# How to cope with snow and ice: winter ecology of feral Greylag Geese Anser anser

SONJA KÄßMANN<sup>1</sup> & FRIEDERIKE WOOG<sup>2</sup>

<sup>1</sup>Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, 70191 Stuttgart, Germany. Email: kaessmann.smns@naturkundemuseum-bw.de <sup>2</sup>Corresponding author. Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, 70191 Stuttgart, Germany. Email: woog.smns@naturkundemuseum-bw.de.

#### Abstract

Unlike most wild goose populations in the Western Palaearctic, the feral Greylag Geese *Anser anser* in Stuttgart, southwest Germany, are not known to migrate. In winter 2004/05, a study was carried out to determine how this resident group copes with snow and ice, since severe weather conditions are not unusual in the region. Changes in activity budgets, feeding behaviour and abdominal fat reserves were investigated. From January to March 2005, frequent snowfall resulted in persistent snow cover. In response to the resulting lack of food, the geese changed their daily feeding patterns, fed less, loafed more and subsequently lost abdominal fat reserves. Although they moved from small park lakes to the ice-free river for roosting, they did not leave the area in search of snow-free feeding sites.

Key words: city ecology, resident population, activity budget, abdominal profile, peck rate.

In the 1980s, feral Greylag Geese Anser anser became established in Stuttgart, southwest Germany. Large parks offer plenty of grazing and small artificial lakes are used by the geese to escape from potential predators, such as dogs. In 1995, a brood of Greylag Geese was recorded for the first time within the city limits at a lake five kilometres north of the parks. Since then numbers increased to 159 individuals by 2004/05. Other resident goose populations are known from cities such as Hamburg, London and Copenhagen (Kreutzkamp 2003, Baker & Coleman 2004, Kampp & Preuss 2005), but little is known about the winter ecology of these feral or reestablished geese.

Unlike most wild goose populations in the Western Palaearctic (Cramp & Simmons 1977, Madsen *et al.* 1999), Greylag Geese in Stuttgart are not known to migrate but movements over short distances may occur that have not yet been documented. They graze exclusively on the extensive lawns of the town's parks, and unlike wild Greylag Geese have not yet used agricultural sites (Carboneras 1992, Ballasus 2005). In wild geese, such as the White-fronted Goose Anser albifrons, it has been shown that frosty temperatures affect vegetation growth and food availability and thus the foraging behaviour of the birds (Owen 1972). Furthermore, wild geese are known to move to areas where foraging is most profitable (Drent & Prins 1987). Given the sedentary habits of the Greylag Geese in Stuttgart, this study focuses on the effect of snow and ice on their activity budgets, the feeding behaviour and abdominal fat reserves. Thus it aims to determine how the geese cope with wintry weather conditions.

# Methods

#### Study area

Field work was carried out between October 2004 and March 2005 in Stuttgart, southwest Germany. With its numerous public gardens and parks, Stuttgart is among the "greenest" towns in Europe. The parks extend over eight kilometres through the inner city. Five kilometres to the north along the river Neckar the geese use a 600 m long lake that is surrounded by open pasture. During of the 1970s, a bird sanctuary was established in the northwest part of this former gravel pit, which includes a few small islands that the geese use for nesting. The study area covered three separate parts of the city: the lake and surrounding pasture, the banks of the adjacent river Neckar, and the large park in town.

## Coloured leg bands

Since 2002, about a third of the 159 Greylag Geese in Stuttgart have been ringed with blue plastic ("Darvic") leg bands, each engraved with a unique white three letter code for identification of individual birds. As the birds were rather tame the codes could frequently be read with the naked eye or using binoculars.

## Activity budgets

Behavioural observations were carried out two to four times a week between 4 November 2004 and 8 March 2005 for a total of 40 days. To compare activity budgets on days with and without snow, respectively, nine observation days each were selected from the period of January and February 2005 for a total of 150 hours. The classification "snow cover"/"no snow" was measured as present/absent. Days with snow cover were characterised by colder temperatures (mean minimum temperature =  $-5.2 \pm 3.2$  °C, mean maximum temperature =  $7.3 \pm 0.4$  °C) and higher precipitation (mean precipitation =  $8.2 \pm 0.7$  mm) than days without snow cover (mean minimum temperature = -2.3 $\pm$  1.1 °C, mean maximum temperature = 9.6  $\pm$  1.1 °C, mean precipitation = 3.5  $\pm$  0.2 mm).

The behaviour of all geese present in an area was determined by taking scan samples from dawn to dusk (Martin & Bateson 1986). An audio beeper gave a signal every 10 minutes and the behaviour of all geese present in the area at that time was recorded. Behavioural categories were modified from those used by Inglis (1977), the main activities being feeding, vigilance, loafing, locomotion, preening and social interactions (mostly aggression).

Since day length varies, only data recorded during the daylight hours of 08:00 h to 17:00 h were used for analysis.

## Peck rates

Peck rates indicate the relative effort an individual bird expends in a certain time to acquire a certain amount of food and are dependent on vegetation height and social status (Ebbinge et al. 1975, Black et al. 1991). Peck rates (pecks/min) were used to compare frequencies of food intake in vegetation covered by snow, vegetation of different height and for birds of different social status. Feeding bouts were recorded by monitoring a bird's activities continuously over a threeminute period using a dictaphone. Time intervals between the records were random. During the three-minute periods, active feeding was often interrupted by other activities, such as vigilance or walking. Only active feeding time within the three-minute samples was used to calculate peck rates. Between 26 November 2004 and 18 February 2005 a total of 121 peck rate samples were recorded for 58 individuals.

After recording peck rates, at least 10 vegetation height measurements were made per pasture, using a set square, at random locations within the areas where the geese had been feeding. Sward heights were divided into two classes: short (mean height < 7 cm) and medium (mean height 7 - 12 cm). The lawns in the parks are mown regularly so grazing in grass longer than 12 cm was rarely observed. The classification "snow" was used when vegetation was covered by snow.

To test the effect of social status, the birds were classified into three social groups:

single (unpaired) birds, paired geese and family groups (parents with goslings of unknown sex). Most goslings stay with their parents throughout the winter until the onset of the breeding season (Cramp & Simmons 1977). For each three-minute observation period a bird was selected at random from the group. To test whether time of day influenced the peck rates the days were divided into "morning" (08:00 h – 11:00 h), "midday" (11:01 h – 14:00 h) and "afternoon" (14:01 h – 17:00 h).

# Abdominal profiles

The relative increase or loss of weight in geese can be determined according to the "Abdominal Profile Index" (API) used to assess their body conditions in the field (Owen 1981). Since abdominal fat is a good indicator of overall body fat, the API also gives a useful estimate of changes in overall body mass (Wiersma & Piersma 1995, Zillich & Black 2002). The API is an alternative method to direct weighing and allows the repeated assessment of individually-marked birds without capturing and causing stress to the animals. The method described by Zillich & Black (2002) was used, where Owen's API scores (0 = concave, 1 = straight, 2 = convex,3 = rounded, thick, 4 = intensely rounded, very fat) are further subdivided by introducing 0.5 unit increments. On determining the API for a goose, the bird was observed until the abdomen was parallel to the ground and easily visible to the observer to avoid bias. Between 12 November 2004 and 9 March 2005, abdominal profiles of all ringed geese present were determined once a week.

Changes in abdominal profiles of individually-marked geese of different social status were compared throughout the winter.

## Weather data

Daily weather records were available from the Environmental Office in Stuttgart (Amt für Umweltschutz, Stuttgart). The weather station is located in town close to the study area. From the daily records we calculated the weekly mean, minimum and maximum temperatures, and also the mean precipitation (rainfall and snowfall) within the city for each week, for inclusion in the analyses.

## Statistics

Minitab software (Ryan *et al.* 2005) and GLIM (NAG) were used for analysis of variance and general linear models.

Variation in the time that the geese spent feeding, loafing or being vigilant was compared using analysis of variance with a binomial error distribution in GLIM (Crawley 1993, NAG 1993). Because the data recorded for the different behavioural categories were not independent of each other, each type of behaviour was tested separately. For instance, the mean number of birds feeding within an hour was the response variable, and the mean number of birds monitored within an hour was the binomial denominator. Explanatory variables tested in the models were snow cover, location and hour (time of day). As location did not cause a significant increase in deviance, data from all locations were pooled in the analyses presented here.

Initial fits to the models indicated that the behavioural data were over-dispersed.

Constraints imposed by specifying a binomial error distribution therefore were adjusted using the scale parameter, which in turn was estimated by dividing the Pearson  $\chi^2$  value of the final model (*i.e.* the system scalar) by the degrees of freedom (Crawley 1993). Variables that caused a significant increase in deviance (P < 0.05) were retained in the model. Insignificant terms were removed. Biologically meaningful interaction terms such as an interaction between time of day and presence of snow were tested but none were significant.

Peck rate data were analysed using one-way ANOVAs. Only one peck rate per individual was used to avoid pseudoreplication. For pair-wise comparisons two-sample *t*-tests were used. There was no effect of location on peck rates; data from different sites therefore were pooled. Abdominal profile data were analysed in a general linear model and the following explanatory variables tested: week, social status, weekly mean minimum temperatures (°C) and weekly mean rain/ snowfall (mm).

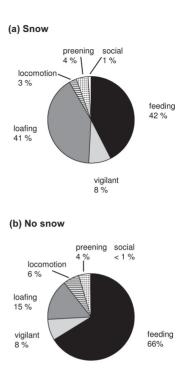
# Results

In November and December 2004, there were only nine days with sub-zero temperatures and no days with snow cover. In contrast, in the second half of the winter from January to March 2005 daily average temperatures dropped to below zero on 27 days (7 days in January, 12 days in February, 8 days in March) and frequent snowfall caused a continuous snow cover for 46 days (8 days in January, 24 days in February, 14 days in March). The distribution of the geese changed as a result but, although the birds moved from the frozen lakes to the ice-free river for roosting, they did not leave the city limits in search of snow-free feeding sites. Almost all banded birds were resighted within the study area throughout the winter (Käßmann 2005). In the snow, the geese had to cope with the resulting lack of food. As a consequence, their activity budgets, peck rates and abdominal profiles changed during the winter.

#### Activity budgets

The daily percentage of activities was different on days with snow cover as opposed to days without snow (Fig. 1). Without snow the birds fed more (66%) than when confronted with a continuous snow cover (42%) ( $F_{1.168} = 23.6, P < 0.01$ ). They also loafed almost three times more (41%) on days with snow ( $F_{1.168}$  = 41.1, P < 0.01) than on days without (14%). Furthermore, they moved less in snow (3% as opposed to 6% without snow;  $F_{1.168} = 24.68, P < 0.01$ ) and showed more social interactions, mostly aggression, in snow (1% as opposed to 0.3% without snow;  $F_{1.168} = 30.8$ , P < 0.01). When feeding in snow, the geese were frequently seen sitting down and, whilst sitting, they pecked holes into the snow in order to reach the vegetation.

Diurnal activity patterns differed between days with and without snow (Fig. 2). In the snow, geese loafed mainly during the morning and evening hours with a peak at 08:00 h (70%), when only 24% were feeding. Most individuals were feeding around midday, with a peak at 13:00 h (56%), when loafing was at its minimum (24%). In contrast, on days without snow

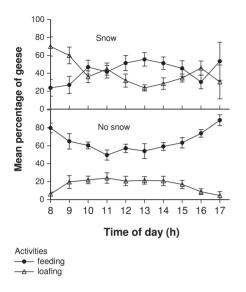


**Figure 1.** Activity budgets of Greylag Geese on (a) days with snow (n = 9) and (b) days without snow (n = 9). The percentages of time recorded for different activities are shown (n = 75 hours each, for (a) and (b) respectively).

the percentage of feeding was high in the morning (maximum 84%) and in the evening hours (maximum 86%), when loafing was low. These differences in diurnal pattern were significant for loafing (snow  $F_{1,159} = 44.8$ , P < 0.01; hour  $F_{9,167} = 3.19$ , P < 0.01), but not for feeding (snow  $F_{1,159} = 23.8$ , P < 0.01; hour  $F_{9,167} = 1.85$ , n.s.).

#### Peck rates

Geese pecked most rapidly in short vegetation and most slowly in the snow



**Figure 2.** Greylag Goose activity (feeding and loafing) throughout the day on days with snow (n = 9) and days without snow (n = 9).

 $(F_{2.118} = 34.01, P < 0.01;$  Fig. 3). Peck rates ranged from 78-123 pecks/min in short vegetation, from 74-107 pecks/min in medium vegetation and from 61-91 pecks/min in snow. Peck rates also varied with social status ( $F_{4.116} = 12.67, P < 0.01$ ). Parental males pecked most rapidly (n = 8;89-123 pecks/min) followed by unpaired birds (n = 12; 85–117 pecks/min) and paired geese (n = 14; 64–119 pecks/min). Peck rates of parental males and paired geese did not differ significantly (t =0.37-0.87, d.f. = 11-21, n.s.), but peck rates of parental females (n = 8; 69–102 pecks/min) and goslings (n = 16; 61–102 pecks/min) were similar ( $t_{15} = 1.06$ , n.s.) and lower than those of parental males (parental females:  $t_{13} = 2.23$ , P < 0.04; goslings:  $t_{14} = 3.47$ , P < 0.004). Splitting the birds into social groups reduced the sample sizes to a level where it was not possible to control for social status and varying vegetation height/snow at the same time. Peck rates did not change significantly with time of day  $(F_{2,120} = 2.87, \text{ n.s.})$ .

#### Abdominal profiles

Abdominal profiles changed throughout the winter and decreased during periods with continuous snow cover in most social groups (week:  $F_{16\,1054} = 14.77, P < 0.01;$ social status:  $F_{51043} = 41.76$ , P < 0.01; Fig. 4). Climate variables such as weekly mean minimum temperatures and rain/snowfall affected abdominal profile indices (social group:  $F_{51057} = 36.84$ , P < 0.01; minimum temperature (°C):  $F_{1,1053}$  = 64.92, P < 0.0001; rain/snowfall (mm):  $F_{1\,1053} = 4.54$ , P < 0.05), but were not significant in models including snow cover. Abdominal profiles of male and female geese changed over time (paired females  $F_{16,126} = 2.12$ , P < 0.01, paired males  $F_{16,197} = 9.29$ , P < 0.01, parental females  $F_{16\,112} = 3.1, P < 0.01$ , parental

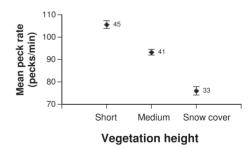
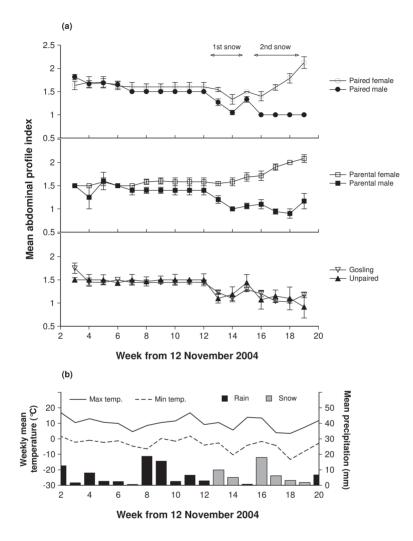


Figure 3. Mean peck rates in short and medium-length vegetation and in snow. Geese pecked most slowly in the snow. Sample sizes indicate the number of recorded peck rates.



**Figure 4.** Changes in the abdominal profile scores recorded for Greylag geese in relation to winter weather conditions. (a) Abdominal profile indices for geese of different social status during the winter (12 November 2004 – 09 March 2005). Sample sizes (*n*) for each week in consecutive order (week 3 - 19): paired females (15, 5, 5, 8, 5, 10, 10, 5, 5, 5, 11, 6, 10, 5, 11, 7, 4), paired males (19, 12, 8, 10, 12, 15, 15, 10, 6, 12, 13, 10, 15, 10, 16, 7, 8), parental females (3, 2, 6, 2, 6, 12, 10, 6, 6, 6, 11, 6, 8, 7, 10, 6, 6), parental males (3, 2, 5, 2, 5, 10, 10, 5, 5, 5, 10, 5, 8, 5, 9, 5, 3), goslings (6, 10, 18, 10, 18, 36, 36, 18, 19, 18, 37, 20, 29, 15, 35, 19, 17), unpaired geese (22, 11, 7, 8, 11, 14, 13, 9, 5, 10, 10, 8, 8, 7, 10, 5, 6). (b) Weather data recorded during the winter. With the beginning of snowfall in week 13, simultaneous loss of weight in most geese became apparent.

males  $F_{16.96} = 2.98$ , P < 0.01) and between sexes (female versus male paired geese  $F_{1,324}$ = 34.58, P < 0.01, female versus male parents  $F_{1,209} = 78.1$ , P < 0.01). From weeks 2 - 12 there was no snow cover and temperatures were higher than in weeks 13 - 19 (Fig. 4b). During this early part of the winter, abdominal profiles remained constant apart from some fluctuations in weeks 3 - 4 (Fig. 4a). With the beginning of snowfall in week 13 (24 January 2005) a simultaneous decline of abdominal profiles became apparent in most geese (Fig. 4a,b), except for females in family groups which gained weight throughout the winter. With higher temperatures in week 15, the snow melted and the geese became fatter for a short time. In the second snow period, from week 16 onwards, again a decline of abdominal profiles was observed in paired males (with and without young), goslings and unpaired geese (Fig. 4a,b). However, parental females and paired females gained weight steadily during that period at the end of winter.

## Discussion

Three different methods were used to show that resident Greylag Geese in Stuttgart changed their behaviour and feeding habits in response to a continuous snow cover. The geese spent less time feeding and probably obtained less energy on days with snow due to the lack of food. Their food intake (measured as peck rates) was lower and their fat reserves (measured from their abdominal profiles) also diminished in snow conditions.

The changes of diurnal patterns in feeding and loafing on days with snow compared to days without snow may reflect

a behavioural adaptation. In snow, a feeding peak was reached around midday when the sun was at the zenith and temperatures were highest. Snow became softer during this time of day, making it easier for the geese to reach food plants. Most individuals loafed during the very cold morning and evening hours when the snow cover was frozen. During these hours, searching for food probably required a great deal of energy and was thus not profitable. On days without snow the diurnal pattern of feeding and loafing was similar to that of wild Greylag Geese wintering in south western Spain (Amat 1986) and wild White-fronted Geese wintering at Slimbridge, England (Owen 1972). In both of these studies, feeding and loafing activity were inversely correlated. Feeding activity was highest during the morning and evening hours, while the peak of loafing activity was reached around midday when the guts presumably were full and the geese were digesting vegetation taken during the morning. In winter, the digestibility (%) and metabolic energy (kJ/g)of food plants are lower than in other seasons, usually resulting in an increase in the time geese spend feeding to cover daily energy requirements (Prop & Vulink 1992). However, in our study the proportion of time that the Greylag Geese spent feeding decreased in snow. This is surprising as, especially in the cold season and with short day lengths, it is important for wild geese to feed as much as possible to build up body fat reserves. Apparently this was not possible for the resident geese when plants were covered by snow and thus not easily available. Fat deposition is strongly correlated with food availability and this in turn depends on weather conditions and season, such as the breeding season and during migration (Owen 1981). Since the geese in Stuttgart are residents, they need fat reserves primarily for the following breeding season and not, so far, for migratory flight.

Due to icy temperatures and continuing snowfall from the end of January onwards, food became scarce and the geese used their body fat reserves resulting in a visible loss of weight. Thawing at the beginning of February improved food availability briefly, causing an immediate accumulation of fat. Abdominal profiles dropped again with renewed snowfall. Such a rapid change in abdominal profile has also been shown in other studies (Zillich & Black 2002). The increase in abdominal profile of parental females throughout the winter and of paired females in the second snow period may have been due to the approaching breeding season, though it is not clear how they achieved this increase given their lower food intake in snowy conditions. Fattening prior to migration or before the breeding season is also known in Barnacle Geese Branta leucopsis (Owen 1981) and Hawaiian Geese Branta sandvicensis (Zillich & Black 2002). Paired males in family groups could not accumulate fat reserves in late winter, probably because they spent much energy defending the feeding space around their partner (Owen 1981). Unpaired birds, being at the bottom of the pecking order (Black & Owen 1989), also were unable to accumulate fat reserves. A similar variation in abdominal profile in relation to social class was found in Bewick's Swans (Bowler 1994).

Peck rates of all geese were lower when

snow cover limited food availability. These results fit well with the observed weight losses. Geese are selective in choosing their food plants and prefer those which are highest in proteins and nutrients (Owen 1976, Prop & Deerenberg 1991, Gadallah & Jefferies 1995, Bos *et al.* 2005). However, snow cover prevented the birds from finding food visually. To reach vegetation they dug holes into the snow with their bills. Despite this effort, the type and number of available plant species remained limited and geese had difficulties grazing on the frozen vegetation (Käßmann 2005).

After being "trapped" in the snow it may not be possible energetically for the Greylag Geese to leave the area in search of snowfree feeding sites, particularly if they wait too long for the thaw. Alternatively, it may not be necessary. The severe winter conditions did not cause mortality, but could have had indirect effects on the fitness of each individual. Further studies on the effect of body condition at the end of winter on the birds' subsequent breeding success are needed to clarify this issue.

## Acknowledgements

We are most grateful to Prof. Dr. J. Steidle (Universität Hohenheim) for supervising this study, to Prof. Dr. C. König, M. Grabert and I. Heynen (Staatliches Museum für Naturkunde Stuttgart) for their support throughout and to Jnr. Prof. Dr. C. Randler and his students (Pädagogische Hochschule Ludwigsburg) for their help in catching the moulting geese. We thank Baz Hughes from the Wildfowl & Wetlands Trust for comments on earlier drafts of the manuscript. All necessary permits to carry out this research were obtained by the German authorities.

#### References

- Amat, J.A. 1986. Numerical trends, habitat use and activity of Greylag Geese wintering in southwestern Spain. *Wildfowl* 37: 35–45.
- Baker, H. & Coleman, D. 2004. Status of the Canada Goose, the Greylag Goose and other naturalised geese in Greater London. *London Bird Report* 65: 199–205.
- Ballasus, H. 2005. Habitatwahl und -präferenz der Bless- und Saatgans Anser albifrons, A. fabalis am Unteren Niederrhein – Historische Veränderungen und mögliche Ursachen. Vogelwarte 43: 123–131.
- Black, J.M. & Owen, M. 1989. Agonistic behaviour in barnacle goose flocks: assessment, investment and reproductive success. *Animal Behaviour* 37: 199–209.
- Black, J.M., Deerenberg, C. & Owen, M. 1991. Foraging behaviour and site selection of Barnacle Geese *Branta leucopsis* in a traditional and newly colonised spring staging habitat. *Ardea* 79: 349–358.
- Bos, D., Drent, R.H., Rubinigg, M. & Stahl, J. 2005. The relative importance of food biomass and quality for patch and habitat choice in Brent Geese *Branta bernicla*. Ardea 93: 5–16.
- Bowler, J.M. 1994. The condition of Bewick's Swans *Cygnus columbianus bewickii* in winter as assessed by their abdominal profiles. *Ardea* 82: 241–248.
- Carboneras, C. 1992. Greylag Goose Anser anser. In J. del Hoyo, A. Elliott & J. Sargatal (eds.), Handbook of the Birds of the World. Vol. 1. Ostrich to Ducks, Plate 41. Lynx Edicions, Barcelona.
- Cramp, S. & Simmons, C.M. (eds.) 1977. Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palaearctic. Vol. I. Ostrich to Ducks. Oxford University Press, Oxford.

- Crawley, M.J. 1993. *GLIM for Ecologists*. Blackwell Scientific Publications, Oxford.
- Drent, R.H. & Prins, H.H.Th. 1987. The herbivore as a prisoner of its food supply. In J. Van Andel, J.P. Bakker & R.W. Snaydon (eds.), Disturbance in grasslands – causes, effects and processes, pp. 131–148. Dr. W. Junk Publishers, Dordrecht, Boston, Lancaster.
- Ebbinge, B., Canters, K. & Drent, R. 1975. Foraging routines and estimated daily food intake in Barnacle Geese wintering in the northern Netherlands. *Wildfowl* 26: 5–19.
- Gadallah, F.L. & Jefferies, R.L. 1995. Comparison of the nutrient contents of the principal forage plants utilized by Lesser Snow Geese on summer breeding grounds. *Journal of Applied Ecology* 32: 263–275.
- Inglis, I.R. 1977. The breeding behaviour of the Pink-Footed Goose: behavioural correlates of nesting success. *Animal Behaviour* 25: 747–764.
- Kampp, K. & Preuss, N.O. 2005. The Greylag Geese of Utterslev Mose. *Dansk Ornitologisk Forenings Tidsskrift* 99(1): 1–78.
- Käßmann, S. 2005. Winterökologie der Graugans Anser anser in Stuttgart: Verteilungsmuster und Habitatnutzung im Winter 2004/05. Diploma thesis, University of Hohenheim, Stuttgart.
- Kreutzkamp, I. 2003. Die Entwicklung der Brutpopulationen von Graugans (Anser anser), Kanadagans (Branta canadensis) und Nilgans (Alopochen aegyptiacus) im Hamburger Berichtsgebiet von 1990 bis 2002. Hamburger Avifaunistische Beiträge 32: 153–186.
- Madsen, J., Cracknell, G. & Fox, T. 1999. Goose Populations of the Western Palaearctic. A review of status and distribution. Publ. No. 48, Wetlands International, Wageningen, The Netherlands, and National Environmental Research Institute, Rønde, Denmark.

Winter ecology of feral Greylag Geese 39

- Martin, P. & Bateson, P. 1986. *Measuring behaviour: an introductory guide*. Cambridge University Press, Cambridge.
- NAG 1993. The GLIM system: generalised linear interactive modelling. B. Francis, M. Green, M. & C. Payne (eds.). Clarendon Press, Oxford.
- Owen, M. 1972. Some factors affecting food intake and selection in White-Fronted Geese. *Journal of Animal Ecology* 41: 79–92.
- Owen, M. 1976. The selection of winter food by White-fronted Geese. *Journal of Applied Ecology* 13: 715–729.
- Owen, M. 1981. Abdominal profile a condition index for wild geese in the field. *Journal of Wildlife Management* 45: 227–230.
- Prop, J. & Deerenberg, C. 1991. Spring staging in Brent geese *Branta bernicla*: feeding constraints and the impact of diet on the accumulation of body reserves. *Oecologia* 87: 19–28.

- Prop, J. & Vulink, T. 1992. Digestion by Barnacle Geese in the annual cycle: the interplay between retention time and food quality. *Functional Ecology* 6: 180–189.
- Ryan, B.F., Joiner, B.L. & Cryer, J.D. 2005. *Minitab*® *Handbook. 5th Edition*. Duxbury Press, University of Iowa, Iowa.
- Wiersma, P. & Piersma, T. 1995. Scoring abdominal profiles to characterize migratory cohorts of shorebirds: an example with Red Knots. *Journal of Field Ornithology* 66: 88–98.
- Zillich, U. & Black, J. 2002. Body mass and abdominal profile index in captive Hawaiian Geese. *Wildfowl* 53: 67–77.