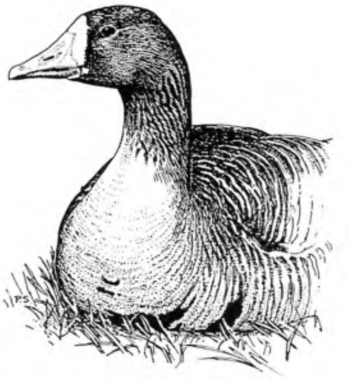
Behaviour and energy budget of wintering geese in the Lower Rhine area of North Rhine-Westphalia, Germany



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The most important activity of wintering geese in the Lower Rhine area is feeding, which accounts for approximately 55% of a 24-hour day. Almost 40% of this feeding takes place at night. Sleeping occupies about 30% of a 24-hour day, more than 80% of which takes place during the hours of darkness distributed among 4-5 sleeping bouts of 1-1¼ hours each. The remainder is spent drinking/preening (about 8%) and in bouts of alertness, social behaviour and flying (about 2% each).

The average flight distance of the geese between roosts, roost and feeding site and between feeding sites is 5.1 km, the average flight velocity is 43.8 km/h.

A White-fronted Goose (mean weight 2.4 kg) requires about 1500 g fresh weight (300 g dry matter) and a Bean Goose (mean weight 3.5 kg) about 1950 g fresh weight (390 g dry matter) of grass daily respectively. A gooseday (gd) is therefore a variable quantity, depending on the species. The feeding intensity measured in goosedays per hectare (gd/ha) only has validity for a specific goose species.

The disturbance of geese promotes activities with a high energy consumption and reduces all activities that save energy. In addition every disturbance prevents food intake and thereby energy intake and fat deposit accumulation. Nocturnal feeding and roosting on land are common for the geese of the Lower Rhine area and maybe are also more common for geese feeding mainly on grassy vegetation at other wintering sites than has been assumed. Both phenomena can be explained by the high energy costs of roosting on cold water during the night (about 1000 kJ, i.e. almost 25 g of body fat).

The Lower Rhine (Unterer Niederrhein) is the biggest Ramsar site in North Rhine-Westphalia (Fig. 1) and a traditional goose wintering area. Besides old farm names, such as "Gansward" and Gänseward", or fields, like "Gänsekuhl" and "Gänsespeck", there are several references in the older literature (Hartert 1887, Le Roi 1906, Le Roi & Geyr von Schweppenburg 1912) which indicate that the Lower Rhine has been a wintering area for the tundra race of the Bean Goose *Anser fabalis rossicus* since the 19th century. Neubaur (1957) stated that the wintering population of the Lower Rhine, numbering about 1000 Bean Geese during the 1950s, was smaller than it had been previously. White-fronted Geese *Anser albifrons albifrons* were only seen irregularly and in very small numbers. At the beginning of the 1960s, a gradual increase in Bean Goose numbers began, continuing to the winter of 1978-79 when a peak of about 20,000 individuals was reached. In the next two winters, the peak was 40,000 to 50,000 birds, and numbers have decreased since then.

Since the beginning of the 1960s, an appreciable number of White-fronted Geese have wintered in the Lower Rhine area. Their numbers rose slowly to about 3000 individuals (winter 1973-74) and then stabilised for some years (winter 1973-74 to 1977-78). In the following four winters, there was a rapid increase to about 20,000 geese (winter 1978-79 to 1981-82), followed by a period of explosive growth to almost 140,000 individuals in the winter of 1987-88. To date, there are some signs that this rate of increase is slowing down (Fig. 2, Mooij 1982a, 1991, 1992).

The enormous increase in goose numbers brought many complaints from the farmers of the region and, since the early 1970s, claims for financial compensation as

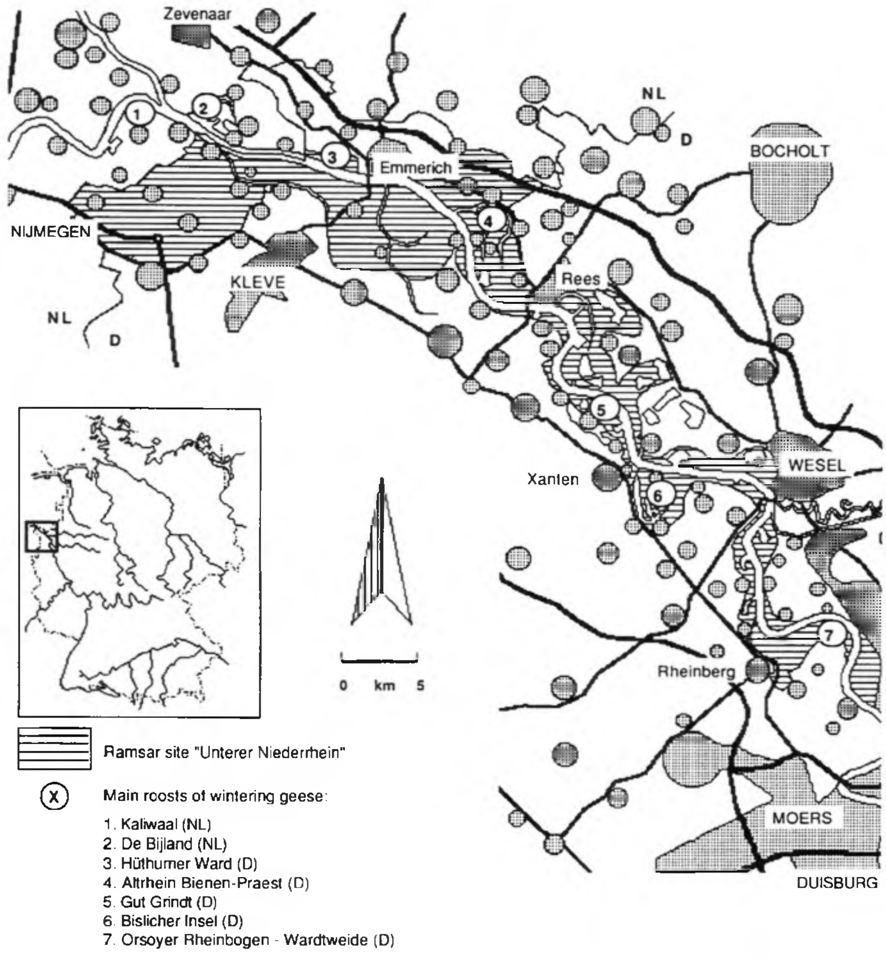

Figure 1. Ramsar site "Unterer Niederrhein" (Lower Rhine) in North Rhine-Westphalia (D) with main roosts of wintering geese.

well as requests to reopen goose hunting have been made. These developments made it necessary to start a programme to investigate goose feeding ecology, to attempt to assess goose damage and to develop management schemes for these refuging birds.

Before we can investigate the problem of goose damage and develop management schemes, it is important to know how much energy a goose needs, how it uses this energy and how much food must be consumed daily to sustain energy expenditure.

Methods

For 40 days (14 in December, 10 in January, eight in February and eight in March) a total of 14,552 wild geese (in 64 flocks) was observed for a total of 440 hours on their feeding sites from the moment they arrived until they flew off spontaneously. Data from White-fronted and Bean Geese were recorded separately. To minimize the influence of disturbance on the behaviour of the geese only those groups were observed that were feeding at a distance of more than 350 m from a source of disturbance (see Mooij 1982b). At half-hourly intervals, the activities of these birds were recorded to following categories: feeding (standing or sitting), sleeping (standing or sitting), drinking/preening, alertness, flying and social behaviour (i.e. greeting, threatening etc.). The period between these observations of group activities was used to observe single geese in these flocks for a longer period. All their activities as well as the production of droppings were recorded in a time table. All field observations were made with the help of binoculars (9x63) and a telescope (20-60x70).

The results of all these observations were compared with the results of about 300 hours of observation of eight captured geese (two pairs Bean and two pairs White-fronted Geese) feeding on pasture.

of droppings per heap as well as recording the positions of these heaps on the roost after the geese left for the feeding sites.

In order to obtain information about behaviour of the geese during flight within the wintering site (flying speed, flight distance, flight time etc.) almost two million geese in more than 8000 flights were followed and observed during flight (morning flights, drink flights and evening flights). The speed of flying goose flocks was measured by means of speedometer and by recording the flight time of known distances. Flights as a result of disturbance were not used for this part of the study.

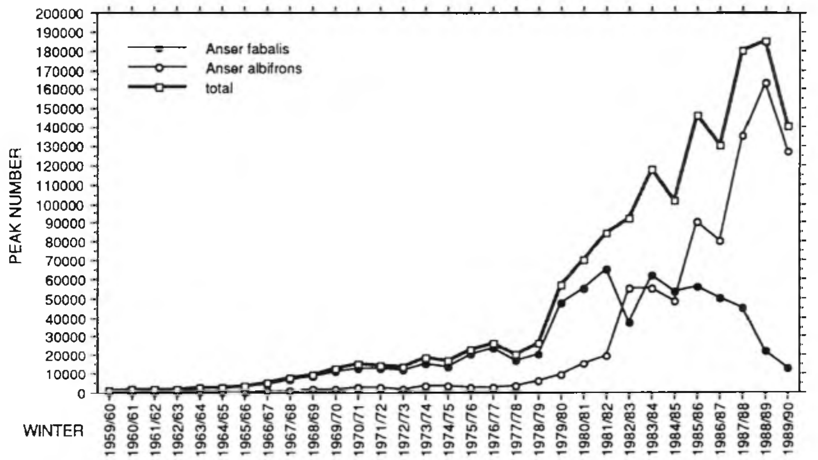

Figure 2. Peak numbers of Bean and White-fronted Geese in the Lower Rhine area from winter 1959/60 to 1989/90.

For 20 nights the geese were observed on their roost. The nights were selected at random and covered both moonlit and moonless, cloudless and cloudy nights. Although it was difficult to see all activities during the night - especially on cloudy and moonless nights - (there was no light-intensifier available and all field observations were made with the help of binoculars (9x63)), it was possible to record night-time activities. A total of 4522 geese (depending on the light conditions about 100-280 birds per night) out of sleeping groups of several thousands was observed for a total of 320 hours. It was noted at half-hourly intervals how the activities of the birds were distributed over following categories: feeding (standing or sitting), sleeping (standing or sitting), drinking/preening, alertness, flying and social behaviour (i.e. greeting, threatening etc.). Besides optical observations of geese in the direct neighbourhood of the observer information was gained by acoustic observations and by counting the number

Results

Roost sites

All the roosts of the Lower Rhine goose wintering site are close to water, although no geese were found sleeping on water. Two of the seven roosts are situated on the banks of a former gravel pit, all the others and their alternatives lie on the banks of the River Rhine and its old river arms. Without exception, roosts are open grasslands, hard to reach by man and seldom disturbed.

After leaving their feeding site in the evening, the geese did not fly directly to the roost, but flew first to drink and bathe on the Rhine, one of its old river arms or, more seldom, on gravel pits.

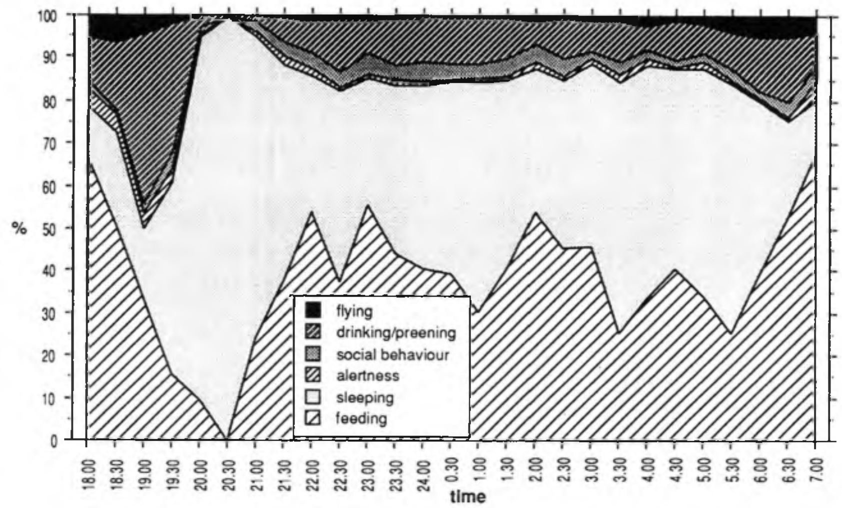

Figure 3. Night-time activities of geese on the roosts of their wintering site at the Lower Rhine.

Roost activities

After the birds land, they commence drinking and bathing (Fig. 3), with much associated calling, family social interaction and aggression. After 10-30 minutes most of the geese swim to the shallow edge of the water and start preening. This activity, in the course of which the feathers are cleaned, combed and oiled, takes 10-20 minutes. After this time the birds walk up the bank to find a place to sleep. If this bathing-drinking place is at a greater distance from the roost the birds fly to their roost.

If the geese are not disturbed, at the latest ½ - ¾ hour after the arrival of the majority of the geese on the roost, everything is quiet. Most of the birds sleep sitting on the ground, bill between the feathers of the back, feet hidden between the feathers of the belly. Some birds sleep standing on one leg.

By acoustic and optical observation it was found that the first resting phase of a night took 1½ - 2 hours. During this period almost all geese slept and the silence on the roost was only occasionally disturbed by the sounds of birds that arrived later (Fig. 3).

During the night geese continue to produce droppings which, when the birds stay on one spot (e.g. sleeping on land or ice) are produced in a heap. As the droppings are produced at regular intervals (see later) the average number of droppings per heap is used as a unit of measurement for the time the geese sleep or rest on one spot.

At six roosts of the geese wintering at the Lower Rhine the number of droppings per heap was counted in 543 heaps. The average number of goose droppings per heap is 9.43 (Fig. 4). More than 55% of the heaps contained 2-7 droppings. A mixed group of captured geese (four White-fronted and four Bean Geese) produced 2246 droppings during six nights of 11.5 hours each, i.e. each member of this group produced 46.8 droppings per night, thus producing one dropping every 15 minutes.

During 417 daily and nightly hours these captured geese produced 22,763 droppings, i.e. 2845 droppings per goose or 164 droppings per goose per day. This means that each goose produced 6.8 droppings per hour or one dropping every 8-9 minutes.

From the observation of 16 grazing geese on the feeding site for 39 hours it was calculated that these birds had an average production of 10.7 droppings per hour and goose, i.e. one dropping every 5-6 minutes. This would mean a daily production of almost 260 per goose.

With the help of these values for the daily dropping production and the average number of droppings per heap, it can be stated that the geese rest 1-2½ hours, i.e. an average of 1½ hours on one spot.

After this first quiet sleeping period some geese started feeding again, at the begin-

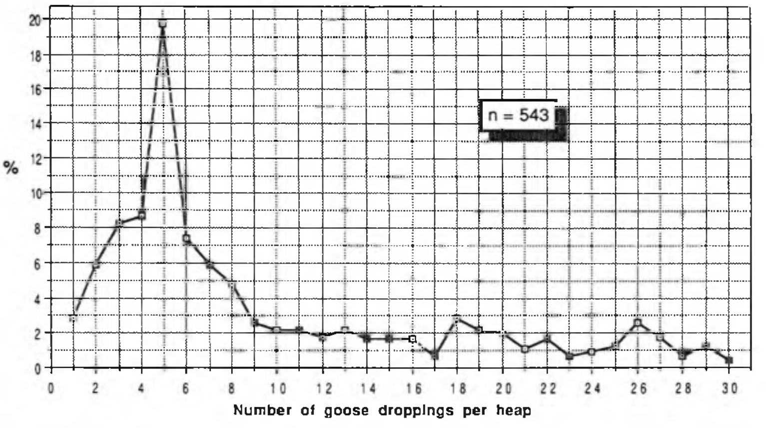

Figure 4. Number of goose droppings per heap on the roosts of the goose wintering site at the Lower Rhine.

ning in a lying position, but after a short time walking between their (still) sleeping companions. Some birds started calling softly and gradually more and more geese joined in. Some geese walked to the water to bathe and drink, but most of the birds started feeding again. Now and then there were aggressive interactions, perhaps because sleeping geese were disturbed by feeding birds.

During the night 4-5 sleeping phases alternated with feeding periods (Fig. 3). With the exception of the first sleeping phase there were always noises of active geese to be heard. Only the first sleeping phase seems to coincide for all geese of a roost, during the others there are always some geese sleeping while others are active. Some nights the noises of active geese were so loud the whole time that it was impossible to decide if the majority of the geese had a sleeping or a feeding phase without optical observations.

Roost activity budget

Based on the half hourly observations of goose behaviour on the roost (Fig. 3), it was calculated that the geese use their time as follows:

The average time that the geese are on the roost is about 13½ hours, used for (rounded off to ¼ hour):

- SLEEPING (44.3%)	6 hours
- FEEDING (38.7%)	5¼ hours
- DRINKING/PREENING (10.6%)	1½ hours
- SOCIAL BEHAVIOUR (2.8%)	¼ hours
- FLYING (2.0%)	¼ hours
- ALERTNESS (1.6%)	¼ hours
TOTAL	13½ hours

Assuming these six hours of sleep are distributed among 4-5 sleeping phases, this means that one sleeping phase takes 1-1½ hours.

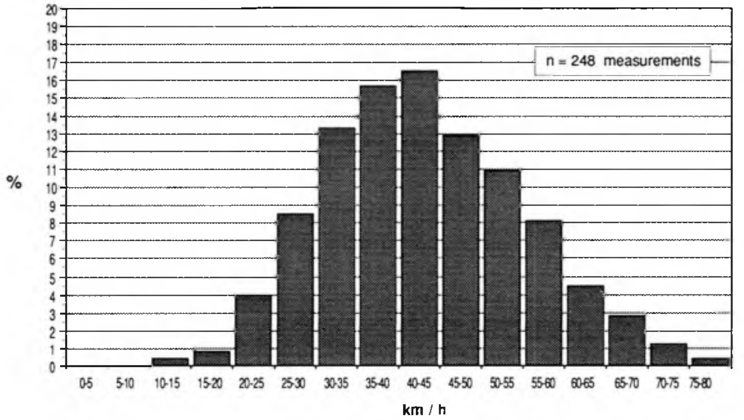

Figure 5. Velocity of flying goose flocks in the goose wintering site at the Lower Rhine.

Flight speed

The goose flocks flew with a velocity of 10-80 km/h over the Lower Rhine wintering site (Fig. 5). About one third of the flights had a velocity between 35 and 45 km/h and more than half of all registered flocks flew with a velocity between 30 and 50 km/h. The average flight velocity of all flocks was 43.8 km/h (n = 248 flocks).

Table 1. Distance between main roosts and feeding sites at the goose wintering site of the Lower Rhine area.

Roost	Distance between main roost and feeding site	
	Range	Average
Kaliwaal De Bijland Hüthumer Ward	0-20 km	7.2 km
Altrhein Bienen-Praest	0- 8 km	3.1 km
Gut Grindt	0- 7 km	3.2 km
Bislicher Insel	0- 4 km	1.5 km
Orsoyer Rheinbogen-Wardtweide	0- 5 km	2.8 km
Average distance between roost and feeding site		5.1 km

Flight distance

The geese of the Lower Rhine area usually flew short distances between roost and feeding site (Table 1). More than a quarter of all flights were shorter than two kilometers and about half of all flights shorter than five kilometers. Less than 5% of the flights were longer than 10 km. The average flight distance was 5.1 km (n = 63.457 flocks).

This means that an average flight between roost and feeding site takes about seven minutes.

Feeding site activities

With the exception of the time they spend on the roost and in the air the geese are to be found on the feeding site. This means that they spend an average of 9 hours 30 minutes in November, 8 hours 45 minutes in December, 9 hours 30 minutes in January, 10 hours 30 minutes in February and 12 hours in March on the feeding site. There were no differences in behaviour between White-fronted and Bean Geese, except for the selection of feeding site (Mooij 1992).

Every winter both goose species spend an average of 10 hours 30 minutes a day on the feeding sites. The number of feeding geese declines during the day and reaches its lowest level between 12.00 and 14.00 h

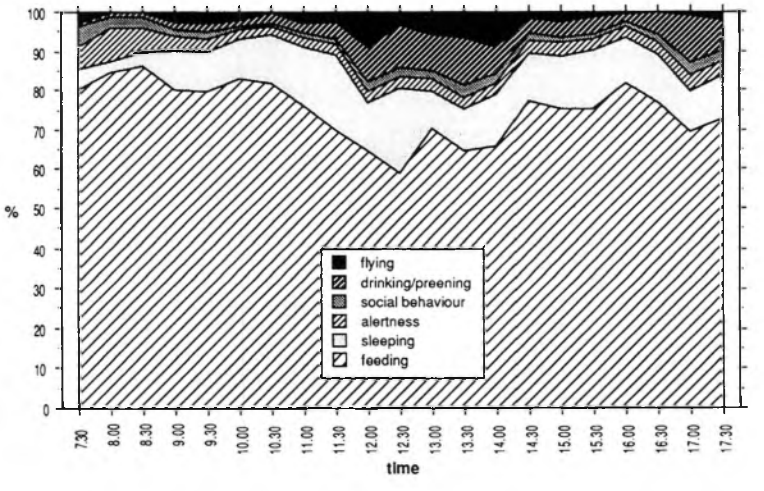

Figure 6. Day-time activities of geese on the roosts of their wintering site at the Lower Rhine.

(Fig. 6). In this period most of the geese make a drinking flight.

The geese of the Lower Rhine wintering site sleep almost 30% of the day: 82.2% of these sleeping hours are during darkness and 17.2% during daylight (Table 2). The sleeping phases on the feeding site lasted 10-65 minutes with an average of 15.7 minutes (n = 127 geese). This means that the geese need 4-5 sleeping phases on the feeding site to reach a total of 75 minutes,

Feeding site activity budget

This average period of 10½ hours the geese spend on the feeding site, are used as follows (rounded off to ¼ hour):

- FEEDING (75.0%)	8 hours
- SLEEPING (11.5%)	1¼ hours
- DRINKING/PREENING (5.1%)	½ hours
- ALERTNESS (3.5%)	¼ hours
- SOCIAL BEHAVIOUR (2.7%)	¼ hours
- FLYING (2.2%)	¼ hours
TOTAL	10½ hours

Table 2 shows that the most important activity of the geese on the roost is sleeping and on the feeding site is grazing. At the same time it becomes clear that of all activities feeding is the most important and takes 13 hours and 15 minutes daily of which 60% takes place on the feeding site and 40% on the roost.

Dropping production as an indicator of daily consumption

Captured geese produced an average of 46.8 droppings per goose and night of 11.5 hours, i.e. one dropping every 15 minutes, i.e. 4 droppings/hour. During 417 daily and nightly hours these captured geese produced 164 droppings per goose and day, i.e. one dropping every 8-9 minutes or 6.8 droppings/hour. During 75 nightly hours these birds were mainly resting and produced 4 droppings/hour, during 342 daylight hours being active 7.5 droppings/hour. From these data it becomes clear that geese produce more droppings during the time they are active than during times of rest, as was also found by Owen (1972) and Rutschke (1983).

From the observation of free-living geese on the feeding site it was calculated that these birds had an average production of 10.7 droppings per hour and goose, i.e. one dropping every 5-6 minutes. Drent *et al.* (1978) stated that the food consumption of captured geese is about 75% of that of free-living birds. This would mean that (assuming dropping weight being constant) the dropping production of captured birds would also be about 75% of free-living ones. It follows that free-living geese do not produce an average of 46.8 but of about 62 droppings per night of 11.5 hours (5.4 droppings per hour and goose) and not 164 droppings per 24 hours but about 219 droppings per day (9.1 droppings per hour and goose).

During 24 hours, the geese of the Lower Rhine area slept for 7¼ hours and were active for the remaining 16¾ hours (mainly feeding).

During the active phase of the day the free-living geese of the Lower Rhine area produced 10.7 droppings per hour and goose. This means for the active time of the day:

- 10.7 droppings/h x 16.75 hours = 10.7 droppings/h x 1005 minutes = 1 dropping every 5.6 minutes and about 180 droppings altogether.

During the inactive phase of the day wild geese produce 5.4 droppings per hour and goose. This means for the inactive time of the day:

Table 2. Average time spent during a 24-hour period by the geese of the Lower Rhine wintering site on their main activities. (All data are rounded off to ¼ hour.)

	Place of activity		
Kind of activity	Feeding site	Roost	Total
Feeding	8 hours (33.3%)	5¼ hours (21.9%)	13¼ hours
Sleeping	1¼ hours (5.2%)	6 hours (25.0%)	7¼ hours
Alertness	¼ hours (1.1%)	¼ hours (1.0%)	½ hours
Social behaviour	¼ hours (1.1%)	¼ hours (1.0%)	½ hours
Drinking/preening	½ hours (2.1%)	1½ hours (6.3%)	2 hours
Flying	¼ hours (1.0%)	¼ hours (1.0%)	½ hours
Total	10½ hours (43.8%)	13½ hours (56.2%)	24 hours

- 5.4 droppings/h x 7.25 hours = 5.4 droppings/h x 435 minutes = 1 dropping every 11.1 minutes and about 40 droppings altogether.

Thus these free-living Lower Rhine geese (mixed groups of White-fronted and Bean Geese) produce about 220 droppings in 24 hours.

This value corresponds closely to the corrected value of the caged geese and the data of Rutschke (1983), who found an average daily dropping production of 230 droppings for the Bean Goose. Given that Bean Geese produce 230 droppings per day and that in the Lower Rhine area we found an average dropping production of 220 droppings for mixed groups of White-fronted and Bean Geese, this means that White-fronted Geese have a daily production of 200-210 droppings.

Having arrived at a reliable value for the daily dropping production, we can now make a first assumption of the daily consumption of free-living geese.

A dropping of a White-fronted Goose has an average dry weight of 0.87 g (Kear 1963, Kear in Atkinson-Willes 1963) and of a Bean Goose of 1.0 g (Rutschke 1983). Based on these data it can be calculated that the daily faecal production of a White-fronted Goose is about 180 g and of a Bean Goose is about 230 g dry weight. By a mean digestive efficiency of 30% (Owen 1972, Ebbinge *et al.* 1975, Drent *et al.* 1978, Vorobeva 1982) and a dry matter percentage of the grass of 19-20% (Kear in Atkinson-Willes 1963) this would mean a daily food intake for a White-fronted Goose of about 257 g dry and 1300 g fresh weight and for a Bean Goose of about 330 g dry and 1700 g fresh weight.

In the next section these approximations for the daily food intake of free-living geese will be compared with estimates made on the basis of energetic calculations and values found by other workers.

Daily energy expenditure

White-fronted geese have a mean body weight of 2.4 kg and Bean Geese of 3.5 kg (Bauer & Glutz 1968, Cramp & Simmons 1977). Because of the mixture of these species in the Lower Rhine area, it is tenable in this region to assume a mean body weight of wintering geese of about 3 kg.

Based on the data of Drent *et al.* (1978) and Rutschke (1983) a goose with a body weight of 3 kg needs about 830 kJ per day to maintain its basal metabolism (Basal metabolic rate = BMR) and 2.5-2.6 x BMR to live and be active, i.e. a goose of 3 kg has a daily energy requirement (Daily Energy Expenditure = DEE) of 2000-2200 kJ/day.

With the help of the metabolic weight (body weight $kg^{.75}$) it is possible to estimate the DEE of other goose species:

- *Branta bernicla*, body weight 1350 kg, 55.1% of 2100kJ/day is 1160 kJ/day,
- *Anser erythropus*, body weight 1500 kg, 59.5% of 2100 kJ/day is 1250 kJ/day,
- *Branta leucopsis*, body weight 1900 kg, 71.0% of 2100 kJ/day is 1500 kJ/day,
- *Anser albifrons*, body weight 2300-2400 kg, 82.0-84.7% of 2100 kJ/day is 1750 kJ/day,
- *Anser caerulescens*, body weight 2600 kg, 89.9% of 2100 kJ/day is 1890 kJ/day,
- *Anser fabalis*, body weight 3500 kg, 112.3% of 2100 kJ/day is 2360 kJ/day.

These data were put together in a graph (Fig. 7) and show a clear correlation:

$\mathbf{y} = 5.4\,\mathbf{x}^{0.745}$ or $\ln \mathbf{y} = \ln 5.4 + 0.745 \ln \mathbf{x}$ (1)

Based on this formula we can calculate the following general values:
- a goose of 1 kg body weight has a DEE of about 0.93 kJ/g & day,
- a goose of 2 kg body weight has a DEE of about 0.78 kJ/g & day,
- a goose of 3 kg body weight has a DEE of about 0.70 kJ/g & day,
- a goose of 4 kg body weight has a DEE of about 0.65 kJ/g & day.

According to Owen (1972) the grass that is grazed by the geese has an energy content of 17.7 kJ/g dry matter. Assuming the geese can utilize all the energy included in the food they consume, they would need a daily intake of about 120 g dry matter of grass in order to cover their energy requirements of 2100 kJ/day. With a portion of about 20% dry matter this means about 600 g fresh weight. Taking into account the quality of grass in winter and the digestibility of grass in winter and the digestibility of grass for geese as discussed by Drent *et al.* (1978), Ebbinge *et al.* (1975), Owen (1972) and Vorobeva (1982), it is realistic to say that the geese can only digest about 30% of the food they consume in winter. This means that they have to take up more than three times the amount of grass that was previously calculated. Thus the daily food requirement of a mean goose in the Lower Rhine area is about 2000 g fresh weight or 400 g dry matter of grass. A mean White-fronted Goose weights 2400 g (metabolic weight 1930 g, i.e. 85% of 2280 g) and needs 85% of 2000 g, which is about 1700 g fresh weight or 340 g dry matter of grass daily. A mean Bean Goose of 3500 g (metabolic weight 2560 g, i.e. 112% of 2280 g) needs 112% of 2000 g, i.e. about 2240 g fresh weight or 450 g dry matter of grass daily.

After these theoretical reflections we will compare the above approximations with the estimates of other authors.

Owen (1972) found for the DEE of White-fronted Geese at Slimbridge (body weight 2300 g) a value of 1365 kJ/day, using a value of the BMR of 525 kJ calculated by Lachlan. Compared to the BMR found by Rutschke (1983) this value is substanially too low. If we replace the value of the BMR of Lachlan by the BMR-value calculated by Rutschke, the DEE of Owen (1972) for the White-fronted Goose is 1725 kJ/day instead of 1365 kJ/day. Rutschke (1983) calculated 2400 kJ/day for the Bean Goose and 1700 kJ/day for the White-fronted Goose.

Several authors calculated the DEE of other goose species. For a Snow Goose *Anser caerulescens*, with an average weight of about 2.6 kg (Cramp & Simmons 1977), Frederick & Klaas (1982, in Frederick *et al.* 1987) calculated a DEE of about 1760 kJ/day and Bedard & Gauthier (1989) a mean value of 1690 kJ/day. All these values are very well comparable with the estimates found above. Dijkstra & Ebbinge (in Drent *et al.* 1978) calculated 842 kJ/day for a Brent Goose *Branta bernicla* (mean body weight 1350 g), Vorobeva (1982) 900 kJ/day for a Lesser White-fronted Goose *Anser erythropus* (mean body weight about 1500 kg) and Ebbinge *et al.* (1975) 943 kJ day for a Barnacle Goose *Branta leucopsis* (mean body weight 1900 g). All these values are substantially lower than the estimates found in this study.

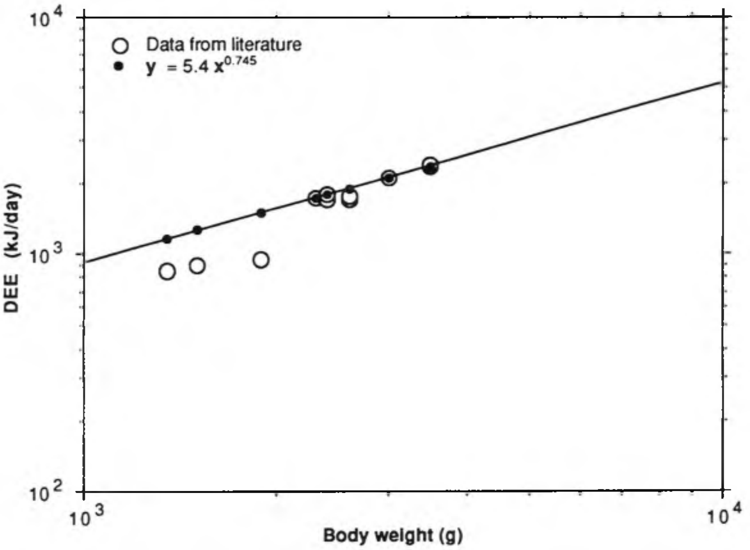

Figure 7. Relationship between body weight (g) and daily energy expenditure (= DEE, kJ/day) in geese after data of Bedard & Gauthier 1989, Drent *et al.* 1978, Ebbinge *et al.* 1975, Frederick *et al.* 1987, Owen 1972 (corrected), Rutschke 1983, Vorobeva 1982 and own data.

These data and those gathered by Drent *et al.* (1978), Ebbinge *et al.* (1975), Walsberg (1983) and Vorobeva (1982) were assembled in one graph (Fig. 8). In this way we can compare the total DEE of almost 80 bird species with a body weight of 3.2-25,200 g and these data show a clear relationship between DEE (y, in kJ/day) and body weight (x, in g) that is expressed by the following formula:

$$\mathbf{y} = 13.05\ \mathbf{x}^{0.6052} \text{ or}$$

$$\ln \mathbf{y} = \ln 13.05 + 0.6052 \ln \mathbf{x} \quad (2)$$

This formula is not new, but was already deduced by Walsberg (1983) with the help of data from 41 bird species, most of them

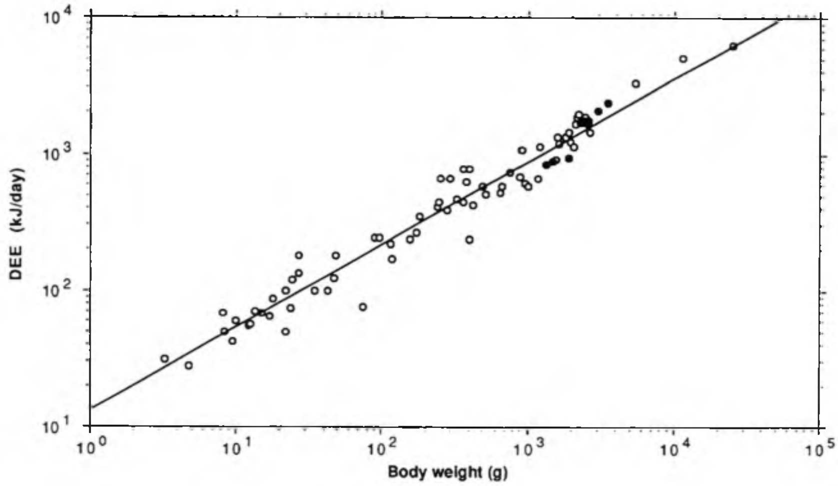

Figure 8. Relationship between body weight and daily energy expenditure (= DEE) in birds, (n = 79). Graph after data of Bedard & Gauthier 1989, Drent *et al.* 1978, Ebbinge *et al.* 1975, Frederick *et al.* 1987, Owen 1972 (corrected), Rutschke 1983, Walsberg 1983, Vorobeva 1982 and own data. (Black points: values of

with a body weight below 1000 g. This analysis shows that there seems to be a general relation between body weight and DEE for all free-living birds, although there can be considerable differences from the predicted value. These differences most likely are caused by the different conditions under which these data were gathered.

As a result of these reflections it should have become clear that a gooseday is a rather variable quantity; a gooseday of Brent Geese means the extraction of about 1 kg fresh weight of vegetation, whereas a gooseday of White-fronted Geese means the extraction of more than 1.5 kg fresh weight of vegetation. A feeding intensity of 1500 goosedays/ha of Brents have to be compared with 1000 goosedays/ha of Whitefronts.

Daily energy budget

As a result of Drent *et al.* (1978) and Rutschke (1983) we know that:

Daily Energy Expenditure (=**DEE**) =

2.55 x Basic Metabolic Rate (=**BMR**) (3)

According to several authors (for instance Bezzel 1977) there are great differences between the metabolic rate during phases of activity and phases of rest that can reach as much as 20-25%. Apart from the fact that there are no exact data about the extent of these differences in geese, it is possible that they are not very well pronounced in geese, because they have no marked day-night rhythm. Phases of activity and resting alternate in geese during day and night and it is possible that the fluctuations in metabolic rate are equally spread over 24 hours.

Therefore the possible fluctuations in the metabolic rate are not taken into consideration in the following theoretical reflections and we can state that the mean Hourly Metabolic Rate (= HMR) is theoretically 1/24 of the BMR:

$$\text{BMR} = 24 \times \text{HMR} \quad (4)$$

A combination of the formulae 3 and 4 results in:

$$\text{DEE} = 2.55\ \text{BMR} = 2.55 \times 24 \times \text{HMR} = 61.20\ \text{HMR} = 2100\ \text{kJ} \quad (5)$$

$$\text{HMR} = 2100 : 61.20 = 34.31\ \text{kJ} \quad (6)$$

Theoretically the Hourly Energy Expenditure (= HEE) is 1/24 of the DEE:

$$\text{DEE} = 24 \times \text{HEE} \quad (7)$$

This means that:

$$\text{HEE} = 2.55 \times \text{HMR} \quad (8)$$

According to Lachlan (in Owen 1972) and Bezzel (1977) the metabolic rate during flight is ten times higher than the HMR, so that for every hour of flight HEE = 10 x HMR instead of 2.55 times. When a bird sleeps the HEE is much lower than the HEE of an active bird, but because the bird has to maintain its temperature and to digest the contents of its intestines the HEE cannot return to the level of the HMR. That is why in this theoretical calculation the HEE of a sleeping bird is calculated as being 1.5 x HMR.

The following formula is based on these reflections:

$$HEE = n \text{ HMR} \quad (9)$$

in which "n" can vary between 10 (flying) and 1.5 (sleeping). The n-values for "feeding", "drinking/preening", "alertness" and "social behaviour" are expected to lie between these extremes. The mean value of "n" for a whole day of 24 hours is 2.55. In order not to complicate the theoretical calculations, it is stated that with the exception of "flying" and "sleeping" for all other activities "n" is the same.

On the basis of ethological observations (Table 2) it is known that the geese of the Lower Rhine area use 24 hours as follows:

- FEEDING	13.25 hours (55.2%)
- SLEEPING	7.25 hours (30.2%)
- DRINKING/PREENING	2.00 hours (8.3%)
- ALERTNESS	0.50 hours (2.1%)
- FLYING	0.50 hours (2.1%)
- SOCIAL BEHAVIOUR	0.50 hours (2.1%)+
TOTAL	24.00 hours

The following calculation for the daily energy budget has been made with the help of these data:

Sleeping: 7.25 x HEE =

$$\left.\begin{matrix} 7.25 \times n \times HMR \\ n = 1.5 \end{matrix}\right\} = 7.25 \times 1.5 \times HMR = 10.88 \text{ HMR}$$

Flying: 0.50 x HEE =

$$\left.\begin{matrix} 0.50 \times n \times HMR \\ n = 10.0 \end{matrix}\right\} = 0.50 \times 10.0 \times HMR = 5.00 \text{ HMR}$$

Total energy for "sleeping" and "flying": 7.75hours 15.88 HMR (10)

The combination of the formulae 5 and 10 means that for other activities, such as "sleeping" and "flying", there remain 16.25 hours and 45.32 HMR.

Other activities:

$$16.25 \times n \times HMR = 45.32 \text{ HMR}$$
$$n = 45.32 : 16.25 = 2.79$$

The daily energy budget is as follows:

- FEEDING			
13.25 x 2.79 x HMR	= 36.96 HMR	= 1268 kJ	(60.4%)
- SLEEPING			
7.25 x 1.50 x HMR	= 10.88 HMR	= 373 kJ	(17.7%)
- DRINKING/PREENING			
2.00 x 2.79 x HMR	= 5.58 HMR	= 191 kJ	(9.1%)
- ALERTNESS			
0.50 x 2.79 x HMR	= 1.39 HMR	= 48 kJ	(2.3%)
- FLYING			
0.50 x 10.00 x HMR	= 5.00 HMR	= 172 kJ	(8.2%)
- SOCIAL BEHAVIOUR			
0.50 x 2.79 x HMR	= 1.39 HMR	= 48 kJ	(2.3%)+
- TOTAL			
24.00 x 2.55 x HMR	= 61.20 HMR	= 2100 kJ	

According to Drent *et al.* (1978) caged birds consume an amount of energy 2 x BMR as so-called "Existence Metabolism". The energy that free-living birds need to survive in addition to this existence metabolism is defined as the "foraging costs", i.e. the energy expenditure that is needed for all activities at obtaining food.

In our case the foraging costs are:

$$FC = 24.00 \times (2.55-2.00) \times HMR$$
$$= 13.20 \times HMR = 453 \text{ kJ} \quad (11)$$

$$\frac{FC}{DEE} = 21.6\% \quad : \quad \frac{DEE}{FC} = 4.6$$

This means that foraging takes 21.6% of the daily energy expenditure and every kilojoule put into foraging activities brings the bird almost five times more energy. These values are much the same as those found for other bird species by Drent *et al.* (1978) and confirms Drent's thesis that in non-breeding birds foraging takes in general about 20% of the DEE.

The geese that winter in the Lower Rhine area have to collect their DEE of 2100 kJ in 13.25 hours, i.e. 158 kJ/hour. This means that they have to ingest 151 g fresh weight/hour or 30.2 g dry matter/hour of vegetation. At the wintering site in the Lower Rhine area the wintering geese have a mean pecking rate of 98.9 pecks/minute (Mooij in prep.). This means that they peck 5934 times in one hour and with every peck take up 25.4 mg fresh weight, 5.1 mg dry matter of grass, with 0.027 kJ of energy.

If we convert the hourly intake to dry matter weight (in gram) per metabolic kilogram (kg body weight to the 0.75 exponent), as practised before by Drent *et al.* (1978), we find a value of 13.2 $g/kg^{0.75}.h$.

Table 3. Hourly food intake by geese.

Species	Body-weight (g)	Food intake per hour (g/birds.hour)	($g/kg^{0.75}$hour)	Author
Branta bernicla	1350	19.9	15.9	Drent *et al.* 1978
Branta leucopsis	1900	20.4	12.6	Drent *et al.* 1978
Anser caerulescens	2950	30.9	19.9	Harwood 1975 in Drent *et al.* 78
Geese of Lower Rhine	3000	30.2	13.2	Mooij
Anser albifrons	2400	24.2	12.6	Mooij
Anser fabalis	3500	35.5	13.6	Mooij

For the White-fronted Goose it follows that they have an hourly intake of 121 g fresh weight and 24.2 g dry matter of grass, with 128 kJ. Converted to dry matter weight per metabolic kg Whitefronts have a value of 12.6 $g/kg^{0.75}$.h. For Bean Geese these values are 177 g fresh weight, 35.5 g dry matter, 181 kJ and 13.6 $g/kg^{0.75}$.h.

These values are very comparable with similar values for other birds gathered by Drent *et al.* (1978) (Table 3). Drent *et al.* suggest that this agreement can hardly be fortuitous "and suggests that there is a limit to the rate of passage of food down the alimentary canal, such that an increase of intake beyond this limiting rate can only be achieved by increasing the length of the foraging period". If this thesis is correct, it means that - based on the extreme values of Drent *et al.* - a mean goose wintering in the Lower Rhine area, with a weight of 3 kg, has a maximum intake of 29-45 g dry matter of grass. This means that these birds, in addition to the necessary hourly intake of 30 g dry matter, can take up at the most another 15 g dry matter of grass; i.e. 80 kJ. This additional amount of energy can be used to compensate energy deficits originating from disturbance, bad weather conditions or migration or can be stored in about 2 g of fat. Under favourable conditions it is possible for the birds to increase their fat deposit daily by 25-30 g, i.e. by 1% of the body weight. It can be assumed that under normal conditions a daily fat increase of about 15 g is within reach.

Comparable values are found by several authors (Prokosch 1981, 1984, St Joseph *et al.* in Ebbinge *et al.* 1982) for other goose species.

This energy budget is calculated for average winter conditions: in the Lower Rhine area the mean winter temperature from November to March is +3.7°C.

Under cold weather conditions the DEE will undoubtedly be much higher (Evans 1976). This additional need of energy can only partly be compensated for by a higher food intake. Most of it must be compensated by economizing on energy consumption.

One of the first reactions is the reduction of the loss of body heat by feeding under cover of hedges or rises in the ground facing to the wind and lying on the ground with the legs protected by the body feathers. Sunshine helps the birds because the dark plumage of the geese absorbs up to 80% of the radiation energy of the sun (Bezzel 1977). Added to this they show a statistically significant higher pecking rate to increase food intake; *Anser albifrons* 101.1 and 116.5 pecks/min, *Anser fabalis* 78.2 and 99.4 pecks/min by temperatures respectively above and below 0°C, Student's t-test; $P<0.01$ (Mooij in prep.).

During periods with frost and closed snow cover a great number of geese shift from grasslands to fields with winter-grains. Although winter grain fields show a lower number of plants per square meter and the leaves have a 9% lower energy content per weight unit compared to grass (Kear in Atkinson Willes 1963), the advantages (plants easy to find under snow cover, relatively long and broad leaves in rosettes) seem to exceed the disadvantages under cold weather conditions.

Under extremely cold weather conditions most of the geese save energy by sleeping on their feeding sites. Dispensable activities like flying, social activities and alertness are reduced at a minimum under these conditions and the theoretical DEE is reduced on the level of the Existence Metabolism, i.e. about 1650 kJ/day. Because of the increased expenditure of energy in order to maintain the body temperature, the DEE can be considerably higher under these conditions. This energy expenditure is covered by the decomposition of body fat. The decomposition of one gram of fat brings the bird about 40 kJ. With a mean body-fat-deposit of 10-15% of the body weight (Bauer & Glutz 1968, Bezzel 1977), i.e. 300-400 g, this means that the geese can theoretically sleep 7-10 days without food, assuming that there is no extra energy needed to maintain the body temperature. In reality most of them leave the area after 2-4 days of extremely cold weather. They do not hold out until the fat deposit is exhausted.

According to the data of Markgren (1963) and Schröder (1975) geese of the size of Bean and White-fronted Goose can take 100-130 g fresh weight of grass or 220 g of grains in their oesophagus and stomach from the feeding site to the roost. In the case of grass, together with the rest of the food in the gut, this food store in the alimentary canal supplies the geese with 130-170 kJ and is enough to cover the energy expenditure of a sleeping goose for 2½-3¼ hours. In the case of grains this amount could be enough to cover the energy expenditure for the whole night, but this food source is not avilable for wintering geese at the Lower Rhine.

Observations show that the average goose of the Lower Rhine wintering site flies seven minutes between feeding site and roost and subsequently spends 15-30 minutes drinking and preening before it goes to sleep. In terms of energy this means that these birds use about 40 kJ for flying and 23-47 kJ for drinking and preening and go to sleep on the banks of the river with a residue of 43-88 kJ, which is just enough to sleep for 50-100 minutes. Sleeping longer would mean consumption of fat. At the Lower Rhine wintering site staying the night on a roost without feeding would mean 13½ hours consumption of energy without energy intake. Such a night would cost 695 kJ, of which 525-565 kJ have to be gained by the decomposition of 13.5-17 g body fat. When these geese are active for at least part of the night, as found by Lebret (1969, 1970), Loosjes (1974), Markgren (1963), Mathiasson (1963) and Philippona (1969, 1972), this waste of fat has to be increased with a quantity of energy up to 250 kJ, i.e. another 6.5 g of body fat.

It would be a poor survival strategy physiologically to roost on cold water for the entire night without feeding and thereby wasting body fat, while being surrounded on the banks of the river/lake by an abundance of food. That is why the geese of the Lower Rhine wintering site sleep on the banks of the water in several bouts of 1½ hours alternating with feeding periods of 1½-2 hours each, as observations showed. As a result of these reflections it seems tenable to state that for geese that mainly feed on grassy vegetations roosting on land and night feeding must be more frequent than has been assumed till now.

Conclusions

These theoretical reflections about the energy budget certainly contain a number of uncertainties, but these do not necessarily cast doubt on the following general conclusions:

- A mean White-fronted Goose weighing 2.4 kg needs 1300-1700 (m = 1500) g fresh weight or 257-340 (m = 300) g dry matter of grass, i.e. 1780 kJ daily and a mean Bean Goose of 3.5 kg 1700- 2240 (m = 1950) g fresh weight or 330-450 (m = 390) g dry matter of grass, i.e. 2360 kJ daily.

  Although bigger geese need more energy than smaller ones, there is a clear correlation between the need of energy per g body weight and the body weight of the birds: the bigger birds need relatively less energy.
- A gooseday is a variable quantity, depending on the goose species. Therefore a feeding intensity measured in goosedays/ha is only valid for a specific goose species and is not freely transferrable to other species.
- For geese mainly feeding on grassy vegetation roosting on land and night feeding are not the exception, but confer physiological advantages.
- Feeding is the most energy consuming activity of the geese. They not only spend about 55% of their time on feeding, they also consume about 60% of their daily energy while feeding. More than 20% of this energy is used for foraging costs. At the same time feeding is the only activity that not only costs but also provides energy.
- There seems to be a limit to the hourly intake of food that is higher than the energetically necessary hourly food intake. The surplus can be used to compensate for energy deficits caused by migration, bad weather conditions or disturbance or it can be deposited in fat.

- Flying is the activity with the highest energy costs per time unit.
- Sleeping is the best way for a free-living goose to save energy. Although the geese use about 30% of their time budget for sleeping, they only consume about 18% of their DEE by sleeping.
- All other activities take about 12.5% of the time budget and almost 14% of the energy budget of the geese.
- The disturbance of geese promotes activities with a high energy consumption and prevents all activities that save energy. Besides this, every disturbance prevents food intake and thereby also the intake of energy and prevents the building-up of fat deposits. Disturbance means a double energy loss for the geese; waste of energy and loss of energy intake.

Discussion

The observations on night-time behaviour were made without a night-sight device. Although it was possible to record each night, depending on the light conditions, the activities of up to 280 birds continuously during the whole night, it cannot be excluded that there were some effects of the author on the roost. However, the acoustic observations of geese at a greater distance from the hide never showed much difference to the optical observations. For this reason the author considers these observations to give a good impression of the night-time activities of the geese of the Lower Rhine area.

The diel activity budget of Snow Geese, studied by Gauthier *et al.* (1988), only shows minor differences to that of the geese of the Lower Rhine wintering site. In this study even a comparable high level of night feeding was found. The overall feeding level of about 55% of the time budget in both studies lies between data of other areas and species, for instance Burton & Hudson (1978) found for Lesser Snow Geese and Ebbinge *et al.* (1975) for Barnacle Geese (about 80% during daylight hours) about 30% of a 24-hour day and for White-fronted Geese Owen (1972) recorded that about 40% (about 95% during daylight hours) and Fox & Madsen (1981) that 68% of diurnal activity was spent feeding. In winter Lesser Snow Geese, mainly feeding on waste grains, spent only about 20% of daylight time feeding (Davis *et al.* 1989), maybe because of the high energetic value of their food source, and in spring Barnacle Geese spent 50-70% of a 24-hour day (70% of 17 hours and 84% of a 20 hours activity budget) feeding (Black *et al.* 1991). Because most of these studies did not record activity budget during the dark hours of the day it cannot be excluded that there was also a certain level of night feeding. Because of the high energy content feeding on wasted grain can shorten feeding time considerably. Also Amat *et al.* (1991) found that the chemical composition and digestibility of the food influenced feeding time.

All these facts show that the calculated activity budget of this study provides a reliable basis for reflections about the energy budget.

Except for the selection of feeding sites (Mooij 1992) there were no behavioural differences found between White-fronted and Bean Geese. This could be a result of the fact that all observations were made in mixed groups and the larger number of Whitefronts on the roosts and feeding sites influenced the behaviour of the Bean Geese.

The energy budget of birds wintering in a specific area is a useful tool for the development of management schemes for these refuging birds (Frederick *et al.* 1987). In spite of the fact that the theoretical reflections of this study about the energy budget of the geese of the Lower Rhine contain a number of uncertainties (for instance: fluctuations of metabolic rate during the day and winter, exact value of "*n*" for several activities, exact influence of cold weather conditions on the DEE) the author considers his conclusions valid because these uncertainties do not influence the overall model.

The value of "*n*" in this study varied between 1.5 (sleeping) and 10 (flying). In a comparable study of Gauthier *et al.* (1984, in Belanger & Bedard 1990) for Snow Geese "*n*" varies between 1.3 (resting) and 15 (flying). Gauthier's value for foraging is somewhat higher and for the other activities somewhat lower, the mean value is about 2.5-2.7. These values are closely comparable with the values found in this study and support the reliability of the model.

Flying is the activity with the highest energy costs per time unit. Human activities in the wintering area modify the distribution of the geese within the site and reduce feeding time by disturbance and by forcing the geese to fly long distances between the roost and various feeding sites. This factor becomes important to the birds from the moment that these energy costs and the reduction of energy intake cannot be compensated for anymore by increased food intake during undisturbed periods (undisturbed feeding sites, night-time feeding). Belanger & Bedard (1990) found that the disturbance rates of 0.5-2.5/hour caused a 2-5-fold increase in flight time. They found that depending on disturbance levels daylight foraging time could be reduced by up to 50%. Therefore the most important aims of goose management at the wintering site have to be to provide the geese with undisturbed roosts and feeding sites, good quality of food in sufficient quantity and short flyways.

The flight velocity of geese flying over the Lower Rhine area lies between 10 and 80 km/h with an average of 43.8 km/h. This value corresponds closely to values found in other studies for the same species, for instance Gerdes *et al.* (1978) found 41-45 km/h, Mathiasson (1963) 60 km/h, Jellmann (1979, in Rutschke 1987) 52 km/h and Wierenga (1976) 44 km/h. For *Anser caerulescens*, a goose of comparable size, average flight velocities of 48 km/h (Frederick *et al.* 1987) and 43 km/h (Cooch 1955 in Philippona 1972) were found.

Less than 5% of the goose flights over the Lower Rhine area were longer than 10 km. The average flight distance was 5.1 km. These short distance flights seem normal for wintering geese. In the Netherlands (Lebret 1959, Philippona 1966, 1972, 1981, Lebret *et al.* 1976, Wierenga 1976) and Southern Sweden (Mathiasson 1963) flight distances between 1 and 15 km were found for wintering White-fronted and Bean Geese, whereas both species in northwest Germany (Gerdes *et al.* 1978) and White-fronts in Great Britain (Owen 1971, Patterson *et al.* 1989) seldom made flights longer than 5 km. In Scotland Pink-footed Geese had average flight distances of about 4 km and Greylag Geese of about 10 km (Bell 1988).

Based on these data it can be stated that daily flight distances between 10 km and 20 km (roost to feeding site and vice versa, with or without drinking flight) are normal for geese wintering on western European inland sites. This means that daily flight times between 15 minutes and half an hour (between 1-2% of the daily time budget) and an energy expenditure between 5% and 10% of the daily energy budget for flying are common in Western Europe. During their studies Gauthier *et al.* (1988) found that Snow Geese in Canada also spent about 2% of their time budget flying.

Management implications

Flight time can be reduced by improvement of feeding conditions by the temporary closure of roads to enlarge undisturbed favourable feeding sites, by temporary damming up of ditches during autumn and winter to create flooded areas or by the creation of permanent shallow waters on the feeding sites where the geese can drink, preen and roost and by a total ban on hunting at the wintering site. Also a good farming strategy on agriculturally used feeding sites could help to shorten flyways and to increase energy output of feeding. The favourite feeding sites of the geese can be made more attractive to them by the cultivation of interim crops on fallow fields, the transformation of arable land into grassland in the central parts, the improvement of grasslands and guaranteed undisturbed feeding. By this type of management and farming strategy the energy budget of wintering geese can be improved and the risk of goose damage be reduced.

A management plan for the wintering sites only makes sense within the scope of a “Western Palearctic Goose Management Plan”. This plan - that has to be developed within the scope of the “Western Palearctic Waterfowl AGREEMENT” under the Bonn Convention - has to concentrate on creating a network of protected areas, throughout their annual cycle and along their whole migration route, where geese can breed, moult, roost, feed and winter with a minimum of disturbance.

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