The digestion of fibre in herbivorous Anatidae - a review

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Numerous studies on the ability of herbivorous Anatidae to digest fibre from a variety of food types (foliage, seeds, tubers) have yielded variable results. Herbivorous ducks and geese have the capacity to digest some components of fibre (between 0% and 85%, depending on the study and the fibre components analysed), in particular hemicellulose. Hemicellulose may be partially digested by acid hydrolysis early in the digestive tract, and the small particles of the fluid digesta obtained may undergo a limited fermentation in the caecae (with the aid of symbiotic microflora). Two sources of variation in the digestibility of fibre identified by the studies are discussed: experimental factors (in particular the differences in the method used) and biological factors. In the latter some of the variation in fibre digestibility reported by the studies is probably due to diet-based factors: differences in structural and chemical properties of the plant species consumed. But other factors, unrelated to diet, may be taken into account. Consumer-based factors, such as seasonal variation (in relation to the retention time of food in the gut) and differences in body mass or caecal length of the bird species, must also be considered. The use of fibre as a marker in studies of food digestibility in herbivorous Anatidae is discussed.

Key Words: herbivorous Anatidae, digestibility, fibre, fermentation, caecae

One of the main components of plant tissues is fibre, which constitutes the cell walls. As digestion of fibre plays an important role in the energy balance of herbivorous birds, it has received particular attention (Gasaway 1976; Herd & Dawson 1984; Buchsbaum *et al.* 1986; Sedinger *et al.* 1995; Bairlein 1999). Measures of fibre digestion can have important implications for understanding foraging behaviour and habitat use of herbivores (Boudewijn 1984) because (a) fibre is a non-negligible source of energy since it represents half of the biomass of the green parts of plants (Van Soest 1982; Sedinger & Raveling 1984), and (b) if cell walls can be digested, the cell content is more accessible and digestion more complete (Rybicki & Lubanska 1959).

Vertebrates are not capable of secreting cellulase, the enzyme which digests cellulose, but many herbivores, including some birds, rely on symbiotic micro-organisms in their gut. This necessitates a suitable site for the retention of plant material and fermentation of fibre (ie the breakdown of cellulose into volatile fatty acids; see below). Birds possess a lateral pair of sacculate tubes called caecae between the small and large intestines, where cellulolytic fermentation may occur (Mattocks 1971). The ability to digest fibre varies among groups and taxa (Bairlein 1999). It is significant in some bird species which have enlarged caecae as fermentation chambers, such as species in the family Tetraonidae (grouse and ptarmigan), the ratites (the Australian Emu *Dromaius novaehollandiae*), and the Hoatzin *Opisthocomus hoazin* (Moss 1977; Herd & Dawson 1984). The possession of an effective, large, heavy fermentation chamber, however, impacts on flight energy costs, which increase directly with body mass.

Anatidae often make long migratory flights. As their caecae contain a prolific microbial fauna (Mattocks 1971; Vulink 1980; Prop & Vulink 1992), these organs have long been assumed to be centres of cellulolytic fermentation, and functionally analogue to a rumen (Lorenz 1952; Miller 1976). However, microbial fermentation is a lengthy process (ie it takes several hours: about 12 hours in cows, sheep and goats, for example), and the rapid rate of passage of food in the gut of herbivorous Anatidae [two hours in the Greylag Goose *Anser anser* on grass (Mattocks 1971); 70-75 minutes in Wigeon *Anas penelope* on grass (Mayhew & Houston 1993); 3.2 hours in Lesser Snow Goose *Chen caerulescens caerulescens* on Alfalfa *Medicago sativa* and 7.5 hours on corn (Post *et al.* 1998)] is likely to limit the opportunities for fibre breakdown.

After a brief introduction on the nature of dietary fibre, this paper reviews what is known about the ability of herbivorous ducks and geese to digest the fibre of a variety of food types (foliage, seeds, tubers), and the underlying digestive mechanisms. The review will then discuss the potential sources of variation in fibre digestibility in herbivorous Anatidae and the potential reasons for these variations, as reported in the studies. The use of fibre as an internal marker as a means to calculate food digestibility will also be discussed.

The fibre content of plant material

Fibre is made up of three main components: cellulose, hemicellulose and lignin (Van Soest 1982). Cellulose is a carbohydrate composed mainly of glucose units linked together. Hemicellulose is made up of diverse groups of polysaccharides, and has a different and more complex configuration than cellulose. Lignin is a polyphenol.

Many studies have explored the chemical composition of food consumed by grazing Anatidae, ie mainly the exposed parts of grasses and forbs (Ebbinge *et al.* 1975; Sedinger 1989; Amat *et al.* 1991; Prop & Vulink 1992), but also seeds, tubers and rhizomes (Bélanger *et al.* 1990; Mathers & Montgomery 1997; van Eerden & Munsterman 1998). For instance, the fibre content of temperate grasses varies according to species, maturity and season (Van Soest 1982) and, in general, ranges from 50% to 60% of dry matter. Cellulose and hemicellulose are the main components of cell walls (45-50% and 40-45%, respectively) (Van Soest 1982). Lignin is less abundant (5-10%).

Measurements of the fibre content of plants are made using the detergent fibre method (Gauthier *et al.* 1991; Van Soest 1982). This method is based on the division of food components into soluble metabolites and cell wall constituents (mainly hemicellulose, cellulose and lignin). The NDF fraction (neutral detergent fibre) contains cellulose, hemicellulose and lignin whereas the ADF residue (acid detergent fibre) contains only cellulose and lignin. In general, the NDF and ADF contents of plant material follow the relationship: NDF=[1.5-2.5]xADF (van Eerden & Munsterman 1998). Lignin (ADL: acid detergent lignin) is determined as the ash-free residue left after treating ADF with sulphuric acid. The distinction between NDF and ADF is often made, since ADF is the fraction of the cell wall which is the least digestible (ie in NDF, hemicellulose is the fraction which is quite well digested by Anatidae, see below). Moreover, this distinction is useful in the partitioning of the different cell wall components; the difference between NDF and ADF values is often used to evaluate hemicellulose content, and cellulose can be determined by removing lignin (and ash) from ADF (Sedinger *et al.* 1995).

The digestion of fibre in herbivorous Anatidae

Fibre digestibility is defined as the fraction of dietary fibre that is digested and converted into usable energy or nutrients (several other terms are frequently used in the literature: assimilation efficiency, utilisation efficiency, digestion efficiency, metabolisability coefficient, etc. but all are used as synonyms). To estimate the digestibility of fibre, two principal methods are used: 1) the input/output method and 2) the marker method (**Tables 1 & 2**). The input/output method is a direct one and involves the use of captive birds. The birds' food intake and excreta are directly measured over a period of several days. The measure of the fibre composition of the food and droppings gives the quantity of fibre eaten (intake) and excreted (output) by the birds. Fibre digestibility (%) is then calculated as: (intake-output)/(intake)*100 (Sedinger *et al.* 1989, 1995).

The other method uses a marker, and is an indirect method. A marker is a substance that remains unchanged during the passage through the digestive tract of an animal. A marker may be 'internal' (produced from the plant) or 'external' (administered to the animal) (Mayes *et al.* 1995). The marker method is based on assessment of the percent marker in the food and the droppings. Percentage fibre digestibility is then estimated as:

$$1-[(\%\text{marker}_{\text{food}}/\%\text{marker}_{\text{droppings}})*(\%\ \text{fibre}_{\text{food}}/\%\ \text{fibre}_{\text{droppings}})*100]$$

This method (Buchsbaum *et al.* 1986) has the advantage of being applicable either with captive or with free-ranging birds (ie in a field situation). For Kotb & Luckey (1972), "inertness and lack of absorption or metabolism occurring in the digestive tract" were the most important criteria for a component to be a reliable marker. The choice of a marker is important because a marker that is partly digested will give an underestimation of digestibility.

Eighteen papers were found that reported studies on the digestion of fibre in herbivorous Anatidae, with a large number of species covered (four species of ducks, eight species of geese and three species of swans; see **Tables 1 & 2**). In the early twentieth century, geese were considered to make little use of dietary fibre. The first work on the digestion of fibre in geese was carried out with domestic geese derived from the genus *Anser*, and showed that geese digested less than 1% of fibre (Weiser & Zeitscheck 1902). Subsequently, fibre digestibilities ranging from negative values for rice to positive values for maize (33.5%) were obtained in studies with cereals, legumes or roots and protein concentrates (Nehring & Nerge 1966). Later, Marriott & Forbes (1970) showed that Cape Barren Geese *Cereopsis novaehollandiae* fed with lucerne pellets (Alfalfa, with less than 35% of fibre) did not digest significant amounts of cellulose and lignin (0.8%). Recent investigations

Table 1: Review of foliage fibre digestion in herbivorous Anatidae. Values are given as % of DM (±S.D., or S.E.)

Species	Mass (kg)	Food	Method used	Digestibility (%)					Period	References
				hemi-cellulose	cellulose	lignin	NDF	ADF		
Wigeon *Anas penelope*	0.6	foliage	marker: ADF	17.0-33.0	-	-	-	-	winter-autumn-spring	Bruinzeel *et al.* 1998
Wigeon *Anas penelope*	0.6	grass	input/output	-	-	-	30.8±4.1	5.0±3.0	autumn	This study
Australian Wood Duck *Chenonetta jubata*	0.9	grass, forbs	marker: manganese	74.0	11.0	4.0	40.0	9.0	no indication	Dawson *et al.* 1989
Brent Goose *Branta bernicla*	1.1	Alfalfa pellets	input/output	-	1.3±1.7	negative	15.5±1.6	negative(*)	winter	Sedinger *et al.* 1989
Brent Goose *Branta bernicla*	1.6	*Spartina patens*	marker: lignin	13.0±10.7(*)	30.8±8.9(*)	-	18.0±10.3(*)	20.8±14.5(*)	May	Buchsbaum *et al.* 1986
Brent Goose *Branta bernicla*	1.6	*Spartina alterniflora*	marker: lignin	38.7±16.8(*)	32.9±13.4(*)	-	29.0±5.6(*)	22.3±6.5(*)	May	Buchsbaum *et al.* 1986
Barnacle Goose *Branta leucopsis*	no indication	graminoids	marker: lignin	20.4±5.9 47.3±11.3(*)	-	-	-	0.3±3.2 26.2±7.7(*)	winter-summer	Prop & Vulink 1992
Barnacle Goose *Branta leucopsis*	1.8	foliage	marker: ADF	50.0±56.0	-	-	-	-	winter-autumn-spring	Bruinzeel *et al.* 1998
Magpie Goose *Anseranas semipalmata*	1.8-2.0	grass	input/output method	32.0±6.0	-	-	27.0±7.0	19.0±8.0	no indication	Dawson *et al.* 2000
White-fronted Goose *Anser albifrons*	2.0	foliage	marker: ADF	32.0±55.0	-	-	-	-	winter-autumn-spring	Bruinzeel *et al.* 1998
Lesser Snow Goose *Chen c. caerulescens*	>2.0	Alfalfa pellets	input/output method	52.6±2.7	44.6±6.0	7.8±6.4	30.9±2.8	16.3±2.8	autumn	Sedinger *et al.* 1995

Table 1: Continued

Species	Mass	Food	Method used	Digestibility (%)					Period	References
	(kg)			hemi-cellulose	cellulose	lignin	NDF	ADF		
Greylag Goose *Anser anser*	2.6	*Phragmites australis*	marker: ADF	21.0-34.0(*)	no digestion'	-	-	-	June 1998a	van Eerden *et al.*
Greylag Goose *Anser anser*	3.3	foliage	marker: ADF	12.0-67.0	-	-	-	-	winter-autumn-spring	Bruinzeel *et al.* 1998
Greylag Goose *Anser anser*	3.4	grass	input/output	-	-	-	28.4±10.2	10.7±9.3	autumn	This study
Cape Barren Goose *Cereopsis novaehollandiae*	3.7	chaffed lucerne	input/output	-	-	-	-	0.8	no indication	Marriott & Forbes 1970
Canada Goose *Branta canadensis*	4.0	*Spartina alterniflora*	marker: lignin	22.6±6.7(*)	29.7±2.4(*)	-	22.0±3.8(*)	21.3±11.7(*)	August	Buchsbaum *et al.* 1986
Canada Goose *Branta canadensis*	4.0	*Juncus geradii*	marker: lignin	25.5±6.3(*)	18.1±6.3(*)	-	17.9±2.5(*)	12.4±10.7(*)	April	Buchsbaum *et al.* 1986
Domestic Goose *Anser* sp.	5.3	pelleted grass	no indication	-	-	-	7.2	-	no indication	Koram & Greenhalgh 1982
Bewick's Swan *Cygnus c. bewickii*	6.0	foliage	marker: ADF	30.0-55.0	-	-	-	-	winter-autumn-spring	Bruinzeel *et al.* 1998
Bewick's Swan *Cygnus c. bewickii*	5.7-6.4	grass	marker: ADF	55.9	-	-	-	-	autumn	van Eerden *et al.* 1998b
Whooper Swan *Cygnus cygnus*	8.7	foliage	marker: ADF	45.0-73.0	-	-	-	-	winter-autumn-spring	Bruinzeel *et al.* 1998
Mute Swan *Cygnus olor*	10.7	foliage	marker: ADF	30.0	-	-	-	-	winter-autumn-spring	Bruinzeel *et al.* 1998

Table 2: Review of seed and tuber fibre digestion in herbivorous Anatidae. Values are given as % of DM (±S.D., or S.E.).

Species	Mass (kg)	Food	Method used	Digestibility (%)					Period	References
				hemi-cellulose	cellulose	lignin	NDF	ADF		
Young domestic ducks *Anas* sp.	no indication	maize, barley wheat, rye	input/output	27.8±12.4	-	-	18.1±8.6	2.8±10.0	no indication	Jamroz *et al.* 1996
Teal *Anas crecca*	0.3	seeds, tubers	marker: ADF	45.0	-	-	-	-	winter-autumn-spring	Bruinzeel *et al.* 1998
Wigeon *Anas penelope*	0.6	seeds, tubers	marker: ADF	35.0	-	-	-	-	winter-autumn-spring	Bruinzeel *et al.* 1998
Barnacle Goose *Branta leucopsis*	1.8	seeds, tubers	marker: ADF	0-29.0	-	-	-	-	winter-autumn-spring	Bruinzeel *et al.* 1998
Magpie Goose *Anseranas semipalmata*	1.8-2.0	rice grain	input/output	21.0±3.0	-	-	19.0±3.0	18.0±4.0	no indication	Dawson *et al.* 2000
Greylag Goose *Anser anser*	3.3	seeds, tubers	marker: ADF	3.0-71.0	-	-	-	-	winter-autumn-spring	Bruinzeel *et al.* 1998
Greylag Goose *Anser anser*	no indication	*Scirpus littoralis*	marker: lignin	56.8	17.1	-	-	-	autumn-winter	Amat *et al.* 1991
Greylag Goose *Anser anser*	no indication	*Scirpus maritimus*	marker: lignin	65.7	31.0	-	-	-	autumn-winter	Amat *et al.* 1991
Domestic Goose *Anser* sp.	no indication	maize, barley, wheat, rye	input/output	34.1±12.9	-	-	23.2±8.6	5.9±9.4	no indication	Jamroz *et al.* 1996
Domestic Goose *Anser* sp.	?	carrots	?	-	-	-	16.1	-	?	Pres *et al.* 1957
Domestic Goose *Anser* sp.	?	oats	?	-	-	-	14.1	-	?	Brüggemann 1931
Domestic Goose *Anser* sp.	?	maize	?	-	-	-	22.6	-	?	Brüggemann 1931
Bewick's Swan *Cygnus c. bewickii*	6.0	seeds, tubers	marker: ADF	47.0-77.0	-	-	-	-	winter-autumn-spring	Bruinzeel *et al.* 1998
Bewick's Swan *Cygnus c. bewickii*	5.7-6.4	sago tubers	marker: ADF	85.6	-	-	-	-	autumn	van Eerden *et al.* 1998a
Bewick's Swan *Cygnus c. bewickii*	5.7-6.4	sugarbeet	marker: ADF	6.5	-	-	-	-	autumn	van Eerden *et al.* 1998b
Whooper Swan *Cygnus cygnus*	8.7	seeds, tubers	marker: ADF	83.0	-	-	-	-	winter-autumn-spring	Bruinzeel *et al.* 1998

? means that the results of the study were reported elsewhere, with no further information available.

confirm, however, that Anatidae can in fact digest fibre to variable extents, and the presence of bacteria in the caecae and the colon was demonstrated in domestic geese (Vulink 1980).

The results of the studies on the digestion of fibre from foliage, seeds and tubers are given in **Tables 1 and 2**. Fibre digestibility varies greatly (0-85%) according to the study and the fibre components considered. The cellulose digestibility (44%) found by Sedinger *et al.* (1995) in Alfalfa pellets is one of the highest values for birds reported in the literature (Hupp *et al.* 1996). Fibre can be an important source of energy and Buchsbaum *et al.* (1986) found that the digestion of cell walls provided up to 31% of the energy geese extract from food plants. This is consistent with a study performed on Australian Wood Duck *Chenonetta jubata* (c. 870g) foraging on grasses and forbs, which is among the few studies on herbivorous ducks (Dawson *et al.* 1989). The authors showed that fibre digestion contributed 30% of the assimilated energy, with most coming from hemicellulose (74% of digestibility). The comparison of fibre digestibility in herbage and seeds by Bairlein (1999) showed that in herbivorous birds the fibre content of seeds is better digested than that of herbage (55% vs. 19%).

The mechanics of fibre digestion in herbivorous Anatidae

Herbivorous ducks and geese thus have some capacity to digest components of fibre, in particular hemicellulose. However, the mechanics and location of fibre degradation are not well known. Fermentation is the process by which the structural polysaccharides (cellulose) are converted by symbiotic microflora into metabolisable short chain volatile fatty acids (VFAs). Ducks and geese have few gross morphological adaptations for fibre fermentation within the gut, and the caecae are not well developed compared to those of grouse of similar size (Owen 1980; Barnes & Thomas 1987; Dawson *et al.* 1989, 2000; Sedinger 1997).

One of the explanations for the significant level of digestion of hemicellulose in Anatidae is that some fibre components may be digested by non-microbial processes prior to fermentation (Herd & Dawson 1984). Dawson *et al.* (1989) found high levels of hemicellulose digestion in the proximal small intestine of the Australian Wood Duck. Dawson *et al.* (1989, 2000) suggested, therefore, that hemicellulose may be partially digested by acid hydrolysis within the proventriculus (glandular gizzard), the gizzard (mechanical gizzard) and the proximate part of the small intestine (duodenum). This process would allow fibre to be placed in solution, and then transported to the caecae for rapid fermentation

(<12 hours, Clemens *et al.* 2000). Fermentation also occurs in the rectum and cloaca (Dawson *et al.* 2000). According to these authors, since it is a complex of polysaccharides, it is possible that hemicellulose is digested by both mechanisms (ie acid hydrolysis and fermentation).

The particle size of the digesta is clearly an important variable in fermentation (Bjorndal *et al.* 1990). Indeed, the caecal orifice (ie a kind of ileo-caecal sphincter) may separate the digesta, leaving the small intestine with a fraction containing mainly fluid, dissolved substances and small particles (resulting from the hydrolysis) (Clemens *et al.* 1975; Björnhag & Sperber 1977; Dawson *et al.* 1989, 2000). This mechanism for selective retention of fluid digesta in the caecae is well known in other species of herbivorous birds (ptarmigan, grouse, turkey) and mammals (rabbit, hare, lemming). It slows the flow of water soluble substances and fine particles (the more digestible parts of the food) in order to effect a satisfactory microbial fermentation. The larger (less digestible) particles pass rapidly into the large intestine. Herbivorous ducks and geese probably show this mechanism of selective retention (see study of McWilliams (1999) on geese) but further studies are necessary to explore this.

The argument for the existence of a process of bacterial fermentation (in the caecae, rectum and cloaca) in herbivorous Anatidae, even if limited, is supported by:

1) bacteria present in the caecae that are capable of hemicellulose and cellulose fermentation (Vulink 1980; Prop & Vulink 1992); see also studies on digestive enzyme activity on geese in Nitsan *et al.* (1973) and McWilliams (1999);

2) the presence of volatile fatty acids (VFAs) produced in the gut by geese during digestion, VFAs being the principal end-products of fermentative digestion (the amounts of VFAs vary among bird species, Clemens *et al.* 1975; Dawson *et al.* 1989; Jamroz *et al.* 1996). VFAs are then absorbed in the caecae;

3) the homogeneous and viscous dark-green paste found among droppings of ducks and geese (Dawson *et al.* 1989; Mattocks 1971; pers. obs.), which has a pronounced smell and a rich microflora similar to that in the caecae (indicating its caecal origin; Mattocks 1971).

Such a mechanism for fibre digestion is probably associated with retrograde movements of the fluid digesta between the small intestine and the gizzard and proventriculus and/or from the cloaca to the colon, caecum and distal part of the small intestin. This was demonstrated by Clemens *et al.* (1975) in domestic geese (see also Dawson *et al.* 2000), but also in turkeys (Duke *et al.* 1989). These movements probably enhance the digestion of fibre by increasing its retention time in the gut, but the existence of such a mechanism in herbivorous birds needs further investigation.

Variation in the extent of fibre digestion

Studies on fibre digestion in herbivorous Anatidae show that the extent of digestion varies strongly (0-85%). There are both experimental and biological reasons for this.

From an experimental point of view, it may be problematic to make comparisons between these studies. First, the method used to assess digestion of fibre differs from one study to another: data are generally derived from the input/output method or by using a marker (see **Tables 1 & 2**). Second, studies using markers were carried out with both captive and wild birds, and the markers vary (ADF, lignin or manganese).

The variations in fibre digestibility are also likely to be caused by biological factors. First, the plant species concerned (Bruinzeel *et al.* 1998), the part of the plant, structure of its tissues and its degree of maturity are likely to play a role in how its fibre is digested by birds (Buchsbaum *et al.* 1986). This can be attributed to variations in the fibre content of the various foods and differences in the structural and chemical composition of cell walls (Mangold 1934). Second, there are also consumer-based factors that are likely to play a role in the variations in the ability of herbivorous birds to digest fibre. The digestive efficiency of a given diet or quantity is a positive function of retention time (Prop & Vulink 1992). However, increasing retention time has costs for a bird: it increases the bird's mass and thus its flight costs; it also reduces the mass of food that can be ingested, and hence energy that can be assimilated. Moreover, birds should maintain the smallest functional gut size because smaller organs reduce metabolic energy expenditure (Moss 1974) and because theoretical studies predict that extra mass is associated with higher predation risk (Lima 1986). This is certainly why the retention time and the length of the digestive tract are both highly plastic in birds (Miller 1975; Burton *et al.* 1979; Kehoe *et al.* 1988). For instance, gut size varies with the volume/quality of the food consumed (Ankney 1977; Karasov 1990). This suggests that there is a complex interplay (based on trade-offs) between the nutritional requirements of herbivorous birds, their flight costs, food quantity/quality and gut size or retention time that determines the optimal digestion strategy and leads to adjustments in their digestive physiology. The seasonal changes in assimilation efficiency reported in herbivorous Anatidae illustrate this concept well. They are probably due to a change in food use (Bédard & Gauthier 1989; Boudewijn 1984) or variations in gut morphology throughout the annual cycle. For example, in female Lesser Snow Geese the intestines decrease in length during laying and incubation (Ankney 1977). It is then likely that geese compensate for this reduction in gut size by an increase in food retention time, in order to improve the digestibility of fibre. Prop &

Vulink (1992) demonstrated that Barnacle Geese *Branta leucopsis* did not digest ADF in winter but were able to retain food (mainly grasses and bryophytes) in the digestive tract for longer (ie up to four times longer) in summer, when food is rare and of poor quality, in order to improve the digestibility of ADF (up to 26%). Evidence for the causal link between ADF digestibility and retention time was also obtained in studies carried out in spring in captive Brent Geese *Branta bernicla* (Prins *et al*. 1981) and Barnacle Geese (Van Marken Lichtenbelt 1981). Even if further research is needed to determine the exact relationship between changes in food intake and quality, gut size, food retention time and fibre digestibility throughout the year, it seems certain that the flexibility of the digestive system of herbivorous Anatidae can be regarded as an adaptation to differences in energy requirements and environmental conditions.

At an interspecific level, differences in fibre digestibility are likely to occur because in vertebrate herbivores metabolic requirements, gut volume and the ability to process and digest food are strongly correlated with body mass (Demment & Van Soest 1985). Whether body size influences the processes by which the food is digested in herbivorous birds is, however, not clear (McWilliams 1999). This hypothesis has been tested recently among Anatidae species over a large range of body sizes (from Teal *Anas crecca*, 300g, to Mute Swan *Cygnus olor*, 11kg) and a variety of foods (seeds, tubers and leaves) (Bruinzeel *et al.* 1998). Digestibility of hemicellulose also correlated significantly with body mass. However, separate analyses for seeds and leaves showed that body size had no effect. The effect of retention time on fibre digestibility is clear, however (see above). Due to their longer retention time, larger birds should be able to digest fibre more efficiently than do smaller ones (Bruinzeel *et al.* 1998) unless, in order to reduce the predicted allometric constraints and to compensate for evident flight constraints that might prevent them from having long retention times, smaller herbivorous Anatidae could: 1) increase retention of the most digestible fibre only (ie through the fermentation in the caecae of small particles from the selective retention of fluid digesta) while maintaining relatively fast passage rates, and 2) have a higher rate of microbial activity. These hypotheses are drawn from the review by McWilliams (1999) on avian herbivores but more data are needed to test them. Since body size is thought to limit the quality of food ingested, Bruinzeel *et al.* (1998) suggested that it is possible that smaller birds compensate for their apparent restricted ability to digest fibre by selecting plants of higher quality (ie containing a higher proportion of proteins and soluble carbohydrates and a lower fibre content).

Anatidae species also vary in caecal length (Bruinzeel *et al.* 1998; Kehoe &

Ankney 1985; Kehoe & Thomas 1987; DeGolier *et al.* 1999). It is known that gut and caecal lengths increase with the amount of fibre in the diet of gallinaceous birds (Moss 1972) and Anatidae (Kehoe *et al.* 1988; Miller 1975; Whyte & Bolen 1985). In gallinaceous birds, the length of the caecae is generally indicative of the degree of cellulolytic fermentation (Gasaway 1976). However, the potential relationship between caecal length and fibre digestion is unknown in herbivorous Anatidae.

Practical implications

This review has important implications for the choice of a reliable marker to quantify food passage and to assess the digestive efficiency of food in herbivorous Anatidae (Grajal & Parra 1995). The works of Marriott & Forbes (1970) and Mattocks (1971) are often cited to affirm that fibre is not digested by herbivorous Anatidae, and thus to use fibre as an internal marker. NDF has been widely used (Halse 1984; Bédard & Gauthier 1989; Mayes 1991; Black *et al.* 1992). However, hemicellulose, which is a component of NDF, is digested in relatively large proportions (Sedinger *et al.* 1995), and can make a large contribution to energy acquisition, in particular in foliage (ie 26% in Bruinzeel *et al.* 1998; see also Dawson *et al.* 1989). For these reasons, it seems that NDF is not a reliable marker.

Since ADF is in general less digestible than NDF, it is potentially a more effective marker (Gadallah & Jefferies 1995); it is also a major component of plant tissue, which reduces measurement error. For example, the Australian Wood Duck is able to digest 40% of NDF (because of the high hemicellulose content of NDF), whereas the digestion of ADF is only 9%, Summers & Grieve (1982) showed that food digestibility values obtained by their input/output method or by the use of ADF as a marker are similar (25% vs 25%). They concluded that ADF is a reliable marker, and it has been used in many studies (Prop & Deerenberg 1991; Manseau & Gauthier 1993; Gadallah & Jefferies 1995; Bruinzeel *et al.* 1998; van Eerden *et al.* 1998a). ADF (and cellulose) have the advantage of being easy to use in field situations (Prop & Deerenberg 1991; Gauthier 1996;). However, ADF (and fibre in general) seems to undergo variation in its digestibility through the annual cycle (Prop & Vulink 1992; van Eerden *et al.* 1998b). There is, therefore, a need for more work on this aspect in order to ascertain the most reliable marker to use in ecological studies.

Since digestion of cellulose can occur to some extent, other workers have prefered to use lignin (Buchsbaum *et al.* 1986; Dawson *et al.* 1989; Amat *et al.* 1991; Prop & Vulink 1992). Indeed, lignin is very resistant to degradation (Buchsbaum *et al.* 1986): almost all lignin ingested by Barnacle Geese was found in the faeces (97%) (Prop & Vulink 1992). However, lignin is difficult to measure accurately (Van

Soest 1982), particularly in the young tissues of grasses and forbs consumed by geese and grazing ducks, since it is present in low concentrations. For some authors, however, lignin is a reliable marker provided that its minimal concentration in the forage is 6-7% of dry matter (Soest 1982: p. 131; Buchsbaum *et al.* 1986; Van). The suitability of lignin as an indigestible marker seems, however, to be in need of reassessment (Van Soest 1982; Sedinger *et al.* 1989; Gadallah & Jefferies 1995).

Conclusion

Variations in the results of the numerous studies reported in this review indicate the need for more measurements, especially on ducks and swans. New studies on the digestibility of fibre throughout a species's annual cycle are essential since ADF (and fibre in general) undergoes variations in its digestibility according to the season. This should increase the understanding of the adaptive significance of such variations. Moreover, the interspecific factors of variation (ie body mass, caecal length) of fibre digestibility are not clear. The priorities for future research should be experiments making simultaneous comparisons of fibre digestibility in various species that vary in body size and gut morphology under standard conditions. Such studies would permit a better understanding of the role of this phenomenon in energy budgets, foraging behaviour and habitat use in avian herbivores as well as resource partitioning between species.

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