The food habits of Greylag and Barheaded Geese in the Keoladeo National Park, India

BETH A. MIDDLETON and A.G. VAN DER VALK

Introduction

More than 6,000 geese overwinter in the Keoladeo National Park, Bharatpur, Rajasthan, India. The Eastern Greylag Goose *Anser anser rubrirostris* is the most common goose, with a peak population of about 5,000 birds. They arrive in the Park by early November and leave by mid March, a pattern which is typical of northern India (Ali and Ripley 1968). The Barheaded Goose *Anser indicus* at between 500–1,000 individuals is less numerous. They arrive in numbers by late December and leave by mid April. This goose has undergone a significant population decline in the past several decades (Gole 1982).

The food habits of Greylag and Barheaded Geese have never been quantified for any part of their overwintering grounds on the subcontinent of India. Some factors contributing to seasonal food selection (i.e. availability versus physiological needs for migration and breeding) also need to be explored.

It was not possible to kill geese in a National Park, so faecal analysis was used, a method which enables the population to be resampled throughout the season (Storr 1961; Stewart 1967). Geese digest relatively little of the plant material ingested, compared to other vertebrate herbivores (Mattocks 1971; Owen 1975). They digest about 28% of the cellulose and 25% of the hemi-



Figure 1. Location of study site, Keoladeo National Park, Bharatpur, Rajasthan, India (upper left). Areas grazed by goose flocks of more than 100 birds, November 1985–April 86 (lower right). Shaded are Greylag goose areas, darkened are Barheaded areas abandoned by Greylags. Letters correspond to area (block) names.

Wildfowl 38 (1987); 94-102

celluloses in their diets (Buchsbaum *et al.* 1986). Undigested food can pass through a goose in as little as one hour (Owen 1975; Ebbinge *et al.* 1975; Dorozynska 1962). In short, it appeared that the food habits of geese could be described adequately through faecal analysis.

Methods

Study site

The Keoladeo National Park (27° 13'N 77° 32'E) near Bharatpur, 50 km west of Agra (Figure 1), lies in the floodplain of the Gambhir and Banganga Rivers. This wetland lies in a natural depression, but each year the water depth is enhanced by adding rainwater through a floodgate from a reservoir, the Ajun Bund. The park is under the control of the State Government of Rajasthan Forestry Department. Prior to 1973, when it was declared a wildlife sanctuary, the area was used as the Maharajah of Bharatpur's private shooting reserve (Ali and Vijayan 1986).

Water levels in this wetland fluctuate both within and between years. After the monsoon (June–September), water levels are at their annual maximum. As the monsoon waters recede during the autumn and winter, parts or all may become dry (Gopal 1973). After a poor monsoon, the whole wetland may be dry for the entire year. In a very heavy monsoon year, the water may be more than two metres deep, with most of the Park's 29 km² area inundated for at least one month.

This wetland is dominated by one species of grass, Paspalum distichum (Maheshwari 1963). This became much more prevalent after the banning of cattle and buffalo grazing in 1981 (Ali and Vijayan 1986). Only the deepest parts of the wetland are now free of this grass; these are dominated by submerged plant species such as Potamogeton indicus and Hydrilla verticillata. Savanna areas which tend to be flooded for only short periods after a heavy monsoon are dominated by the tall grass species, Vetiveria zizanioides, with occasional trees, primarily Acacia nilotica. Geese, most typically found in the P. distichum dominated areas, have also been recorded in the other two vegetation types in Bharatpur. In V. zizanioides stands, they tend to be found in the wetter depressions that are free of tall grasses.

Collection of Goose Droppings and their analysis

Goose droppings were collected every month from wherever goose flocks were currently grazing. To ensure a good sampling over the population, 100 fresh droppings were collected over a wide area in a given location. Greylag Goose droppings were distinguished from those of Barheaded Geese on size, colour, texture and location. Typically, the two goose species prefer to graze in separate but adjacent flocks in a single area (Figure 1).

The 100 droppings were taken to the laboratory, carefully cleaned of debris, and then mixed. This composite sample was homogenized in an electric blender on the same day that it had been collected in the field. Homogenization improved the quality of the slides by clearing dark pigments from the material. After mixing for one minute, the material was washed for about five minutes through a 0.1 mm (200 mesh) screen until thoroughly cleaned. This cleaned material was dried in an oven at 72°C for future slide preparation or immediately mounted on slides (Scott and Dahl 1980).

Five duplicate slides were prepared for each monthly composite sample (n) following a method described by Baumgartner and Martin (1939). A small amount of faecal material was boiled in a drop of Hertwig's solution over a small burner. Next, a few drops of Hoyer's mounting medium were put on the boiled material, heated and covered with a 22 x 50 mm cover slip while still hot. The material was spread evenly over the slide to minimise fragment overlap. Completed slides were then dried at room temperature or at 55°C in a drying oven. This method does not work during humid weather conditions due to the hydrophilous nature of the mounting medium.

A reference plant collection for the purpose of identifying faecal fragments was constructed. Samples of known plant species were first chopped, then ground in a blender followed by the same cleaning and mounting methods used for the faecal material. Because leaves, stems, seeds and roots are readily distinguishable from each other, a reference slide was made for each plant part. Certain species changed slightly in microscopic appearance during the season (e.g. trichomes in *P. distichum*) so several series of slides were prepared as necessary.

Slide reading followed the sequence described by Scott and Dahl (1980). Starting at the upper left hand corner of the slide, each fragment was recorded in a microscope field where three identifiable fragments occurred until 50 fields had been read. From this information, percentages for each slide were obtained. For both goose species, five duplicate slides were read and averaged for each monthly composite, in each goose grazing location with more than 100 geese. The components of variance for the means of the plant fragments in the goose diet were analysed using the Proc Varcomp option in SAS (Statistical Analysis System 1982).

The method provides estimates in terms of surface area only. Since the relationship between area and volume or weight varies widely among plant parts, the results give only an approximate measure of the contribution of the various plants to the diet.

Results

Greylag Diet

The main source of variation in food habits derives from the month collected rather than goose feeding location or duplicate slides (Table 1). Seasonal diet differences are apparent. Early in the overwintering season, seeds are common in the diet of Greylag Geese. Seed ripening occurs for many plants during the postmonsoon con-

Table 1. Components of variance of selected plant species in the diets of Greylag and Barheaded Geese.

| | Variance Month | Component Area | Estimate Sample |
|---|-------------------------|-----------------------|--------------------|
| GREYLAG GOOSE Paspalum distichum Nymphaea nouchali Oryza rufipogon | 598.3 180.2 293.6 | 130.2 32.5 76.9 | 12.2 7.0 7.5 |
| BARHEADED GOO Paspalum distichum Pisum sativum | SE 1434.2 939.7 | 20.0 6.7 | 8.7 13.7 |

ditions in November and December and seeds made up 64.7% and 58.4% of the diet in these months. Most of these seeds are from Nymphaea nouchali, Oryza rufipogon, Nymphoides cristatum, and P. distichum. When seeds become scarce (they contributed only 1.5% in January and less subsequently), grasses increase in importance, to form almost all of the diet (Figure 2) from January until migration. Most of the grass contribution comes from the stems and leaves of the one species, P. distichum, 68% over the entire season. In all, at least 21 plant species are eaten by Greylag Geese, with additional, minor contributions from insects and snails (Table 2).

Barheaded Goose Diet

Striking differences are seen in the seasonal eating patterns of this species (Figure 2 and Table 3). Grasses are important in January and February but drop sharply in March and April when herbaceous plants and seeds become important. In January, the main constituent of the diet is Wheat Triticum aestivum (Table 3). In February, when field crops are not available, native P. distichum predominates. Overall, its leaves comprise 45% of the overwintering diet. By March and April, once again the diet is mostly field crops, but chiefly of Peas Pisum sativum and Grams Cicer arietinum instead of wheat. Seeds then make up 41.9% and 73.3% of the diet, having been insignificant in the two earlier months. Barheaded Geese utilised a total of 21 different plant species, 3 of which were of agricultural origin. Insects and snails constitute a very low percentage of the diet throughout the season (Table 3).

Barheaded Geese were thus less dependent than Greylag Geese on native wetland plants and only in February did these comprise all their diet, 95% of it being *P*. *distichum*. In parts of the season, Barheaded Geese relied on agricultural crops. Overall, they utilised 52% wild plants in their diet, whereas Greylag Geese used nothing but wild plants.

Discussion

Geese feed on a wide variety of plants (McFarland and George 1966; Pollard and



MONTH OF THE YEAR

Figure 2. Monthly comparison of fragment type in the faeces of Greylag (bottom) and Barheaded Geese (top), November 1985–March 86, in the Keoladeo National Park, Bharatpur, Rajasthan, India. Number of composite samples from goose flocks (n).

98 Beth A. Middleton and A.G. Van Der Valk

Table 2. Food habits of the Greylag Goose, Keoladeo National Park, Bharatpur, India, 1985–86. Averages for all plant species in diet, given by percent. This percent divided between leaves, stems, seeds (in parenthesis). * = <0.1%.

| MONTH | | | | | | | |
|---------------------|--------|----------|---------|--------|----------|----------------|--|
| Plant | Nov | Dec | Jan | Feb | Mar | Average | |
| Paspalum | | | | | | | |
| distichum | 29.4 | 31.2 | 90.0 | 92.2 | 96.1 | 67.8 | |
| leaves | (8.4) | (1.9) | (33.4) | (11.7) | (13.5) | (13.8) | |
| stems | (8.4) | (17.3) | (55.5) | (80.4) | (82.2) | (48.7) | |
| seeds | (12.6) | (11.9) | (1.1) | (0.2) | (0.4) | (5.2) | |
| Nymphaea | | | | | · · · | · · · · | |
| nouchali | 55.1 | 9.4 | 0.1 | - | - | 12.9 | |
| leaves | (3.0) | (0.8) | - | _ | _ | (0.8) | |
| seeds | (52.1) | (8.6) | * | _ | _ | (12.1) | |
| Orvza | | | | | | , í | |
| rufipogon | 1.2 | 46.7 | 2.3 | 0.9 | 0.8 | 10.4 | |
| leaves | (1.2) | (11.6) | (2.1) | (0.9) | (0.8) | (3.3) | |
| seeds | _ | (35.1) | (0.2) | - | (0.1) | (7.1) | |
| Іротоеа | | (((()))) | (0.2) | | () | (,) | |
| aquatica | 1.2 | 0.9 | 0.9 | 2.8 | 0.5 | 1.3 | |
| leaves | (1.2) | (0.8) | (0.9) | (2.8) | (0,5) | (1.2) | |
| seeds | - | (0.0) | ((),)) | (2.0) | (0.5) | (1.2) (0.1) | |
| Sagittaria | | (0.1) | | | | (0.1) | |
| guavanensis | 2.4 | 2.5 | :Br | | | 1.0 | |
| leaves | (2,4) | (1.8) | (*) | - | | (0.8) | |
| seeds | (2.7) | (0.7) | (_) | | | . , | |
| | — | (0.7) | - | _ | _ | (0.1) | |
| Nymphoides | 7.8 | 1.7 | 0.1 | * | 0.1 | 1.0 | |
| cristatum leaves | | | 0.1 | | 0.1 | 1.9 | |
| | (7.8) | (0.3) | | (*) | - | (1.6) | |
| seeds | - | (1.5) | (0.1) | (*) | (0.1) | (0.3) | |
| Scirpus | | 07 | 0.5 | 0.4 | A | 0.2 | |
| tuberosus | | 0.7 | 0.5 | 0.4 | 0.1 | 0.3 | |
| Cynodon | | 0.5 | 0.5 | 0.1 | 0. | 0.2 | |
| dactylon | - | 0.5 | 0.5 | 0.1 | 0.1 | 0.2 | |
| Panicum | | | | | | | |
| paludosum (stem) | - | 0.5 | 1.7 | 1.1 | 0.6 | 0.8 | |
| grass seed | _ | 0.3 | - | _ | - | 0.1 | |
| Paspalidium | | | | | | | |
| flavidum | - | 0.2 | 0.5 | 0.6 | 0.3 | 0.3 | |
| Sporobolus sp. | - | 0.1 | 0.8 | 0.1 | 0.3 | 0.2 | |
| herbaceous seed | _ | 0.1 | - | - | _ | 20 | |
| Hemiadelphus | | | | | | | |
| polyspermus | - | 0.1 | 4 | 0.1 | sit | sic | |
| Scirpus | | | | | | | |
| littoralis | - | - | 1.4 | 0.4 | 34: | 0.4 | |
| Eleocharis | | | | | | | |
| palustris | - | - | 0.3 | 0.1 | 0.1 | 0.1 | |
| Utricularia sp. | _ | 2 | 0.1 | 0.1 | _ | * | |
| Ceratophyllum | | | | | | | |
| demersum | _ | _ | * | 0.1 | _ | * | |
| Cyperus | | | | | | | |
| alopecuroides | _ | _ | 0.3 | * | _ | 0.1 | |
| grass stem | _ | _ | | _ | * | * | |
| Insects & snails | 3.0 | 5.3 | 0.6 | 0.7 | 0.9 | 2.1 | |
| maceta et anana | 5.0 | 5.5 | 0.0 | V. / | 0.7 | ا.ن | |

Walters-Davies 1968; Owen and Kerbes 1971; Owen 1976; Burton *et al.* 1979; Prevett *et al.* 1979; Summers and Grieve 1982). The particular species of plants consumed depends on the flock's geographic

location and on plant availablility.

In the Keoladeo National Park, Barheaded Geese eat more gramineous leaves than they are reported to do elsewhere. In their nesting range in the Soviet

| Table 3. Foods habits of the Barheaded Goose, Keoladeo National Park, Bharatpur, India, 1986. | |
|---|--|
| Averages for all plant species in diet, given by percent. This percent divided between leaves, stems, | |
| seeds (in parenthesis). * = $<0.1\%$. | |

| | MONTH | | | | | | |
|----------------------|--------|--------|--------|--------|---------|--|--|
| | Jan | Feb | Mar | Apr | Average | | |
| Paspalum | | | | | | | |
| distichum | 10.8 | 95.0 | 49.5 | 26.4 | 45.4 | | |
| leaves | (10.3) | (94.9) | (49.5) | (26.4) | (45.3) | | |
| stems | - | - | - | _ | _ | | |
| seeds | _ | (0.1) | _ | - | (*) | | |
| Pisum | | | | | | | |
| sativum | 4.6 | - | 44.5 | 72.3 | 30.2 | | |
| seed | - | - | (42.2) | (72.1) | (28.5) | | |
| stems & leaves | (4.6) | - | (2.3) | (0.2) | (1.8) | | |
| Cicer | | | | | | | |
| arietinum | 3.1 | - | 2.7 | 0.6 | 1.6 | | |
| seed | - | - | (0.1) | (0.6) | (0.2) | | |
| stems & leaves | (3.1) | - | (2.6) | - | (1.4) | | |
| Triticum | | | | | | | |
| aestivum | 65.1 | - | - | - | 16.3 | | |
| Cynodon | | | | | | | |
| dactylon | 5.5 | 0.7 | 1.5 | 0.3 | 2.0 | | |
| Ipomoea | | | | | | | |
| aquatica (leaves) | 0.8 | 0.2 | 0.1 | - | 0.3 | | |
| Paspalidium | | | | | | | |
| flavidum | 2.0 | 0.4 | 0.6 | - | 0.8 | | |
| Panicum | | | | | | | |
| paludosum | 2.1 | 0.3 | 0.6 | - | 0.8 | | |
| Ceratophyllum | | | | | | | |
| demersum | - | 0.3 | - | - | 0.1 | | |
| Sporobolus sp. | 1.4 | 0.2 | - | 0.2 | 0.5 | | |
| Scirpus | | | | | | | |
| tuberosus | 2.6 | 0.4 | 0.3 | | 0.8 | | |
| Nymphoides | | | | | | | |
| cristatum | 0.2 | 0.1 | - | - | 0.1 | | |
| Scirpus sp. | _ | 0.2 | - | - | 94 | | |
| Sagittaria | | | | | | | |
| guayanensis (leaves) | 0.2 | 0.1 | - | - | 0.I | | |
| Scirpus | | | | | * | | |
| littoralis | | - | 0.1 | - | * | | |
| Eleocharis | | | | | * | | |
| palustris | - | - | - | 0.1 | | | |
| Utricularia sp. | 0.5 | - | - | - | 0.1 | | |
| Hemiadelphus | 0 - | | | | * | | |
| polyspermus | 0.2 | - | - | - | 25 | | |
| Nymphaea | 0.2 | | | | * | | |
| nouchali (seed) | 0.2 | - | - | - | | | |
| herbaceous leaf | 0.4 | - | - | _ | 0.1 | | |
| Insects & Snails | - | 2.2 | 0.3 | 0.1 | 0.7 | | |

Union, they feed mostly on terrestrial vegetation, including the seeds of grasses and legumes; in tidal areas they eat seaweeds, erustaceans and invertebrates (Dement'ev and Gladkov 1952).

Greylag Geese in the Keoladeo National Park cat seeds early in the winter season and grass parts in later months, not greatly different from reports of the Eastern Greylag diet in the Soviet Union. Dement'ev and Gladkov (1968) reported that they eat grasses of various sorts (winter rye, hair grasses, awnless broom grass *Leerzia* sp.), the fruits of *Potamogeton pectinatus* and the seeds of *Polygonum* sp. and oats. In the Netherlands (Loosjes 1974) and in Spain (Amat 1986) Greylag Geese eat a wild plant diet of mostly *Scirpus lacustris* root pieces and the tubers or rhizomes of *Scirpus* maritimus. Western Greylag Geese A. a. anser in Scotland eat mainly grasses but in late summer switch to ripening oats (Newton and Kerbes 1974). In the winter, they primarily feed in agricultural fields where they eat oat and barley seeds, later switching to potato crops (Newton and Campbell 1973; Newton et al. 1974).

Greylag Geese in the Keoladeo National Park have very different food habits from the Barheaded Geese grazing in the same area. Large-billed species such as the former are adapted for rooting, whereas smaller-billed geese like the latter may be better suited for grazing on shorter grasses (Reed 1976) in shallower water. Other studies have demonstrated that goose species in one area may have very different food habits due to differences in food preference (Craven 1984) as well as morphological differences.

The Greylag Geese maintain themselves on the nearly apple-sized fruits of *Nymphaea nouchali* (and many kinds of seeds) in the early part of their overwintering season. Later in the season, they can be observed forcibly pulling up whole culms of *P. distichum* which may be growing in water approaching 2 metres deep. Barheaded Geese which have a much smaller bill, tend to tear off the leaves of grasses rather than tackle the bulky stems. They can often be seen grazing in shallow areas abandoned by Greylags, perhaps preferring the shorter forage provided.

Barheaded Geese spend most of their time grazing in agricultural fields during certain parts of the winter season, but during the day, they also graze on wild grasses in the wetland. Since more than half of their diet comes from a wild food source, they cannot be thought as being completely dependent on agriculture.

It is not known whether or not *P. distichum* was such an important food item in the diet of geese prior to this plant's spread after the cessation of cattle and buffalo grazing in 1981. It is clear from this study that it is now an important component of the diet for both goose species overwintering in the Keoladeo National Park. Studies now in progress will explore the role of geese in creating openings in this nearly monospecific grass cover.

To some extent, seasonal dietary requirements of geese dictate their choice of food (Ydenberg and Prins 1981; Halse 1984; Hobaugh 1985). These authors suggest that geese choose more nutritious food prior to migration or to breeding in order to accumulate fat reserves. In India, Barheaded Geese do behave in this fashion, in that, prior to migrating to their Himalayan breeding grounds, they eat such nutrientrich foods as peas, grams and, a little earlier in the season, young wheat but then, these plants are only available at this time. During February, between the season of young wheat and that of ripening legumes, the geese return to graze exclusively in the wetland.

One cannot make a case for food selection by Greylag Geese on their overwintering grounds related to migration or breeding requirements. Shortly after they arrive for their five month sojourn, they choose to eat the nutrient-rich seeds available during the post-monsoon period (Nymphaea nouchali, Oryza rufipogon). Just before migrating from India, they switch to grasses when seeds are no longer available. For Greylag Geese then, and to some extent for Barheaded Geese, availability seems to be a major determinant of their seasonal food selection.

Acknowledgements

This study was carried out under Smithsonian Grant No. 4013600. We would like to thank the State Government of Rajasthan Forestry Department for their cooperation with this work, including O.P. Mathur, V.D. Sharma and Rajan Mathur. For help with various technical aspects of this report, we would like to thank Gretchen Scott of Texas Tech, Ted Bailey of the Iowa State and Craig B. Davis of Ohio State University. Comments on drafts of this paper came from Nels Lersten, Bill Clark, Erv Klaas and Jerry Sell. Special thanks to the field assistants in this work: O.P. Mudgal, Laxmi Kant Mudgal, Sunil Mudgal, Kriste Ericeson, Kurt Streeb, Marjorie Bousfield, Nihal Singh, Gopal Singh, Prakash Singh, Bihari Singh and Soren Singh.

Summary

The food habits of overwintering Greylag Anser anser rubrirostris and Barheaded Anser indicus Geese were investigated in the Keoladeo National Park, Bharatpur, India. Greylag Geese eat mostly seeds of Nymphaea nouchali and Oryza rufipogon in November and December but shift to native grasses such as *Paspalum distichum* in January. They eat mostly *P. distichum* until they leave in March. Barheaded Geese eat mostly young wheat in January, native grasses, such as *P. distichum* in February and change to field peas and grams in March and April. Native wetland plants make up most of the diet of Greylag and Barheaded Geese, 100% and 52% respectively. Overall, *P. distichum* is the most important species in the diet of these geese, comprising 67.8% of the Greylag and 45.4% of the Barheaded Goose diet.

References

- Ali, S. and Vijayan, V.S. 1986. Keoladeo National Park ecology study. Summary report 1980–85. Bombay Natural History Society, Bombay, India.
- Ali, S. and Ripley, S.D. 1968. Handbook of the birds of India and Pakistan. Volume 1. Oxford University Press, Bombay, India.
- Amat, J.A. 1986. Numerical trends, habitat use and activity of Greylag Geese wintering in southwestern Spain. *Wildfowl* 37:35–45.
- Baumgartner, L.L. and Martin A.C. 1939. Plant histology as an aid in squirrel food-habit studies. *J. Wildl. Manage.* 3:266–269.
- Buchsbaum, R., Wilson, J. and Valiela, I. 1986. Digestibility of plant constituents by Canada Geese and Atlantic Brant. *Ecology* 67:386–393.
- Burton, B.A., Hudson, R.J., and Bragg, D.D. 1979. Efficiency of utilization of bulrush rhizomes by Lesser Snow Geese. J. Wildl. Manage. 43:728–735.
- Craven, S.R. 1984. Food habits of Canada Geese on the coast of Hudson Bay. J. Wildl. Manage. 48:567–569.
- Dement'ev, G.P. and Gladkov, N.A. 1952. Birds of the Soviet Union, Vol. 4, Moscow.
- Dorozynska, N. 1962. Food intake and defecation in the goose, Anser anser L. Acta Biologiae Experimentalis 3:227–240.
- Ebbinge, B., Canters, K. and Drent, R. 1975. Foraging routines and estimated daily food intake in Barnacle Geese wintering in the northern Netherlands. *Wildfowl* 26:5–19.
- Gole, P. 1982. Status of Anser indicus in Asia with special reference to India. Aquila 89:141-149.

Gopał, B. 1973. A survey of the Indian studies on ecology and production of wetland and shallow water communities. *Polskie Archiwum Hydrobiologii* 20:21–29.

- Halse, S.A. 1984. Diet, body condition and gut size of Egyptian Geese. J. Wildl, Manage. 48:569-573.
- Hobaugh, W.C. 1985. Body condition and nutrition of Snow Geese wintering in southeastern Texas. J. Wildl. Manage. 49:1028–1037.
- Loosjes, M. 1974. Over terreingebruik, verstoringen en voedsel van Grauwe Ganzen Anser anser in een brak getijdengebied. Limosa 47:121–143.
- Maheshwari, J.K. 1963. The flora of Dehli. CSIR. New Dehli, India.

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

- McFarland, L. Z. and George, H. 1966. Preference of selected grains by geese. J. Wildl. Manage. 30:9–13.
- Newton, I. and Campbell, C.R.G. 1973. Feeding of geese on farmland in east- central Scotland. J. *Appl. Ecol.* 10:781–801.
- Newton, I., Campbell, C.R.G. and Allison, A. 1974. Gut-analysis of Greylag and Pink-footed Geese. Bird Study 21:255–262.
- Newton, I. and Kerbes, R.H. 1974. Breeding of Greylag Geese (*Anser anser*) on the Outer Hebrides, Scotland. J. Anim. Ecol. 43:771–783.
- Owen, M. 1975. An assessment of fecal analysis technique in waterfowl feeding studies. J. Wildl. Manage. 39:271–279.
- Owen, M. 1976. The selection of winter food by White-fronted Geese. J. Appl. Ecol. 13:715–729.
- Owen, M. and Kerbes, R.H. 1971. On the autumn food of Barnacle Geese at Caerlaverock National Nature Reserve. *Wildfowl* 22: 114–119.
- Pollard, D.F.W. and Walters-Davies, P. 1968. A preliminary study of the feeding of the Greenland White-fronted Goose Anser albifrons flavirostris in Cardiganshire. Wildfowl 19:108–116.
- Prevett, J.P., Marshall, I.F. and Thomas, V.G. 1979. Fall food of Lesser Snow Goose in the James Bay Region. J. Wildl. Manage. 43:736–742.

Reed, A. 1976. Geese, nutrition and farmland. Wildfowl 27:153-156.

Scott, G., and Dahl, B.E. 1980. Key to selected plant species of Texas using plant fragments. Occasional Papers, The Museum, Texas Tech University, Lubbock, Texas.

Statistical Analysis System 1982. SAS user's guide: statistics. Cary, North Carolina.

102 Beth A. Middleton and A.G. Van Der Valk

Stewart, D.R.M. 1967. Analysis of plant epidermis in faeces: a technique for studying the food preferences of grazing herbivores. J. Appl. Ecol. 4:83–111.

Storr, G.M. 1961. Microscopic analysis of facees, a technique for ascertaining the diet of herbivorous mammals. Aust. J. Biol. Sci. 14:157–165.

- Summers, R.W. and Grieve, A. 1982. Diet, feeding behavior and food intake in the Upland Goose (*Chloëphaga picta*) and Ruddy-headed Goose (*C. rubidiceps*) of the Falkland Islands. *J. Appl. Ecol.* 19:783–804.
- Ydenberg, R.C. and Prins, H.H.Th. 1981. Spring grazing and the manipulation of food quality by Barnacle Geese. J. Appl. Ecol. 18:443–453.

Beth A. Middleton and A.G. van der Valk, Botany Department, Iowa State University Ames, Iowa 50011–1020.

