The bill of evolution : trophic adaptations in anseriform birds

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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.

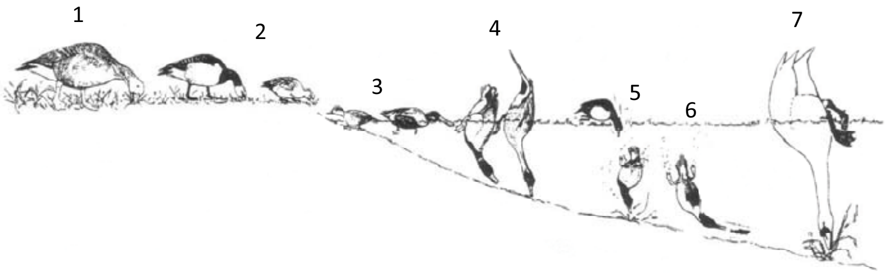

Figure 1.1. Feeding methods of anseriform birds. 1. grubbing (greylag goose), 2. grazing (barnacle goose and Eurasian wigeon), 3. dabbling (Eurasian teal and shoveler), 4, upending (mallard and pintail), 5. diving (tufted duck and common pochard), 6. pursuit diving (goosander), 7. upending (mute swan).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