during filter-feeding. Furthermore, the 'over-tongue' mechanism in geese precludes the continuous throughput of food items as found in filter-feeding duck species. The collection of food items on top of the tongue necessitates a two stage food intake with a food collection phase followed by a swallowing phase (Van der Leeuw et al., 2003). Compared to the continuous process of the 'under-tongue' transport mechanism, the two separate phases slow down intake rates and consequently result in a lesser performance of geese and the mute swans compared to aquatic feeding ducks.

Conclusions

The morphological data as well as the kinematical analyses of feeding in several wildfowl species show that the mechanics of feeding on small water suspended food items differs clearly from that used for the severing of vegetation. Consistent differences are found in the morphological characters related to the intake of food between aquatic or terrestrial

grazing species and aquatic feeding species that forage on food items other than aquatic plants. The morphological adaptations and intraoral transport mechanisms associated with maximal performance for either grazing or filter-feeding are incompatible and prevent maximal performance of both foraging methods at the same time. There is a trade-off between grazing and filter-feeding. Species that mainly filter-feed in the water have a lower grazing performance than species that predominantly graze and vice versa grazers perform worse when filter-feeding compared to filter-feeding specialists.

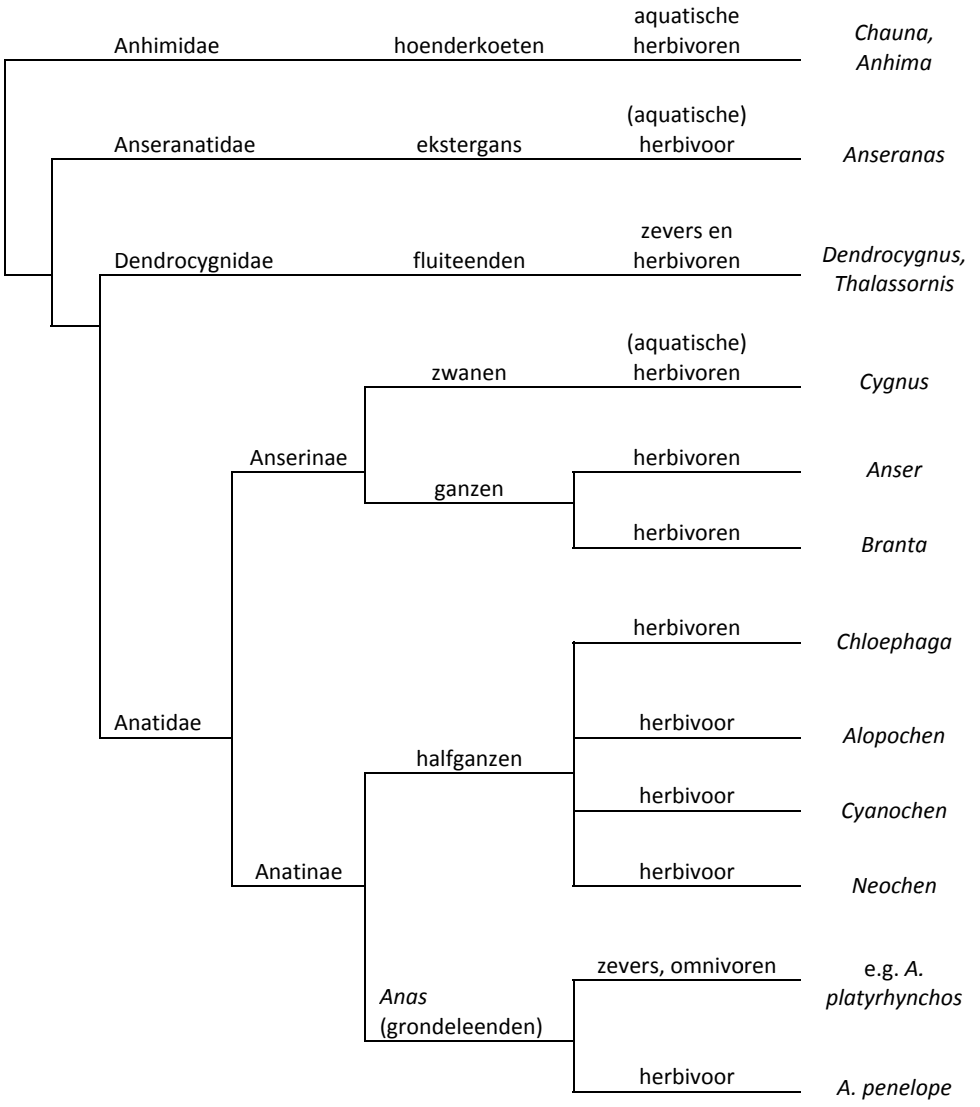
Algemene Samenvatting

De rol van voedselkeuze in de evolutie van eendachtigen

Eendachtigen vormen een diverse groep vogels die over de hele wereld, behalve op de Zuidpool, voorkomen. Deze vogels zijn nauw aan elkaar verwant, en vormen de orde Anseriformes. De orde van Anseriformes is onderverdeeld in vier families (zie figuur 1). De oudste familie (Anhimidae) wordt gevormd door de drie soorten hoenderkoeten (*Chauna chaviaria*, *Chauna torquata* en *Anhima cornuta*). De tweede familie (Anseranatidae) bestaat uit slechts 1 genus (*Anseranas*) met 1 soort: de ekstergans (*Anseranas semipalmata*). Deze soort wordt beschouwd als de overgangsvorm ('link') tussen de Anhimidae en de Anatidae (Brush, 1976; Delacour, 1954; Johnsgard, 1961; Johnsgard, 1978; Livezey, 1986; 1997a, 1997b; Madsen et al., 1988; Olson and Feduccia, 1980; Woolfenden, 1961). Fluiteenden (Dendrocygnidae) vormen de derde familie (Sibley and Monroe, 1990, 1993), maar worden ook wel binnen de Anatidae (eenden, ganzen en zwanen) geplaatst (Donne-Goussé et al., 2002; Livezey, 1997a). De fluiteenden vormen de zustergroep van de eenden, ganzen en zwanen (Donne-Goussé et al., 2002; Livezey, 1997a; Madsen et al., 1988).
De Anatidae zijn weer onderverdeeld in twee subfamilies: de Anserinae en de Anatinae. Onder de Anserinae vallen de ganzen (*Anser* en *Branta*) en de zwanen (*Cygnus*). De Anatinae bestaan uit alle 'echte' eenden (ongeveer 30 genera, waaronder *Anas*) en de Tadornini (de halfganzen (*Cyanochen*, *Alopochen*, en *Chloephaga*) en de eenden van de genera *Tadorna* en *Casarca*).
De Tadornini zijn als eerste afgesplitst binnen de Anatinae en worden gezien als een tussenvorm van de 'echte' eenden en ganzen (Delacour and Mayr, 1945; Donne-Goussé et al., 2002; Johnsgard, 1965, 1978; Livezey, 1986).
Wanneer de eendachtigen zijn ontstaan is niet zeker, maar fylogenetische analyses duiden op het late Krijt (ongeveer 80 miljoen jaar geleden) (Livezey, 1997b; Olson and Feduccia, 1980; Sibley and Monroe, 1990, 1993).

Niet alleen zijn er zeer veel soorten eendachtigen, ook het voedsel van deze vogels kenmerkt zich door een grote variatie. Zo zijn er verschillen tussen soorten, maar ook binnen de soort kan het type voedsel afhankelijk zijn van habitat, jaargetijde, leeftijd en geslacht en zelfs verschillen tussen individuen van dezelfde soort (reviews in Baldassarre and Bolen (1984) en Krapu and Reinecke (1992)).
Hoewel de meeste soorten afhankelijk zijn van water voor hun voedsel, zijn er ook soorten die op het land hun voedsel vinden. De methodes die de vogels gebruiken om voedsel te vergaren hangen samen met de habitat waarin voedsel gevonden wordt en het geprefereerde voedseltype (reviews in Krapu and Reinecke (1992) en Kear, 2005). De twee meest voorkomende methodes zijn zeven en grazen. Zeven is het door de snavel pompen van water waarbij voedseldeeltjes worden verzameld. Deze methode wordt zowel aan het wateroppervlak (slobberen) als dieper (grondelen) gebruikt om ongewervelde diertjes, zaden en delen van waterplanten te bemachtigen (e.g. review in Kear (2005)). Grazen is het plukken van planten op het land of onder water.

De hoenderkoeten eten voornamelijk de bovengrondse delen van waterplanten, terwijl ze waden door het water. Ook de ondergrondse delen worden wel opgegraven. Daarnaast worden ook de boven– en ondergrondse delen van terrestrische planten gegeten (review in Kear (2005)).
De ekstergans foerageert hoofdzakelijk op ondergrondse delen van moerasplanten, maar slobbert en graast daarnaast ook (Marchant and Higgins, 1993).



Figuur 1. Overzicht van de orde der anseriformen met trofische typering. Voor de overzichtelijkheid zijn fossiele families en de meeste eendengenera (Anatinae) niet vermeld. De fylogenie is samengesteld aan de hand van Brush (1976), Delacour and Mayr (1945), Delacour (1954), Donne-Goussé et al. (2002), Johnsgard (1961, 1965; 1978), Livezey (1986, 1997a, 1997b), Madsen et al. (1988), Olson and Feduccia (1980), Sibley and Monroe (1990, 1993), Woolfenden (1961).

Het merendeel van de fluiteenden zeeft voornamelijk zaden uit het water (Petrie and Petrie, 1988; Petrie, 2005), een klein aantal soorten graast vooral op het land (review in Kear (2005)).
Binnen de Anatidae komt het zeven als foerageer methode vooral voor bij soorten uit de subfamilie Anatinae, terwijl de Anserinae voornamelijk grazen; de ganzen op het land, de zwanen vooral in het water, maar ook wel op het land (Bollinger and King, 2002; Brazil, 2003; Chisholm and Spray, 2002; Earnst, 2002; Earnst and Rothe, 2004; Gillham, 1956; Grant et al., 1994; Owen and Kear, 1972). Ook een aantal Anatinae soorten graast op het land, zoals de smienten (*Anas penelope*, *A. sibilatrix* en *A. americana*), de halfganzen en de manengans (*Chenonetta jubata*) (review in Kear (2005)).
Een minder vaak voorkomende foerageermethode is het vangen van vis en/of grote aquatische evertebraten. Er zijn weinig soorten die aquatisch grazen of het eten van grote prooien combineren met het zeven van kleine voedseldeeltjes.
De grote diversiteit aan soorten zou te maken kunnen hebben met het feit dat in verschillende werelddelen andere soorten eenzelfde niche bezetten. Zo zijn de halfganzen de grazers in Zuid-Amerika en de ganzen de grazers van het noordelijke halfrond en vormen soorten in eendengemeenschappen in de nieuwe wereld de tegenhangers van die in de oude wereld (Delacour, 1964; Nudds et al., 1994).

Adaptieve radiatie

De vele soorten eendachtigen met hun specifieke foerageermethoden worden beschouwd als een voorbeeld van adaptieve radiatie. Adaptieve radiatie is het evolutionaire proces waarbij door divergentie vanuit 1 voorouderlijke soort nieuwe soorten ontstaan die zijn aangepast aan verschillende ecologische niches. Elk soort benut andere hulpbronnen (Benkman, 2003; Grant, 1986; Lovette et al., 2002; Schluter, 2000a, 2001).
Drijvende kracht achter divergentie is een uitruil ('trade-off') van de vermogens van de soorten om verschillende hulpbronnen te gebruiken (Doebeli, 1996; Taper and Case, 1992). De verschillen in de efficiëntie waarmee de diverse hulpbronnen worden gebruikt resulteren in verschillen in fitness (Arnold, 1983; Emerson and Arnold, 1989; Lande, 1979). Dit komt doordat adaptaties die gerelateerd zijn aan geprefereerde hulpbronnen ten koste gaan van adaptaties aan andere, minder geprefereerde hulpbronnen. Om het gebruik van bepaalde voedselbronnen te begrijpen is het nodig om een mechanistisch inzicht te hebben in de interactie tussen de adaptaties van de soorten en hun hulpbronnen (Moermond, 1986; Wainwright, 1996).

Conflicterende eisen aan het voedselopnameapparaat

Voor zover bekend zijn er heel weinig soorten eendachtigen die gebruik maken van zowel aquatische als terrestrische voedselbronnen. Aangezien foerageren in water andere eisen aan het voedselopnameapparaat stelt dan het foerageren op land, zouden deze twee manieren van foerageren verschillende, mogelijk tegenstrijdige, aanpassingen van het voedselopnameapparaat kunnen vereisen. Aanwijzingen die deze hypothese ondersteunen zijn gevonden in de manier waarop de wilde eend (*Anas platyrhynchos*, Kooloos et al., 1989; Zweers et al., 1977) en gedomesticeerde gans (*Anser anser*

domesticus; Van der Leeuw et al., 2003) voedsel verzamelen en door de snavel naar de slokdarm transporteren.

Het zeven en transporteren van kleine voedseldeeltjes uit water gebeurt bij de wilde eend via een zogenoemd 'onder-tong' transportmechanisme. Water en voedseldeeltjes worden aan de voorkant van de snavel naar binnen gezogen en tegelijkertijd wordt eerder opgezogen water aan de achterkant van de snavel uitgestoten. Het achterste gedeelte van de tong is steeds tegen de bovensnavel aangedrukt om inslikken van water te voorkomen. Voedseldeeltjes worden langs dit opgeheven gedeelte van de tong naar de slokdarm getransporteerd via groeven aan weerszijden van de tong. Met dit mechanisme kunnen alleen voedseldeeltje tot de grootte van een erwt (Kooloos and Zweers, 1991) worden getransporteerd. Voor grotere voedseldeeltjes wordt een transportmechanisme toegepast dat gebruik maakt van de traagheid van massa. De kop beweegt met gesloten snavel met daarin voedsel naar achter, waarna de snavel wijd opent en het voedseldeeltje vrij door de open snavel richting keel vliegt (Gans, 1969). Tegelijk wordt de kop naar voren bewogen en wordt het voedsel weer opgevangen. Deze methode wordt in het Engels dan ook wel 'catch-and-throw' genoemd. De wilde eend gebruikt dit mechanisme ook voor het transport van gras.

Bij de gedomesticeerde gans is het mechanisme dat zorgt voor transport van afgehapte vegetatie en opgepikte voedseldeeltjes fundamenteel verschillend van het 'onder-tong' mechanisme. Voedseldeeltjes worden op de naar achteren bewegende tong richting keel gedragen. Wanneer de tong weer naar voren gaat drukt deze tegelijkertijd het voedsel tegen kleine naar achteren gerichte uitsteeksels op het monddak aan, zodat het voedsel niet mee naar voren beweegt. Dit mechanisme wordt 'over-tong' transport genoemd. In de zeldzame gevallen dat ganzen voedsel uit het water halen via de zeefmethode wordt ditzelfde 'over-tong' transportmechanisme toegepast.

De tegenstrijdigheid van een glad versus een met stekels bezet monddak en de daarmee samenhangende mechanismen om voedsel door de bekholte te transporteren vormt mogelijk een beperking voor de vogels om beide mechanismen even efficiënt toe te passen.

Onderzoeksvragen

De kennis over de verschillen in morfologie en de verschillen in foerageerprestaties die bij de diverse voedselopnamemechanismen horen is beperkt. Of de diversiteit van eendachtigen het gevolg is van adaptieve radiatie van het voedselopname apparaat is niet zeker: een 'trade-off' tussen de verschillende manieren van voedselopname is nooit aangetoond. Dit proefschrift probeert de kennis over de functionele uitruil tussen grazen en zeven bij eendachtigen te vergroten. Hiertoe wordt voor een aantal soorten onderzocht of er inderdaad een uitruil bestaat tussen de efficiëntie waarmee dieren grazen (hoofdstuk 5) en zeven (hoofdstuk 6). Als voor zowel zeven als grazen de opname van voedsel gemaximaliseerd wordt maar een maximale inname van beide typen voedsel niet mogelijk is, betekent dit bovendien dat er elkaar uitsluitende aanpassingen te verwachten zijn in de structuren die voor voedselopname zorgen.

Zo zal bijvoorbeeld bij eendachtigen die voornamelijk zeven een zo groot mogelijk volume per pompbeweging moeten worden gerealiseerd, terwijl grazende soorten een aanzienlijke kracht op de snavel moeten kunnen leveren om zoveel mogelijk plantenmateriaal per hap te plukken. Voor zevers zal de snavel dus lang (en breed) moeten zijn, maar voor grazers juist kort om een zo groot mogelijke kracht te kunnen uitoefenen op het gras. Het verband tussen deze en andere conflicterende functionele eisen en verschillen in de bouw van het kaak-, tong- en spierapparaat zijn onderzocht door een gedetailleerde vergelijkende analyse te maken van
1. de vorm van de schedel en de daarin voorkomende botstructuren (hoofdstuk 2),
2. de grootte van de vijf functionele kaakspiergroepen bij aquatisch en terrestrisch foeragerende eendachtigen (hoofdstuk 3) en
3. de morfologie van de snavel en tong (hoofdstuk 4).

Hieronder worden de gebruikte methoden en resultaten per hoofdstuk samengevat.

Vorm van de kop

In hoofdstuk 2 is een vergelijking gemaakt van de vorm van de schedel tussen gespecialiseerde zevers en grazers op basis van geometrische morfometrie. Deze vergelijkingsmethode is gebaseerd op de coördinaten van homologe kenmerken, zoals snavelpunt of gewrichten tussen botten. Na het elimineren van grootte-verschillen tussen soorten toont een kwantitatieve vergelijking tussen zevers en grazers aan dat de posities van veel kenmerkende schedelpunten statistisch verschillen. Echter de vormverschillen tussen de soorten zijn op veel plaatsen zeer klein.

Een aantal grote verschillen is duidelijk gerelateerd aan de methode van foerageren. Om het grote aantal variabelen (3 coördinaten van 33 kenmerken) te reduceren en inzicht te krijgen in hun onderlinge samenhang is op de data een principale componenten analyse uitgevoerd. Deze analyse geeft aan dat er tenminste 3 onafhankelijke factoren zijn die effect hebben op de vorm van de schedel. De eerste component beschrijft verschillen in onder andere de hoogte van de schedel, de positie van de oogkas, de positie van de verbinding tussen snavel en hersenschedel (craniofaciale scharnier) en de lengtes van twee schedelbotjes (palatinum en pterygoid) die samen veranderen (covariëren). Een aantal van deze eigenschappen is gerelateerd aan het uitoefenen van kracht tijdens grazen. Berekeningen met behulp van een 2D-statische krachtenmodel geven aan dat de meer naar achteren gelegen positie van de craniofaciale verbinding bij grazers leidt tot het kunnen weerstaan van een grotere externe kracht op de punt van de bovensnavel. Bovendien wordt met het naar achteren schuiven van de craniofaciale verbinding dit scharnier ook breder en kan daardoor beter reactiekrachten in het gewricht weerstaan. Hetzelfde 2D-model geeft ook aan dat de relatieve verschuiving in de lengtes van palatinum en pterygoid de reactiekrachten in de verbindingen van palatinum en ‘jugale’ (jukboog) met de bovensnavel zou kunnen verminderen bij grazers. Om dit realistisch te kunnen modelleren zijn echter metingen van werkelijke trek- en bijtkrachten noodzakelijk. Andere meevariërende eigenschappen zijn niet zonder meer in verband te brengen met foerageermethode. De positie van het oog hangt samen met de hoogte van de schedel, maar de betekenis van schedelhoogte is niet duidelijk. Grazende eendachtigen hebben een relatief hogere schedel dan zevers, een eigenschap waarvan wel verondersteld wordt

dat dit het oppervlak voor spieraanhechting, en daarmee de maximale spierkracht, vergroot. Het onderzoek naar spiergrootte (hoofdstuk 3) laat echter zien dat er geen rechtstreeks verband is tussen schedelhoogte en spiergrootte.

In de tweede principale component covariëren lengte, breedte en de hoek van de snavel met de schedel, de breedte van het cranium, de positie van de achterhoofdsknobbel en opnieuw de positie van de craniofaciale verbinding. Gespecialiseerde zevers hebben een relatief langere, rechte en breed uitlopende snavel, een meer naar voren gelegen positie van de craniofaciale verbinding en een smalle hersenschedel. De relatief grote omvang van de snavel stelt deze vogels in staat om een groot volume aan water met daarin zwevende voedseldeeltjes op te pompen. Grazers hebben een relatief korte, spits toelopende en iets meer omlaag gerichte snavel en een brede schedel. De kortere snavel vergroot de kracht die door de nekspieren uitgeoefend kan worden tijdens het lostrekken van gras (kleinere lastarm) en vergroot de bijtkracht waarmee het gras in de snavel kan worden geklemd. Berekeningen in het 2D-model geven aan dat het effect van de kortere snavel op de kracht die kan worden uitgeoefend op het gras veel groter is dan het effect van het naar achteren schuiven van de craniofaciale verbinding. Een meer omlaag gerichte snavel vergroot de bijtkracht (van der Meij, 2004), en ook een bredere schedel is in verband gebracht met een grotere bijtkracht bij Galapagos vinken (Herrel et al., 2005b).

In de derde principale component is er variatie in de vorm van de achterkant van de hersenschedel in combinatie met de breedte van de craniofaciale verbinding. Deze variatie is gerelateerd aan lichaamsgrootte. Er lijkt geen verband te zijn tussen de vorm van de achterkant van de schedel en foerageermethode. Grazers zijn meestal groter dan gespecialiseerde zevers en hebben een bredere craniofaciale verbinding. De reactiekrachten die tijdens het lostrekken van vegetatie gegenereerd worden kunnen hierdoor over een groter oppervlak worden verdeeld, zonder dat de beweeglijkheid van de verbinding door botverdikking hoeft te worden belemmerd.

Wanneer de mate van aanpassingen in de vorm van de schedels van de verschillende terrestrisch grazende genera met elkaar worden vergeleken, blijkt er een verband te zijn met evolutionaire geschiedenis. Recente soorten, smienten en halfganzen, vertonen alleen aanpassingen in de snavel, terwijl de meest basale soorten (ganzen) daarnaast ook verschillen in de hersenschedel laten zien.

De kaakspieren

Naast verschillen in de vorm van de schedel kunnen ook de spieren van het voedselopname apparaat aanpassingen vertonen aan de wijze van foerageren. Zo hebben zevers een grotere snavel (hoofdstukken 2 en 4) en worden de cyclische bewegingen van open en sluiten van de snavel tijdens foerageren met verschillende snelheden uitgevoerd: 20 Hz bij gespecialiseerde zevers (Kooloos et al., 1989) en 2 Hz bij grazers (Durant et al., 2003). De hoogfrequente bewegingscycli van de ondergedompelde snavel van gespecialiseerde zevers genereren mogelijk aanzienlijke reactiekrachten van het water op de snavel. Grazende eendachtigen daarentegen moeten tijdens het lostrekken van vegetatie de snavel krachtig gesloten houden om wegglippen van blaadjes tijdens de

trekbeweging van de kop en nek te voorkomen. Tegelijkertijd moet de kracht op de ten opzichte van de schedel beweegbare bovensnavel tijdens het lostrekken van gras worden weerstaan.

In hoofdstuk 3 zijn van 45 soorten eendachtigen de gewichten van de 5 functionele kaakspiergroepen bepaald. Gebaseerd op literatuurgegevens werden de vogels opgesplitst in twee groepen: een aquatisch foeragerende groep en een terrestrisch foeragerende groep. Hoewel het gewicht van alle kaakspieren samen in beide groepen op dezelfde manier afneemt met lichaamsgrootte (negatieve allometrie), is het relatieve gewicht aan kaakspieren steeds anderhalf keer groter bij aquatisch foeragerende eendachtigen dan bij terrestrisch foeragerende soorten. Niet alle spiergroepen dragen bij aan dit verschil. De spieren die de ondersnavel omlaag (depressoren) en de bovensnavel omhoog bewegen (protractoren) zijn in aquatisch foeragerende soorten ongeveer 2 keer zo groot. De spieren die tegelijk de onder- en bovensnavel sluiten (pterygoid spieren) zijn 1.4 keer zo zwaar. De twee resterende snavelsluitende spiergroepen verschillen niet tussen de trofische groepen.

De verklaring voor de grotere kaakopener en -sluiter spieren bij aquatisch foeragerende soorten lijkt niet te liggen in de grotere weerstand die een bewegende snavel in het water ondervind. Omdat de snavel van aquatisch foeragerende soorten groter is dan van terrestrisch grazende soorten zal ook los van de omgeving waarin voedsel wordt verzameld een grotere kracht nodig zijn om het traagheidsmoment van de snavel te overwinnen. Schattingen van de benodigde spierkracht laten zien dat de grotere spieren in aquatisch foeragerende soorten net voldoende zijn om te compenseren voor de grotere snavel. Bovendien zijn de pterygoid-spieren van beide trofische groepen, ondanks hun onderlinge verschil, kleiner dan die van andere soorten vogels, die voornamelijk terrestrisch foerageren.

Ook is er geen direct verband tussen schedelvorm en spiergrootte. Het relatief grotere oppervlak gevormd door een hoger en breder cranium in terrestrische foeragerende eendachtigen gaat niet gepaard met daar aanhechtende grotere adductor spieren. Evenmin wordt de relatief grotere beschikbare ruimte tussen oogkas en palatinum-pterygoid ingenomen door grotere spieren. In tegendeel, de pterygoidspieren zijn relatief klein bij terrestrisch grazende soorten. En ondanks een relatief smalle en lage schedel zijn de depressoren bij aquatisch foeragerende soorten relatief groter.

Er zijn duidelijke verschillen in relatieve spiergewichten tussen soorten die op het land dan wel in het water foerageren, terwijl er toch aanzienlijke variatie in het soort voedsel binnen de aquatische groep is. Ongeveer eenvijfde van deze soorten voedt zich hoofdzakelijk met kleine deeltjes. De helft van de aquatische groep voegt hieraan delen van waterplanten toe, en sommigen eten juist voornamelijk waterplanten. Mogelijk lijkt de manier waarop waterplanten worden benut op de manier waarop landplanten worden begraasd, met bijbehorende langzamere bewegingen. Dat de vorm van de schedel van de waterplantetende zwanen neigt naar die van terrestrische grazers ondersteunt dit idee. Dit zou dan de relatief kleinere depressoren in de voornamelijk waterplantetende soorten kunnen verklaren. Relatief grote adductorspieren, zelfs groter dan die van vele soorten uit de terrestrische groep, worden gevonden in eendachtigen die hoofdzakelijk schaaldieren

of vis eten. Het losmaken van schaaldieren van het substraat of het vasthouden van een spartelende vis gaan mogelijk gepaard met krachten op de snavel die groter zijn dan tijdens het filteren van kleine voedseldeeltjes of het grazen van terrestrische vegetatie.

Ook de als terrestrisch foeragerend getypeerde eendachtigen eten niet allemaal hetzelfde. Allen begrazen bovengrondse plantendelen, terwijl sommigen (ganzen uit het genus *Anser*) ook ondergrondse delen eten. Voor het blootleggen van deze subterrestrische delen wordt de aarde omgewroet met de snavel door middel van spreidacties van de snavel (Glazener, 1946). De relatief grote kaakopener spieren in *Anser* soorten zou hiermee verband kunnen houden.

Morfologie van de bekholte

Zowel het doorpompen van water als het transport van gras door de snavel lijken verbonden met aanpassingen van de tong en mondholte. Uitgebreide kinematische analyse heeft laten zien dat in de wilde eend het aanzuigen van water en het 'onder-tong' transport van voedseldeeltjes geassocieerd is met een glad monddak voor de 'zuigerwerking' van de tong en een groeve langs de zijkant van het verdikte achterste gedeelte van de tong (het zgn. tongkussen) om het zeven niet te hoeven onderbreken om voedsel in te slikken. In de tamme gans ontbreken deze groeven en zijn op het monddak kleine stekels aanwezig die het gras tegenhouden als het met voor/achterwaartse bewegingen van de tong door de mondholte naar achteren wordt getransporteerd. In een vergelijkende studie over een groot aantal soorten is nagegaan of de functionele eisen van aquatisch foerageren en terrestrisch foerageren heeft geresulteerd in gelijksoortige morfologieën binnen dezelfde trofische groep.

De bestudeerde eendachtigen zijn op basis van literatuurgegevens onderverdeeld in twee groepen: degene die vooral op het land grazen, en degene die in het water foerageren. Het type voedsel in deze laatste groep is echter gevarieerd, vooral wat betreft grootte. Het merendeel van de 19 onderzochte soorten aquatisch foeragerende eendachtigen heeft de typische kenmerken behorende bij het 'onder-tong' transportmechanisme: een glad monddak, duidelijke verdikkingen van het voorste gedeelte van de tong en groeves langs weerszijden van het achterste gedeelte van de tong (het zgn. tongkussen). Bijna alle 20 soorten van de terrestrisch foeragerende groep hebben echter uitsteeksels op het monddak en de groeves in het achterste deel van de tong ontbreken.
Andere structuren in de mondholte vertonen ook een relatie met de foerageermethode. In het algemeen hebben de dorsale rij lamellen (dit zijn kamvormige uitsteeksels op de randen van de kaken) van de onderkaak een scherpe bovenrand in de terrestrische foerageerders (beschadigen vegetatie) en een gladde rand in aquatische vogels. Ook hebben aquatische foeragerende eendachtigen een 1.6 maal diepere bovensnavel (volume toename) en is de relatieve grootte van het voorste gedeelte van de tong van aquatisch foeragerende anseriformen groter (zuigerwerking tong).

In beide groepen komen soorten voor die enigszins afwijken van de hierboven beschreven algemene orale morfologie. In de aquatisch foeragerende groep missen veel van de waterplantenetende soorten de groeven aan weerszijden van het tongkussen, maar

hebben wel scherpe lamellen op de onderkaak en uitsteeksels op het monddak. Deze eigenschappen zijn typisch voor grazers met een 'over-tong' transportmechanisme.

Kleine uitsteeksels op het monddak worden ook in een aantal andere aquatisch foeragerende eendachtigen gevonden die wel groeven in het tongkussen hebben. Het voedsel van deze vogels bestaat voor een deel uit grote voorwerpen die niet door de wel aanwezige tonggroeven kunnen worden getransporteerd. Waarschijnlijk maken deze uitsteeksels het mogelijk om het efficiënte 'over-tong' transportmechanisme als dat van de gedomesticeerde gans te gebruiken in plaats van het inefficiëntere 'opgooien-en-vangen', maar of dit werkelijk gebeurt is niet bekend. Combinaties van morfologische kenmerken die behoren bij de verschillende transportmechanismen zijn bijvoorbeeld te vinden bij de smient. Voor deze soort is aangetoond dat ook daadwerkelijk gebruik wordt gemaakt van beide transportmechanismen: 'onder-tong' tijdens zeven en 'over-tong' tijdens grazen (Van der Leeuw et al., 2003).

Prestatie van grazen en zeven

De morfologische kenmerken van de snavel en tong die behoren bij ofwel het 'over-tong' – ofwel het 'onder-tong' transportmechanisme zijn functioneel niet verenigbaar. In grazende eendachtigen zal de aanwezigheid van stekels op het monddak, nodig voor het 'over-tong' transport van gras of grotere voedselobjecten, ertoe leiden dat de tong de mondholte niet goed kan afsluiten en de zuigkracht aantasten die nodig is voor efficiënt zeven van kleine voedseldeeltjes. Ook zal de afwezigheid van groeven aan weerszijden van de tong het gebruik van het 'onder-tong' mechanisme verhinderen. Aan de andere kant missen de meeste aquatisch foeragerende soorten de grote stekels op het monddak, en zullen dus niet via het 'over-tong' mechanisme voedsel over de tong kunnen transporteren. Verwacht mag worden dat deze tegenstrijdigheid limiterend is voor het vermogen van de vogels om beide intraorale transportmechanismen even efficiënt toe te passen. In de volgende twee hoofdstukken zijn de prestaties van grazen en zeven gemeten om te controleren of de verwachte uitruil ('trade-off') daadwerkelijk aanwezig is.

In hoofdstuk 5 is de graasprestatie gemeten van een aantal soorten terrestrische grazers (dwerggans (*Anser erythropus*), brandgans (*Branta leucopsis*) en Canadese gans (*Branta canadensis*)) en van 1 aquatische grazer (knobbelzwaan (*Cygnus olor*)). Individuele vogels begraasden gedurende korte tijd een kleine plag gras en de hoeveelheid opgenomen gras werd zeer nauwkeurig bepaald. Een prestatiemaat werd vervolgens berekend door per hap de hoeveelheid losgetrokken gras, vermindert met de hoeveelheid die verloren werd tijdens transport door de snavel, te vermenigvuldigen met de hapfrequentie.

Bij alle vier de onderzochte soorten neemt de prestatie proportioneel toe als de hapgrootte toeneemt. Echter in de grotere eendachtigen is deze toename kleiner dan in de kleine soorten. Zwaardere eendachtigen met een grotere snavel nemen grotere happen, maar hebben ook een relatief groter verlies en een lagere hapfrequentie. De relatie tussen hapgrootte en hapfrequentie leidt tot een snelle toename van de prestatie bij kleine soorten die kleine happen nemen, terwijl bij grote happen de afname in

hapfrequentie samen met de toename van verlies compenseert voor het effect van hapgrootte, waardoor de prestatie niet verder meer toeneemt of zelfs iets afneemt.

Een vergelijking van de graasprestaties tussen soorten is gemaakt op basis van de lichaamsgrootte-afhankelijke metabolische behoefte. Deze prestatie is gelijk voor twee van de drie soorten ganzen en de knobbelzwaan en eveneens gelijk aan graasprestaties van ganzensoorten vermeld in de literatuur (Durant et al., 2003; Van der Leeuw et al., 2003). Hoewel geen kinematische analyses zijn uitgevoerd, lijkt het waarschijnlijk dat alle vier de soorten het 'over-tong' transportmechanisme toepassen. Er zijn geen grote kopbewegingen zoals in het 'catch-and-throw' mechanisme waargenomen en de morfologische structuren benodigd voor 'over-tong' transport zijn aanwezig.
De brandgans heeft een iets lagere prestatie dan de andere ganzen (in deze en in andere studies (Cope et al., 2005; Durant et al., 2003)). Dit wordt mogelijk veroorzaakt doordat deze soort een andere foerageerstrategie, gericht op de lange termijn, toepast. In plaats van het minimaliseren van benodigde foerageertijd maximaliseren deze vogels hun energieopname.

Een vergelijking met eerdere studies aan eenden laat zien dat de wilde eend, en in mindere mate de smient, een relatief lagere prestatie leveren dan de ganzen en zwaan. Deze lage prestatie wordt bij de smient veroorzaakt door de combinatie van kleine happen en een lage hapfrequentie en in de wilde eend door de lage hapfrequentie en de grote hoeveelheid verlies. Deze relatief lagere prestaties zijn toe te schrijven aan de structuren van de mondholte. Smienten hebben alleen uitsteeksels op een richel in het midden van het monddak en het oppervlak direct daarnaast. Deze structuren maken het wel mogelijk dat de smient het 'over-tong' transportmechanisme kan toepassen, maar de beperkte grootte en verspreiding van de stekels beperken de hapgrootte tot 1 grasspriet. Daarentegen heeft de wilde eend helemaal geen uitsteeksels op het monddak en gebruikt het relatief langzame 'catch-and-throw' mechanisme om afgehapt gras te transporteren, wat zowel het grote verlies en de lage hapfrequentie verklaart.

De zeefprestatie is bepaald bij twee soorten ganzen (de dwerggans en de brandgans) en bij de knobbelzwaan (hoofdstuk 6). Zowel de hoeveelheid voedsel die wordt doorgeslikt ten opzichte van de hoeveelheid die de snavel binnenkomt als het volume aan water met voedseldeeltjes dat de snavel binnenkomt, zijn gemeten. Ondanks een andere techniek van 'filteren' dan bij *Anas*-soorten is de efficiëntie van het filteren van de opgenomen voedseldeeltjes bij de ganzen en knobbelzwaan hoog: meer dan 95% van de binnengekomen zaadjes wordt doorgeslikt. Dit is gelijk aan wat aquatisch foeragerende eenden presteren (Kooloos et al., 1989). Kennelijk is het opvangen van zaden achter de uitsteeksels van het monddak even effectief als het tegenhouden hiervan met behulp van lamellen op de snavelranden. Echter, de soorten die een 'over-tong' transport gebruiken kunnen waarschijnlijk niet selectief verschillende zaadgroottes opnemen, in tegenstelling tot eenden.

Het totale volume aan water met zaadjes dat per bewegingscyclus van de snavel naar binnen komt (ten opzichte van lichaamsgewicht), is veel groter in de aquatisch foeragerende soorten dan in de ganzen en zwaan. In combinatie met de iets hogere

bewegingsfrequenties resulteert dit in een relatief betere totale prestatie van de aquatisch foeragerende eenden.
Hoewel het verschil in volume deels verklaard kan worden uit verschillen in relatieve snavelgrootte, lijkt het transportmechanisme de belangrijkste oorzaak te zijn voor de verschillen in prestatie.

Het 'over-tong' transportmechanisme dat door ganzen wordt toegepast voor zeven werkt op dezelfde manier als voor het transport van gras en heeft een andere coördinatie van tong- en snavelbewegingen dan bij zevende soorten. Tijdens het openen van de snavel en 'aanzuigen' van water staat de tong niet tegen het monddak, zoals bij echte zevers, maar maakt een soort schepbeweging. Door vervolgens de tong tegen het monddak te duwen en naar voren te bewegen worden voedseldeeltjes door de stekels op het monddak vastgehouden en over de tong naar achteren geschoven. Bij zevende soorten wordt de tong juist omlaag gedrukt tijdens het naar voren bewegen. De snavel en tong bewegingen van het 'over-tong' transport blijken minder efficiënt water aan te zuigen dan die van het 'onder-tong' transport van zevers.
Daarnaast maakt het 'over-tong' transport een continu doorvoerproces langs de tong zoals bij zevers onmogelijk. Het verzamelen van voedsel op de tong maakt twee aparte voedselopname-fases noodzakelijk: één voor het verzamelen van voedseldeeltjes, en één voor het inslikken ervan (Van der Leeuw et al., 2003). Het opsplitsen van zeven in twee fases vertraagt de snelheid van voedselinname aanzienlijk ten opzichte van het 'onder-tong' transport, waardoor de zeefprestatie van knobbelzwanen en ganzen vergeleken met eenden slechter is.

Conclusies

De morfologische data en kinematische analyses van voedselopnamegedrag van verschillende eendachtigen laten zien dat de mechanica van de opname van kleine voedseldeeltjes uit water duidelijk verschilt van die van het plukken van gras of waterplanten. Eendachtigen die voornamelijk grazen (zowel op land als in het water) en eendachtigen die voornamelijk aquatisch foerageren (anders dan het grazen van waterplanten) vertonen consistente verschillen tussen morfologische kenmerken van het voedselopnameapparaat die samenhangen met een zo efficiënt mogelijke voedselopname. De morfologische adaptaties en intraorale transportmechanismen die een maximale prestatie voor zeven of grazen mogelijk maken blijken een maximale inname van beide typen voedsel onmogelijk te maken. Directe metingen van prestaties voor zeven en grazen laten dan ook een uitruil ('trade-off') zien in de efficiëntie waarmee beide voedsel types worden opgenomen. De graasprestatie van eendachtigen die veel van hun voedsel verzamelen door zeven is lager dan de graasprestatie van gewoonlijk grazende eendachtigen, en omgekeerd is de zeefprestatie van eendachtigen die vooral grazen lager dan voor soorten die vooral zeven.

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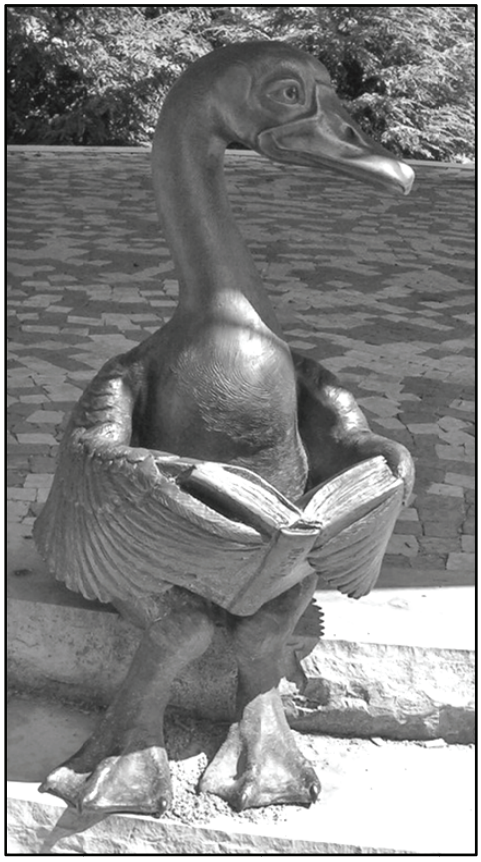

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Curriculum vitae

Carolina Deborah Kurk werd geboren op 31 januari 1973 in Gouda. In 1991 behaalde zij het diploma Atheneum-B aan het Casimir Lyceum te Amstelveen. Hetzelfde jaar begon zij met de studie Biologie aan de Rijksuniversiteit Leiden. Tijdens de doctorale fase volgde ze de richting Organismale Zoölogie, aangevuld met de theoretische vakken van de richting Medische Biologie. Tevens heeft ze drie stages gelopen, alledrie gericht op vogels.
Tijdens de eerste en tevens hoofdstage bij het Nederlands Instituut voor Oecologisch Onderzoek (NIOO) in Heteren werd de consistentie en erfelijkheid van individuele verschillen in exploratief en agressief gedrag van de koolmees onderzocht onder begeleiding van dr. Piet Drent (NIOO) en prof. Dr. Paul Brakefield (Evolutionaire Biologie, EEW, Leiden). De tweede stage betrof de integratie van grazen in de andere voedselopname-systemen van de smient onder begeleiding van drs. Angelique van der Leeuw en prof. dr. Gart Zweers (Ethologische Morfologie, EEW, Leiden). Een studie-bezoek aan het Nederlands Instituut voor Onderzoek der Zee op Texel resulteerde in een tweede nevenstage, over de wijze van prooidetectie van de kanoetstrandloper onder begeleiding van dr. Theunis Piersma (NIOZ) en dr. Herman Berkhoudt (Ethologische Morfologie, EEW, Leiden).
Na het afronden van de studie Biologie in 1996 is Karin opgeleid tot Microsoft Certified System Engineer en heeft vervolgens drie jaar in de automatisering gewerkt.
Begin 2000 keerde ze terug naar de biologie en verrichtte onderzoek aan de Universiteit van Wageningen (Natuurbeheer in de tropen en ecologie van vertebraten) onder begeleiding van dr. Sip van Wieren en prof. dr. Herbert Prins. Bij drie ondersoorten van de Canadese gans werd het effect van lichaamsgrootte op de eigenschappen van voedselopname en competitie bestudeerd.
In 2003 begon ze als AIO bij de vakgroep Evolutionaire Morfologie in Leiden. De resultaten van dit onderzoek staan beschreven in dit proefschrift.
Sinds januari 2007 werkt Karin bij TTP (personele dienstverlening voor de ICT, Informatiemanagement en Inkoop) en heeft met goed gevolg de opleiding Leergang Aankomend Record Manager afgerond. Intussen is ze gedetacheerd geweest bij de gemeente Dordrecht als functioneel beheerder van een post- en archiefapplicatie. Momenteel is Karin gedetacheerd bij de Aloysius Stichting Onderwijs Jeugdzorg en werkt als projectleider aan de implementatie van een post-en archiefsysteem.