Goose feeding and cellulose digestion

JOHN G. MATTOCKS

Introduction

The domestic goose *Anser anser*, in common with many of its wild relatives, is primarily a grazer and it can be raised satisfactorily on grass alone (Bögre 1967; Wright 1942). Some naturalists have assumed that the goose has a cellulose digesting mechanism (Lorenz 1952). Such a capacity would seem to be of real advantage to a grazing animal, for, not only would the cellulose represent an energy source, but the dissolution of the cellulose wall of the grass cells would make the cell contents more readily available for digestion. A literature search failed to give evidence with which to judge the validity of such an assumption and so a study of goose digestion was made (Mattocks 1971). An outline of some of this work is given in this paper.

Review of literature

Cellulose is a carbohydrate consisting mainly of glucose units linked together by $\beta 1-4$ bonds (Rogers and Perkins 1968) and, presumably because the molecule is folded into a zig-zag ribbon which itself is wound into a helix (Manley 1964), it is particularly resistant to hydrolytic cleavage. A complex process involving a number of enzymes is thought to be necessary to convert cellulose to glucose (Norkrans 1967; Reese *et al.* 1950; Gascoigne and Gascoigne 1960), a substance which can be readily used by an animal.

Some insects, such as the silver fish *Ctenolepisma lineata*, are undoubtedly able to produce cellulases (Lasker and Giese 1958), while others are suspected of having this ability. Snails have been shown to digest cellulose (Galli and Giese 1959), but whether the cellulases are of molluscan or microbial origin is an issue not entirely resolved. There is general agreement, however, that no vertebrate is itself capable of secreting cellulases (Marshall 1960; Moir 1965). Horses have evolved large colons and caeca, which house a prolific symbiotic microbial population able to carry out cellulose digestion (Davies 1968). In the rabbit it is the caecum and the appendix which are enlarged for the same purpose, and the overall efficiency of the system is increased by virtue of the fact that the animal eats and digests the faecal pellets it produces during the night (Eden 1940). The ungulates, including the cow, sheep and goat, have developed the most efficient methods. They have capacious rumens in which the food is allowed to ferment for about twelve hours. The cellulose is converted by huge numbers of bacteria (up to 10^{14} organisms/ml.) and ciliates into volatile fatty acids, mainly acetic, propionic and butyric acids, which are absorbed directly into the blood stream (Halliwell 1961; Hungate 1950, 1966; Mann 1968; Walker 1968). The microfauna and microflora are subsequently digested in the rest of the digestive tract.

Cellulose digestion in birds has received very little attention except in the domestic hen. Work done in Germany nearly fifty years ago suggested that cellulose digestion did occur (Mangold 1928, 1931, 1934; Radeff 1928; Henning 1929) but Groebbels (1932) disagreed. More recently cellulose has been found to be so consistently indigestible in cockerels that it has been used as a marker to trace the passage of food in the gut (Bolton 1954). The Ruffed Grouse *Bonasa umbellus* apparently has some ability to digest cellulose but lost weight on a diet of the male flower buds of the trembling aspen *Populus tremuloides* which contain a high proportion of cellulose (Hill *et al.* 1968). In the Red Grouse *Lagopus lagopus* no cellulose and lignin digestion was found when the daily intake was about 80 gm. dry matter per day. If the intake was reduced to 60 gm., however, 20% of the cellulose was digested (Moss 1967).

The question arises as to whether or not there is present in the alimentary canal of a bird an organ wherein cellulose digestion can occur.

Characteristically birds possess a lateral pair of blind-ending tubes called caeca which arise at the junction of the small and large intestines (Figure 1). The variations in form and type have been investigated thoroughly (Mitchell 1901; Maumus 1902; Pinchon 1942). In parrots there is no trace of any caecum and in the falcons and hawks it is very much reduced or absent. By contrast members of the grouse family have very long caeca, that of the Capercaillie *Tetrao urogallus* approaching 1 m. in length. Curiously the herons and their relatives are unique among birds in having a single caecum arising latro-ventrally on the right.

There have been many attempts to classify avian caeca, but basically three

kinds are distinguishable: the plain type which is not well vasculated, usually has much lymphoidal tissue and in which the lumen is small and simple and may contain secretions but never ingesta; the sacculate type in which the lumen is well developed and filled with material from the intestines, and a transitional type. A correlation is found between the possession of large sacculate caeca and a vegetable diet. However, the nocturnal owls have pronounced sacculate caeca, whereas their diurnal counterparts, the hawks and falcons whose food is so similar, have no caeca. Wildfowl have, as might be expected, thin walled, sacculate caeca reaching 10 cm. in most ducks and 30 cm. or more in the swans.

It is very tempting to presume that the avian caecum is functionally a kind of rumen with a cellulose digesting function. Howie and Baker (1952) declared that in non-ruminants the part of the gut most resembling the rumen was the caecum. Both organs contain vast numbers of bacteria (Barnes and Shrimpton 1957; Hungate 1966). Certain groups of bacteria—bacteroides (Barnes and Goldberg 1962), streptococci lactobacilli and coliforms (Barnes and Shrimpton 1957) are found in the caecum of the hen and also in the cow rumen (Hungate 1966). Ciliates abound in the rumen but apparently no protozoa live in the avian caecum except as pathogens (G. Monachon, pers. com.).

Alimentary canal of the domestic goose

A number of varieties of domestic goose was studied, but, since no significant differences were found in them, a single description is given. The bill is strong, and lamellae in the upper and lower jaws arranged in two rows parallel with, and lateral to, the edges of the tongue superficially resemble ungulate molars and premolars. The ridges on the lamellae of the upper jaw running across those on the lower jaw presumably enhance their gripping action. No sideways grinding action can take place in the goose. The thick, spatulate tongue which virtually fills the buccal cavity bears a pronounced fringe of backwardly directed hair-like processes.

The oesophagus (35 cm.), although broadening out a little before joining the proventriculus (7 cm.), has no crop (Figure 1). The gizzard (10 cm.) is very large and its walls consist of concentric arcs of thick muscle fibres. Opposed, thick, cornified, bright yellow patches of keratin-like koilin are present on the inner walls. About 15 gm. of stones and sand together with fibrous residue are found in the gizzard lumen. The small intestine (224 cm.) is fairly uniform in diameter and has a small blind-ending process, Meckel's diverticulum, somewhat posterior to the mid-point. At the junction of the small and large intestine, two lateral caeca arise, the left one being

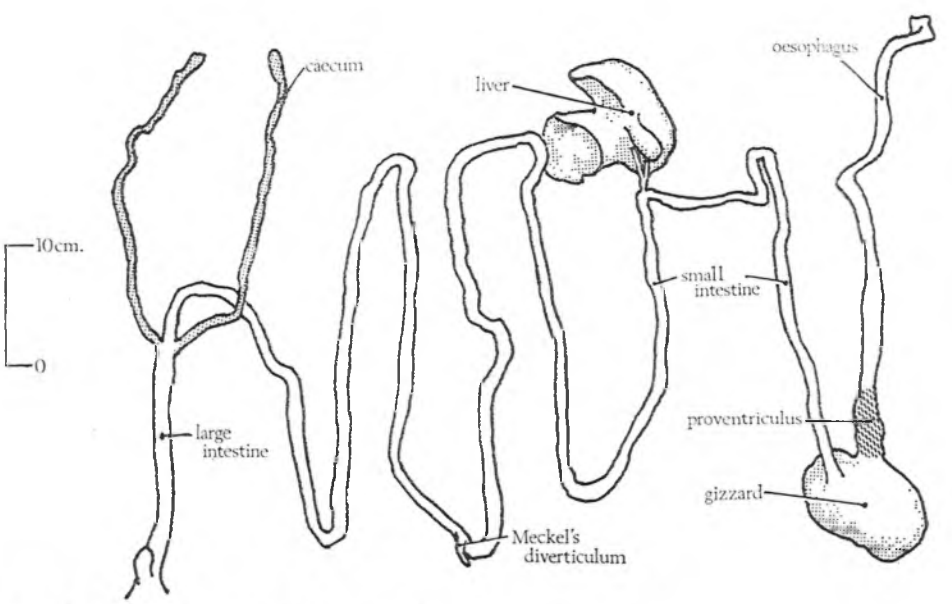

Figure 1. Alimentary canal of a domestic goose.

slightly shorter (21 cm.) than the right one (26 cm.). The lengths given are the average of ten specimens. Most sections of the gut are just under 1 cm. in diameter and variations in length and slight dilations are not uncommon particularly at the distal end. The caeca contain a homogeneous viscous paste with a pronounced smell and of a dark-green, almost black colour. The large intestine or colon is much shorter (about 16 cm.), than the small intestine, but slightly wider in diameter (Figure 1).

Bacteriology of the goose gut

The bacteria present in the various parts of the gut were ascertained by direct microscopical examination of stained smears, and by culturing in various media under anaerobic conditions. Coliforms, relatively plentiful in the oesophagus, decrease in the gizzard and the anterior part of the small intestine, until in the Meckel's diverticulum and onwards they are absent. There is believed to be some form of autosterilisation in the gut (Köhlbrugge 1901; Fuller and Moore 1967), through its own secretions or those of the liver. Lactobacilli were not found, as might be expected in view of the high pH of most of the gut. Faecal streptococci were curiously absent. An abundance of starch-utilizing clostridia was surprising, though their spores probably survive the autosterilisation. It is worth noting that no trace of starch, as determined by the iodine test, was found posterior to the middle of the small intestine. Possibly there is a connection between the rapid digestion of starch and the incidence of clostridia. At no time, in any part of the gut, were protozoa seen, although they were looked for with diligence.

The bacteria of the caeca were examined with especial care in view of their possible function in cellulose digestion. A general habitat-simulating medium (including liver extract, l-cysteine and dithiothretol—Dr. D. J. Jayne-Williams pers. com.) was first used. Sampling was carried out anaerobically in an atmosphere of 99% CO_2 and 1% H_2 the gases having been passed over a cold catalyst to ensure that they were oxygen free. A sterile, needleless, gas-filled plastic hypodermic syringe was used to extract samples below the surface of the exposed caecal contents. Decimal dilution was carried out using small stoppered Astell bottles, gas being passed through continuously whenever the stoppers were withdrawn. Incubation was at 39°C. in Petri dishes placed in McIntosh and Fildes jars containing an atmosphere of 95% H_2 and 5% CO_2 and dry catalysts (palladinised asbestos). The results indicated an overall bacterial count of the order of 10^{10} organisms/gm. wet weight. Niche-simulating media, each suitable for a narrower spectrum of micro-organisms were then used to obtain more specific information. These included Elsden's medium (Elsden *et al.* 1956), ethyl violet medium (Baird-Parker 1957), as modified by Fuller and Lev (1964), Reinforced Clostridial medium, Seeley and Dain (1960) medium and de Man *et al.* (1960) medium. Spread plates were prepared with the ethyl violet and Elsden media and pour plates for the others.

The results, again obtained under carefully anaerobic conditions, indicated that peptostreptococci (2.7×10^9 organisms/gm. wet weight), clostridia (1.7×10^8/gm.), streptococci (2.0×10^7/gm.), bacteroides (9.0×10^4/gm.) and lactobacilli (2.3×10^4/gm.) were present, in descending order of frequency. Clearly the caecum is a congenial place for anaerobic bacteria. Any sterilizing agent produced in the small intestine does not penetrate effectively into the caecum. Starch-utilizing streptococci were found to be about ten times more abundant in the proximal than in the distal end of the caecum; but this ratio was reversed for the bacteroides. The flora of the so-called caecal faeces showed a close correspondence with that of the caecum, confirming their origin.

Tests were now made to see whether any of the anaerobic bacteria present in the goose caecum were capable of cellulose digestion. Bottles containing the medium of Mann (1968) and rolled rectangles, 6 × 5 cm., of filter paper (Whatman's No. 1), were inoculated with caecal material. As before great care was taken to maintain anaerobic conditions during sampling, dilution and incubation. Control bottles were inoculated with the contents of an ox rumen. Both sets were incubated for ten days. The filter paper exposed to goose caecal contents was entirely unchanged. In the ox rumen bottles, however, pits which had appeared in the filter paper within 24 hours continued to increase in size and number and there was production of gas. Microscopical examination revealed concentrations of cocci and other bacteria, all Gram-positive, around the pit margins.

Filter paper is usually considered more susceptible to degradation than its raw counterpart. All factors necessary for

microbial activity were present for not only was their Seitz-filtered rumen liquor present in the medium, but also the initial concentrated inoculum contained plenty of caecal material (0.5 ml.). We can therefore conclude that those bacteria capable of breaking down cellulose which were clearly present in the material from the ox rumen were absent in the goose caecum. Of course there is no guarantee that the medium and technique used was suitable for all kinds of cellulolytic anaerobes.

Goose feeding technique

The birds feed on grass, or meal, for a large proportion of the hours of daylight. The grazing technique is to tilt the head slightly and stretch the neck out to grasp a blade of grass so that it is across the bill. The neck is then withdrawn, the grass fracturing either at the edge of the bill or further down the stem. No mastication of any kind is seen but, by repeatedly moving the head back with the mouth closed and forwards with the mouth open, the birds manoeuvred the grass blade towards the oesophagus. The tongue is also used to manipulate the grass. When feeding on wet meal, no tilting of the head occurs.

Through-put times

The original intention was to determine the time taken for food material to pass through the alimentary canal by using an inert marker. Many such substances have been used including magenta, aluminium powder (Browne 1922), polyethylene glycol (Williams and Wilkins 1968), chromic oxide (Raymond and Minton 1955), lamp black and methylene blue (Kaupp and Ivey 1923). There is some evidence, however, that these substances themselves affect the through-put time (Soergel 1968; Jensen *et al.* 1962) and so other techniques were looked for. Introducing a 'natural' marker gave through-put intervals averaging 82 minutes when grass in meal was used, 122 minutes with cotton strands in grass. X-ray techniques using food containing radio-opaque barium sulphate have been used on the goose (Rybicki 1965) but the adulterant is very dense and the handling of the birds is necessary, so it was thought better to use less drastic methods. Birds killed for dissection in the early morning were all found to have no food left in their alimentary canals. Thus an 'initial' through-put time could be determined by finding the interval between the first morning feed and the passing of the first faeces with food in them. The shortest interval recorded was 26 minutes, but average values were 44 minutes with meal and 71 minutes with grass. If birds which had been feeding on meal only were presented with grass or *vice versa*, the change in faeces was abrupt and easily noted. 'Mid-feed' through-put times on changing from grass to meal averaged 119 minutes and for the reverse change, 137 minutes. All the above averages were based on 10 timings, 5 on one bird, 5 on another. Clearly, food normally stays in the alimentary canal for only about two hours.

Faeces

Four distinct kinds of faeces were produced. The most common was a cylinder of very moist 'chewed' grass with a cap of white uric acid crystals. A small quantity of bile pigment was present but the main colouration was unchanged chlorophyll. The pieces of grass were readily identifiable and apparently very little changed by the bird's digestive processes. The second type appeared when the animal had eaten meal and differed from the first type by being a little shorter and consisting of brown fibrous matter. The uric acid, although present, was less conspicuous than in the grass faeces and there was enough bile pigment to impart a faint green colour to the stool. The third type was very much wetter than the first two types and consisted of a dark brown watery splodge with a pronounced odour and a rich microflora indicating its caecal origin. The last kind consisted of uric acid crystals in a watery mucous medium. The absence of colour or particulate matter other than uric acid crystals suggests that this type is exclusively of renal origin

Discussion

It is clear that in geese no mastication takes place in the mouth. The absence of a crop is to be expected in an animal which grazes most of the day, food being swallowed in small quantities constantly over a long period of time. The oesophagus may, however, serve as a functional crop, particularly towards the end of the day when the rate of feeding tends to rise (Owen 1971). The fact that the grit the gizzard holds contains a high proportion of sand, prompts the suggestion that its principal function is to puncture the grass cells rather than to grind the blades. The appearance of the grass in the faeces shows little evidence of a grinding of the kind exercised by a cow. Lengths of leaf

up to 25 mm. long are quite common and they seem surprisingly intact.

In flying birds, excess weight must be kept to a minimum and so a quick and thorough digestive action is to be expected. Nevertheless, it was a surprise to find that the through-put time for the goose was as short as two hours. In mammals it is measured in days rather than hours, two days being usually quoted for human beings. With such a rapid, piston-like action it is hardly likely that much breakdown of cellulose could take place. The caecum might serve as a reservoir into which food could be shunted to be dealt with in a protracted way, but no trace of any recognisable food-plant tissue nor cells therein were found. Possibly a kind of straining mechanism controlled by the sphincter at the base of the caecum excludes all but the liquid and the most finely divided particles. X-rays of geese fed with meal adulterated with barium sulphate have shown no caecal shadows although traces of barium sulphate left behind in the folds of the oesophagus have been readily seen (Rybicki 1965). It seems unlikely that any large quantity of food enters and is retained by the caecum. The zoning of bacterial types within the caeca argues against any mixing of their contents. In any case, the capacity of the two caeca are less than 20 ml. and they would have to be emptied and refilled many times per day to handle the amount of food ingested.

The failure to find any cellulose-splitting bacteria in the caecum lends weight to the view that cellulose digestion is not a main function of the caecum.

There is a possibility that the caeca assist in the absorption of water or of the soluble products of digestion. Another suggestion has been that excretory nitrogen might be recycled through the caeca. Again, vitamin B_{12} has been shown to be 100 times more plentiful in the caeca of normal chickens than in germ-free ones (Coates *et al.* 1963). Chickens kept on wire, and so prevented from eating their faeces, require a higher proportion in their diet (Shrimpton 1954). It is thus possible that geese might pick up caecal-synthesised B_{12} when grazing on caecally contaminated pastures. In cases where ruminants eat goose-droppings (Kear 1966) one wonders whether the vitamin content might be an attractant as well as undigested grass or phosphates from egested grit.

It might be that the caeca are not concerned with metabolism at all. Ruminants and horses have been shown to contain antibodies in their blood against strains of anaerobic bacteria isolated from the bovine rumen (Sharpe *et al.* 1969). The intestinal flora, providing a small but unremitting source of antigenic stimulation for the production of such antibodies, may be responsible for what might be termed autovaccination. A goose, with its remarkably brief through-put time, would have no resident flora in the alimentary canal. It might be particularly susceptible to an infection were it not for the possession of a cul-de-sac where a prolific flora could be housed.

As a final speculation on caecal function smell seems relevant, for to have kept geese is to be aware that, associated with caecal droppings, there is a pronounced, repugnant odour. Birds mostly have a poor sense of smell and are unlikely to be discommoded. However, geese spend much of their time on the ground and are thus liable to attack by mammalian predators and to competition from mammalian competitors. The caecal discharge might serve the function of deterring such animals, even though Rochard and Kear (1970) have shown any repellent effect is short-lived.

General conclusions

Geese in the wild state are largely, but by no means exclusively, grazers (Kear 1966). It would appear unlikely that cellulose digestion contributes in any significant way to their food up-take. Cell sap appears to be the chief source of nourishment extracted from grass and hence the goose is an inefficient grazer, requiring a much larger *pro rata* intake than a ruminant.

By the reverse token, if geese in captivity are fed on an easily assimilable diet of high calorific value, the through-put rate is so high that the animal is able to grow very rapidly (Monachon 1964). The force-feeding of geese with up to 1000 gm. per day is common on farms in Hungary and France in the interests of the production of *fois gras*.

Acknowledgements

I am most grateful to Dr. R. G. Board and Mr. A. J. P. Goodchild for their guidance of this work, and to Professor L. Broadbent for allowing it to be carried out at the School of Biological Sciences, University of Bath. Much helpful information and stimulation was obtained from Dr. J. Kear and Dr. M. Owen at the Wildfowl Trust, Slimbridge.

Summary

The domestic goose *Anser anser*, a grazing species, takes in considerable quantities of cellulose as part of its food. Investigations were carried out to discover whether cellulose is digested in the gut to any extent. The experiments and techniques for establishing through-put rates are discussed. It is unlikely that cellulose digestion contributes significantly to the goose's food up-take.

References

BAIRD-PARKER, A. C. 1957. Isolation of *Leptotrichia buccalis* and *Fusobacterium* sp. from oral material. *Nature, Lond.* 180 : 1056.

BARNES, E. M. and H. S. GOLDBERG. 1962. The isolation of anaerobic, Gram-positive bacteria from poultry reared with and without antibiotic supplements. *J. Appl. Bact.* 25 : 94.

BARNES, E. M. and D. H. SHRIMPTON. 1957. Causes of greening of uneviscerated poultry carcases during storage. *J. Appl. Bact.* 20 : 273.

BÖGRE, J. 1967. L'importance économique de la race d'oie Landaise. Université des Science Agricoles—chaire de Zootechnie, Gödöllö, Hongrie.

BOLTON, W. 1954. The digestibility of the carbohydrate complex of bran and oats by adult cocks. *Proc. 10th Wld's Poult. Congr. Edinburgh* : 94.

BROWNE, T. G. 1922. Some observations on the digestive system of the fowl. *J. Comp. Path. Ther.* 35 : 12.

COATES, M. E., M. E. GREGORY, J. W. G. PORTER *and* A. P. WILLIAMS. 1963. Vitamin B_{12} and its analogues in the gut contents of germ-free and conventional chicks. *Proc. Nutr. Soc.* 22 : 27.

DAVIES, M. E. 1968. Rôle of colon liquor in the cultivation of cellulolytic bacteria from the large intestines of the horse. *J. Appl. Bact.* 31 : 286.

EDEN, A. 1940. Coprophagy in the rabbit: origin of night faeces. *Nature, Lond.* 145 : 628.

ELSDEN, S. R., B. E. VOLCANI, F. M. C. GILCHRIST and D. LEWIS. 1956. Properties of the fatty acid-forming organisms isolated from the rumen of sheep. *J. Bact.* 72 : 681.

FULLER, R. and M. LEV. 1964. Quantitative studies of the Gram-negative anaerobic bacteria in the pig alimentary tract. *J. Appl. Bact.* 27 : 434.

FULLER, R. and J. MOORE. 1967. The inhibition of the growth of *Clostridium welchii* by lipids isolated from the contents of the small intestines of the pig *J. Gen. Microbiol.* 46 : 23.

GALLI, D. R. and A. C. GIESE. 1959. Carbohydrate digestion in a herbivorous snail *Tegula funebralis*. *J. Exp. Zool.* 140 : 415.

GASCOIGNE, J. and M. GASCOIGNE. 1960. *Biological Degradation of Cellulose.* London: Butterworths.

GROEBBELS, F. 1932. *Der Vögel.* Berlin: Verlag von Gebrüder, Borntraeger.

HALLIWELL, G. 1961. *On Digestion Physiology and Nutrition of the Ruminant.* London: Butterworths.

HENNING, H. 1929. Die Verdaulichkeit der Rohfaser beim Huhn. *Landwn. Vers. Stnen.* 108 : 253.

HILL, D. C., E. V. EVANS and H. G. LUMSDEN. 1968. Metabolized energy of aspen flower buds for captive ruffed grouse. *Wildl. Mgmt.* 32 : 854.

HOWIE, J. W. and F. BAKER. 1952. Rumen and caecal organisms as symbionts. *Proc. R. Soc.* 139 : 193.

HUNGATE, R. E. 1950. The anaerobic mesophilic cellulolytic bacteria. *Bact. Rev.* 14 : 1.

HUNGATE, R. E. 1966. *The Rumen and its Microbes.* London: Academic Press.

JENSEN, L. S., L. H. MERRILL, C. V. REDDY and J. MCGINNIS. 1962. Observations on eating patterns and rate of food passage of birds fed pelleted and unpelleted diets. *Poult. Sci.* 41 : 1414.

KAUPP, B. F. and J. E. IVEY. 1923. Time required for food to pass through the intestinal tract of fowls. *J. Agric. Res.* 23 : 721.

KEAR, J. 1966. The food of geese. *Intern. Zoo Yearbk., Zool. Soc. Lond.* 6 : 96.

KÖHLBRUGGE, J. H. F. 1901. Die Autosterilisation des Dünndarmes und bie Bedeutung des Coecum. *Zentbl. Bakt. Parasitkde* 29 : 571.

LASKER, R. and A. C. GIESE. 1958. Cellulose digestion by the silverfish, *Ctenolepisma lineata*. *J. Exp. Biol.* 33 : 542.

LORENZ, K. Z. 1952. *King Solomon's Ring.* London: Methuen.

MANGOLD, E. 1928. Die Physiologischen Funktionen des Blinddärms, allgemein und besonders bei den Vögeln. *Sber. Ges. naturf. Freunde Berl.*, Dec. : 217.

MANGOLD, E. 1931. Die Verdauung bei den Vögeln. *Proc. 7th Int. Orn. Congr. Amsterdam* : 206.

MANGOLD, E. 1934. Die Verwertung der Planzlichen Rohfaser beim Menschen und den Tieren. *Sber. Ges. Naturf. Freunde Berl.* : 345.

MANLEY, R. ST. J. 1964. Fine structure of native microfibrils. *Nature, Lond.* 204 : 1155.

de MAN, J. C., M. ROGOSA and M. E. SHARPE. 1960. A medium for the cultivation of Lactobacilli. *J. Appl. Bact.* 23 : 130.

MANN, S. O. 1968. An improved method for determining cellulolytic activity in anaerobic bacteria. *J. Appl. Bact.* 31 : 241.

MARSHALL, A. J. 1960. *Biology and Comparative Physiology of Birds.* London: Academic Press.

MATTOCKS, J. G. M. 1971. Some aspects of the problem of cellulose digestion and caecal function in the domestic goose. Unpublished M.Sc. thesis, University of Bath.
MAUMUS, J. 1902. Les Caecums des oiseaux. *Annls. Sci. nat. VIII, Serie Zoologie* 15 : 2.
MITCHELL, P. C. 1901. On the intestinal tract of birds; with remarks on the valuation and nomenclature of zoological characters. *Trans. Linn. Soc. Lond.* 8 : 173.
MOIR, R. J. 1965. *The Comparative Physiology of Ruminant-like Animals.* London: Butterworths.
MONACHON, G. 1964. *Quelque reflexions sur l'élevage et l'habitat des oies.* Domaine Experimental d'Artiguères Banquet, Landes, France.
MOSS, R. 1967. Aspects of grouse nutrition. Unpublished Ph.D. thesis, University of Aberdeen.
NORKRANS, B. 1967. Cellulose and Cellulolysis. *Adv. Appl. Microbiol.* 9 : 91.
OWEN, M. 1971. Some factors affecting food intake and selection in White-fronted Geese. *J. Appl. Biol.* (in press).
PINCHON, R. 1942. Thèses: Contribution a l'étude morphologique des caecums dans la série des oiseaux. Université de Paris.
RADEFF, T. 1928. Uber die Rohfaserverdauung beim Huhn und die Hierbei dem Blinddärm zukommende Bedeutung. *Biochem. Z.* 193 : 192.
RAYMOND, W. F. and D. J. MINTON. 1955. The use of chromic oxide for estimating the faecal production of grazing animals. *J. Br. Grassld. Soc.*, 10 : 282.
REESE, E. T., R. G. H. SIU and H. S. LEVINSON. 1950. The biological degradation of cellulose derivatives and its relationship to the mechanism of cellulose hydrolysis. *J. Bact.* 59 : 485.
ROCHARD, J. B. A. and J. KEAR. 1970. Field trials of the reactions of sheep to goose droppings. *Wildfowl* 21 : 108.
ROGERS, H. J. and H. R. PERKINS. 1968. *Cell Walls and Membranes.* London: Spon Ltd.
RYBICKI, M. 1965. X-ray observations on the passage of food in *Anser anser* L. *Zoologica Polon.* 15 : 2.
SEELEY, H. W. and J. A. DAIN. 1960. Starch hydrolysing streptococci. *J. Bact.* 79 : 230.
SHARPE, M. E., M. J. LATHAM and B. REITER. 1969. The occurrence of natural antibiotics to rumen bacteria. *J. Gen. Microbiol.* 56 : 353.
SHRIMPTON, D. H. 1954. The utilization of the intestinally synthesized riboflavin and vitamin B_{12} by poultry. *Proc. 10th Wld. Poult. Congr. Edinburgh.*
SOERGEL, K. H. 1968. Inert markers. *Gastroenterology* 54 : 449.
WALKER, D. J. 1968. Energy utilization for polysaccharide synthesis by mixed rumen organisms fermenting soluble carbohydrates. *Appl. Microbiol.* 16 : 1672.
WILLIAMS, R. J., and M. W. WILKINS. 1968. Suitability of polyethelene glycol as a dilution indicator in the human colon. *Gastroenterology* 54 : 331.
WRIGHT, M. M. 1942. An observation on the feeding of cut grass to goslings. *Harper Adams Util. Poult. J.* 27 : 117.

J. G. Mattocks, Redland College, Bristol, and School of Biological Sciences, University of Bath, Somerset.