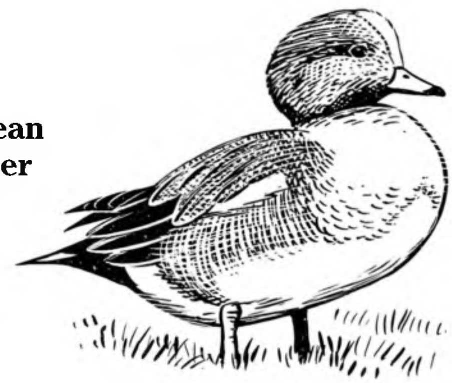
Food throughput time in European Wigeon *Anas penelope* and other grazing waterfowl



PETER W. MAYHEW and DAVID C. HOUSTON

The mean retention time for food passing through the gut of European Wigeon was determined, using a ruthenium isotope as an inert marker, at 74 minutes. This was compared with other published figures for larger grazing geese. The data suggest a relationship between body mass and retention time in grazing wildfowl, although this is not significant, with small species passing food through their guts proportionally more slowly than large ones. This should allow them to sustain a high digestive efficiency.

Grazing geese are known to have extremely low digestive efficiencies (Marriot & Forbes 1970, Ebbinge *et al.* 1975, Drent *et al.* 1979). This is mainly due, in winter feeding conditions, to their inability to digest cellulose (Marriot & Forbes 1970, Mattocks 1971). Fermentation of this compound by microorganisms requires a slow rate of food passage, and wildfowl usually pass food through the gut so rapidly that there is no opportunity for microbial breakdown. The low digestive efficiency of wildfowl requires them to feed almost continuously through daylight hours in winter, and to take high quality plant food (Owen 1980). The problems of extracting sufficient energy from the diet are accentuated for smaller species. Basal metabolic rate increases with body mass at a decreasing rate (Withers 1992), so that small birds need more energy in relation to body weight. The rate at which energy can be extracted from the food, however, is partly a function of gut size and, across a wide range of animal species, gut volume scales linearly with body mass (Demment & Van Soest 1985). Thus small animals need more energy, but have proportionally smaller gut volume with which to obtain it from the food. Demment (1983) predicted from these relationships that small animals should retain food in the gut for disproportionately longer periods than large ones, mainly because digestibility increases with the time food is retained in the gut (Prop & Vulink 1992). The European Wigeon *Anas penelope* is the smallest grazing Anseriform, being about half the size of the smallest of the British geese, the Brent *Branta bernicla*. Wigeon feed, in a similar manner to grazing geese, on short grass swards (Mayhew & Houston 1989). This paper presents some observations on food throughput times in Wigeon, and considers whether there may be a relationship between body mass in grazing waterfowl and food retention time.

Methods

Passage time for the food was measured using a radioactive tracer based on the rare earth element ruthenium. Isotope markers have the advantage of being easy to detect accurately in faecal samples. The ruthenium was in the form of ^{103}Ru tris (1,10 - phenanthroline) ruthenium 11 chloride, a compound which binds, in a non-dissociable complex, to plant fibres so that it travels at the same speed as the digesta (Tan *et al.* 1971, MacRae 1974). Captive birds were used, feeding on a grazing pasture of *Lolium perenne*, *Phleum pratense*, *Festuca* spp. and *Poa* spp.. An isotope solution containing 0.02 µCi/ml was used to prepare grass samples by submerging leaves of grass in the solution for 1 hour at 15°C. The leaves were then removed from the solution and dried for 5 minutes at 50°C. The birds were caught, and ten 3 cm long pieces of marked grass were placed in the bird's oesophagus by inserting a soft rubber tube into the open mouth. The grass pieces were extruded by pushing a narrow piece of rubber inside the first tube to act as a plunger. Once it was clear that the birds had swallowed the food, they were placed back in

Wildfowl 44 (1993): 174-177

the grazing enclosure and watched to record the time at which they started feeding again. Faeces that they produced subsequently were collected about every 20 minutes (more frequent collection caused stress to the captive birds). Radioactive levels in the faeces were measured using a Nuclear Enterprises Scaler-Ratemeter SR5 coupled to a Nuclear Enterprises 663C Scintillation counter. The birds were allowed to graze freely for about two hours before the marker was administered, to ensure that food was passing through the gut normally. Care was taken to minimise the stress to the birds, but they did take several minutes to resume feeding after handling. Although we had a flock of ten birds, we carried out all throughput tests on only one male, because this bird appeared to be least influenced by handling, and started to feed far more rapidly after capture than the other individuals.

Results

The time taken for the food to pass through the gut was found to be influenced by the time taken for the birds to resume feeding after handling. Six trials were run on the same male. On the four occasions when he started to graze normally within 15 minutes of being released, the mean time taken for the first appearance of the marker in the faeces was 31.3 ± 0.8 minutes, and from plots of the cumulative percentage recovery of isotope against time it was found that 50% recovery occurred after 73.5 ± 6.8 minutes and 95% recovery occurred after 115 ± 16.1 minutes. On the two occasions when the bird did not start feeding until 38 and 143 minutes after release, the time for recovery of the faeces was considerably longer, and there was a significant correlation between the time taken for the bird to start feeding and the time taken to record 50% recovery of the marker in the faeces ($t = 4.39$, $df = 4$, $P<0.02$).

Discussion

The maintenance of energy balance is particularly difficult for a small herbivore, because of relatively large energy demands and small gut size which impose a short food retention time. Digestive efficiency is dependent on the speed of food throughput (Ebbinge & Ebbinge-Dallmeijer 1975, Prop & Vulink 1992). We might therefore predict that small species would have relatively longer retention times. European Wigeon are the smallest of all grazing Anseriformes (mean weight 750 g). Their throughput rates reported here can be

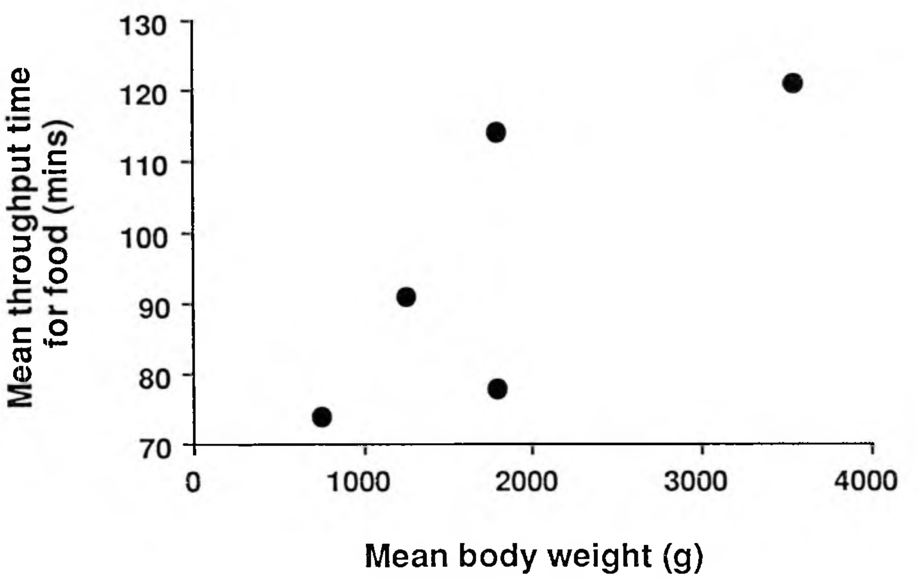


Figure 1. Mean retention time for food in the gut of wildfowl in relation to body weight.

compared with data from other wildfowl species grazing on grass in winter: for Barnacle Geese (mean weight 1800 g) by Owen (1975) and Prop & Vulink (1992), for Red-breasted Geese *Branta ruficollis* (mean weight 1250 g) by Owen (1975), and for Greylag Geese *Anser anser* (mean weight 3550 g) by Mattocks (1971). We have not considered data from species on other diets, because food quality is known to influence throughput time in animals (Lee & Houston in press). Only tentative conclusions can be drawn from comparisons between species in the above studies because there are differences in methodology, and throughput time does vary within species on the same diet. However, Figure 1 suggests that there is a relationship between body mass and throughput time for grazing wildfowl, although this is not quite significant (r = 0.78, N.S.). It does seem, therefore, that smaller wildfowl species retain food in the gut for longer periods, as predicted by Demment (1983). Across species, a four-fold increase in body mass compares with only a two-fold increase in throughput time. Perhaps as a consequence, Wigeon are as efficient at digestion as the larger geese. Mayhew (1988) showed that dry matter digestive efficiency in Wigeon was 28.8%, which compared favourably with that of grazing geese which was generally around 25 to 30% (Sibly 1981, although this is highly variable, see Prop & Vulink 1992). The smallest species can probably only achieve energy balance by retaining food in the gut for a sufficient time to result in an adequate digestive efficiency. This relatively slow digestion accentuates the need to feed for long periods, and Mayhew (1988) showed that Wigeon have to graze for around 13 hours a day in order to obtain sufficient food.

We are grateful to Dr J. MacRae of the Rowatt Research Institute, Aberdeen, for supply of the labelled ruthenium marker compound, and to Dr B.S. Ebbinge and Dr J. Prop for their helpful comments on the manuscript.

References

Demment, M.W. & Van Soest, P.J. 1985. A nutritional explanation for body size patterns of ruminant and nonruminant herbivores. *Am. Nat.* 125:641-672.

Demment, M.W. 1983. Feeding ecology and the evolution of body size in baboons. *Afr. J. Ecol.* 21:219-233.

Drent, R., Ebbinge, B. & Weijand, B. 1979. Balancing the energy budgets of arctic-breeding geese throughout the annual cycle: a progress report. Pp. 239-263 in: (Eds. M. Smart, J. Reichholf & E. Fuchs) *Proc. IWRB Symp. Feeding Ecology of Waterfowl, Gwatt, Switzerland.*

Ebbinge, B.S. & Ebbinge-Dallmeijer, D.A. 1975. Barnacle Geese (*Branta leucopsis*) in the arctic summer - a reconnaissance trip to Svalbard. *Norsk Polarinst. Årbok* 1975:199-138.

Ebbinge, B., Canters, K. & Drent, R. 1975. Foraging routines and estimated food intake in Barnacle Geese wintering in the northern Netherlands. *Wildfowl* 26:5-19.

Lee, W.B. & Houston, D.C. in press. The role of coprophagy in digestion in voles. *J. Funct. Ecol.*

Marriot, R.W. & Forbes, D.K. 1970. The digestion of lucerne chaff by Cape Barren Geese *Cereopsis novaehollandiae*. *Aust. J. Zool.* 18:257-263.

Mattocks, J.G. 1971. Goose feeding and cellulose digestion. *Wildfowl* 22:107-113.

Mayhew, P.W. 1988. The daily energy intake of European Wigeon in winter. *Ornis Scand.* 19:217-223.

Mayhew, P.W. & Houston, D.C. 1989. Feeding site selection by Wigeon *Anas penelope* in relation to water. *Ibis* 131:1-8.

Owen, M. 1980. *Wild geese of the world.* Batsford, Norfolk.

Owen, M. 1975. An assessment of fecal analysis technique in waterfowl feeding studies. *J. Wildl. Manage.* 39:271-279.

Prop, J. & Vulink. T. 1992. Digestion by barnacle geese in the annual cycle: the interplay between retention time and food quality. *J. Funct. Ecol.* 6:180-189.

Sibly, R.M. 1981. Strategies of digestion and defecation. Pp. 109-139 in: C.R. Townsend & P. Calow (Eds.) *Physiological Ecology: an evolutionary approach*. Sinauer Associates, Sunderland.

Withers, P.C. 1992. *Comparative animal physiology*. Saunders, Fort Worth.

Peter W. Mayhew, Royal Society for the Protection of Birds, Etive House, Beechwood Park, Inverness, IV2 3BW.

David C. Houston, Applied Ornithology Unit, Zoology Department, University of Glasgow, Glasgow, G12 8QQ.