Figure 2. Relationship between m (kg) and C (kJ $°C^{-1}$ h^{-1} kg^{-1}) in three species. The upper panel shows the diving posture in water, the middle panel shows the swimming posture, and the lower panel shows the standing posture in air. The left panel represents *Podiceps cristatus* (filled circles). The right panel represents *Aythya fuligula* (dots) and *Aythya marila* (triangles). Regressions of log (C) on log (m) for the standing posture in air: *P. cristatus*, $C = 0.672m^{-0.244}$ ($R^2 = 0.080$, $SE_{slope} \pm 0.195$, $P = 0.227$, $N = 20$); *A. fuligula*, $C = 0.740m^{-0.815}$ ($R^2 = 0.322$, $SE_{slope} \pm 0.199$, $P < 0.005$, $N = 37$); *A. marila*, $C = 0.649m^{-0.639}$ ($R^2 = 0.279$, SE_{slope} ± 0.296, $P = 0.0522$, $N = 14$). Regressions of log (C) on log (m) for the swimming posture: *P. cristatus*, $C = 1.464m^{-0.573}$ ($R^2 = 0.372$, $SE_{slope} \pm 0.181$, $P < 0.01$, $N = 19$); *A. fuligula*, $C = 1.564m^{-1.009}$ ($R^2 = 0.307$, $SE_{slope} \pm 0.260$, $P < 0.001$, $N = 36$); *A. marila*, $C = 1.463m^{-0.514}$ ($R^2 = 0.513$, $SE_{slope} \pm 0.144$, $P < 0.005$, $N = 14$). Regressions of log (C) on log (m) for the diving posture in water: *P. cristatus*, $C = 3.592m^{-0.730}$ ($R^2 = 0.966$, $SE_{slope} \pm 0.041$, $P < 0.0001$, $N = 13$); *A. fuligula*, $C = 3.398m^{-1.114}$ ($R^2 = 0.538$, $SE_{slope} \pm 0.797$, $P < 0.005$, $N = 14$); *A. marila*, $C = 3.442m^{-1.067}$ ($R^2 = 0.796$, $SE_{slope} \pm 0.106$, $P < 0.0001$, $N = 9$).

Table 2. Effect of sex and age on parameters of allometric function ($C = am^b$) relating fresh m (g) to C (kJ $°C^{-1}$ h^{-1} kg^{-1}) in aquatic bird species.

Posture	Age, Sex[a]	N	Constant	Power	P Value
Standing	J, M	10	.689	- .472 ± .125	< .0054
	J, F	15	.748	- .213 ± .094	< .0412
	A, M	56	.709	- .522 ± .065	< .0001
	A, F	31	.698	- .409 ± .068	< .0001
Swimming	J, M	9	.574	- .603 ± .143	< .0031
	J, F	14	1.566	- .511 ± .115	< .0009
	A, M	55	1.560	- .572 ± .063	< .0001
	A, F	28	1.445	- .557 ± .071	< .0001
Diving	J, M	3	3.519	- .510 ± .051	< .0630
	J, F	8	3.564	- .563 ± .058	< .0001
	A, M	26	3.464	- .716 ± .074	< .0001
	A, F	13	3.527	- .572 ± .086	< .0001

Note. Constant and power of the allometric function (am^b) relating C to m were obtained from regression of log(C) on log(m). Values shown are power ± SE. P value indicates significance of the slope (b) of the log-log regression (F-test).
[a] A = adult, J = juvenile, M = male, and F = female.

Table 3. Least-square regression of C residuals on fat mass residuals in the standing, swimming, and diving postures.

Equation	R^2	SE	P	N
$C_{air-res} = 0.002 - m_{fat-res} \times .129$	.0041	.199	.520	104
$C_{swim-res} = 0.028 - m_{fat-res} \times .469$	.0132	.412	.260	98
$C_{dive-res} = 0.100 - m_{fat-res} \times 2.145$	.0436	1.480	.154	48

birds) of the present study. The comparison between the present data and a similar study on terrestrial birds using the same technique (Herreid & Kessel 1967) indicates that aquatic birds have higher C's. Several metabolic studies on aquatic bird species are consistent with this (Table 4). The C's of these aquatic birds are between the predictions of the allometric lines of Herreid and Kessel (1967) and the present study. In addition, the C's obtained by cooling curve analysis of Herreid and Kessel (1967) compare reasonably well over a large range of m's in the compilation of C data by Drent and Stone-house (1971; Fig. 3). These data are mainly obtained by gas exchange experiments, which indicates that comparisons between various data sets of C are not hampered *per se* by methodological differences. The conclusion is that, contrary to what might be expected, aquatic birds do not show any adaptation in C to their cold aquatic environment.

The higher C's in air of aquatic birds raises the question of what might be the cause of this higher level. By living in the water, birds have to prevent the plumage from losing its waterproofing capacity. Deterioration of the waterproofing capacity of the plumage severely increases C in water. We have to

Table 4. Thermal conductance C in various aquatic birds as measured in air.

Species	m (kg)	Measured	Predicted Herreid & Kessel (1967)	Predicted Present study	Measured/Predicted Herreid & Kessel (1967)	Measured/Predicted Present study	Reference
Clangula hyemalis	.490	.76	.69	.99	1.09	.76	Jenssen & Ekker (1989)
Aythya marila	.59-.80	.58	.63-.53	.84-.78	1.09	.76	McEwan & Koelink (1973)
Anas barbariae	.752	.82	.55	.81	1.49	1.01	Barre et al. (1985)
Anas rubripes	.904	.59	.50	.74	1.18	.80	Hartung (1967)
Eudyptula minor	.900	.62	.50	.75	1.24	.80	Stahel & Nicol (1982)
Anas platyrhynchos	1.263	.49	.42	.63	1.17	.78	Hartung (1967)
Somateria mollissima	1.650	.27	.36	.56	.75	.48	Jenssen et al. (1989, 1990)
Spheniscus humboldti	3.870	.28	.23	.38	1.22	.74	Drent & Stonehouse (1971)
Pygoscelis adeliae	4.000	.26	.22	.37	1.18	.70	Chappell & Souza (1988)
Anser anser	5.000	.37	.20	.33	1.85	1.11	Bennedict & Lee (1937)
Cygnus olor	8.300	.29	.15	.26	1.90	1.10	Bech (1980)
Aptenodytes fosteri	24.800	.17	.08	.16	2.01	1.08	Le Maho et al. (1976)

C (kJ $°C^{-1}$ h^{-1} kg^{-1})

Note. Predicted values and measured/predicted values are obtained with either the regression of Herreid & Kessel (1967: $C = 0.322m^{-0.484}$) or the regression for species examined in this study ($C = 0.705m^{-0.461}$).

rely on data on mammals to get an idea of this effect. During diving the C's of the fresh carcasses of two shrew species, *Sorex palustris* and *Sorex cinereus*, and two other small mammals, *Zapus princeps* and *Peromyscus maniculatus*, with artificially water-soaked fur was 9.1 times their C in air instead of 4.6 times C with intact, dry furs (Calder 1969). It is obvious that a twofold increase of the C due to losses of waterproofing capacities must have a great impact on thermoregulatory costs. The water-proofing capacity of the plumage of birds is mainly attributable to the structure of the feather plumage and is optimal when the plumage structure remains intact (Rijke 1969). We suggest that the greater destructive forces of water movements have led in aquatic birds to structural adaptations of the plumage such as thicker shafts, barbs, and barbules of feather, causing a stiffer plumage. These adaptations might explain the higher C's of aquatic birds in air compared with those of terrestrial ones, but it is probably the best solution for their aquatic way of life.

In animals contact with water elevates their C. An approximately twofold increase of the C during swimming compared with the C in air of the present study (Table 2) is also found in metabolic studies of *Somateria mollissima* (Jenssen *et al.* 1989, 1990), *Clangula hyemalis* (Jenssen & Ekker 1989), and *Eudyptula minor* (Stahel & Nicol 1982). Two metabolic studies in birds (*Eudyptes chrysolophus chrysolophus* and *Aptenodytes patagonicus*; Barré & Roussel 1986) and a cooling-constant study in mammals (*S. palustris, S. cinereus, Z. princeps*, and *P. maniculatus*; Calder 1969) show a similar magnitude of an approximately fivefold increase of C during diving with minimal compression compared with the C in air as found in the present study (Table 2). This might suggest that the order of magnitude of increase of C due to water contact is a rather general phenomenon during swimming and diving.

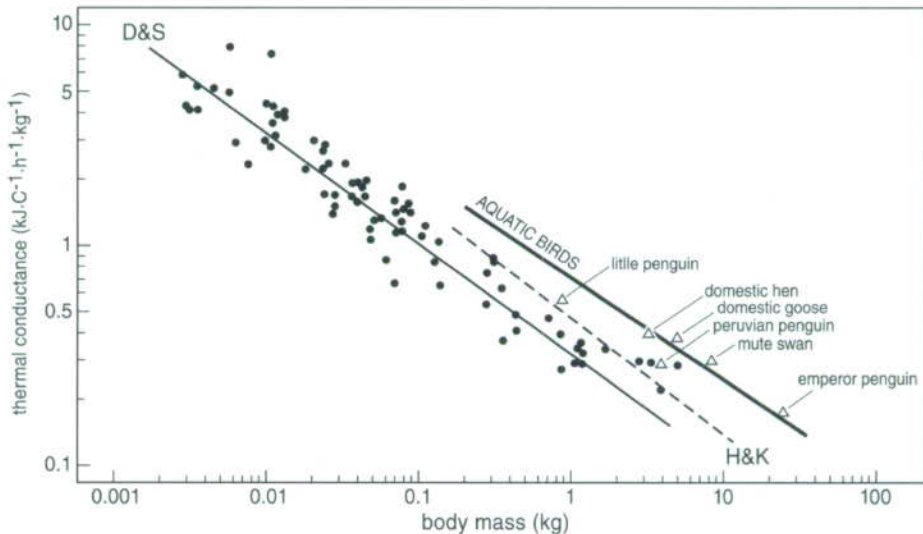Several factors increase the C in water, such as motion of the water, motion in water by animals, and

Figure 3. Comparison between C data in air. The filled circles and the line labelled D&S refer to the regression of the compilation of data obtained by Drent & Stonehouse (1971): $C = 0.430m^{-0.479}$ (C in kJ °C^{-1} h^{-1} kg^{-1}; m in kg). The line labelled H&K refers to the regression of the cooling constant technique (Herreid & Kessel 1967): $C = 0.474m^{-0.536}$. The line labelled AQUATIC BIRDS refers to the warming constant technique of present study: $C = 0.705m^{-0.461}$. The triangles refer to gas exchange studies of single species: Mute Swan *Cygnus olor* (Bech 1980), Domestic Goose *Anser anser* (Bennedict & Lee 1937), Little Penguin *Eudyptula minor* (Stahel & Nicol 1982), Emperor Penguin *Aptenodytes fosteri* (Le Maho *et al.* 1976), and Domestic Hen *Gallus gallus* (Romijn & Lokhorst 1966).

compression of the plumage during diving. Two studies show the considerable importance that these factors might have in thermoregulation. Beginning with motion in water by animals, in *Mustela vison* a swimming speed of 0.25 m s^{-1} increases the heat loss by a factor of three compared with the heat loss during resting in water (Williams 1986). With regard to compression, in *Pygoscelis adeliae* a hydrostatic pressure of 2 atm elevates the diving C by 30% (Kooyman *et al.* 1976). Therefore, the mode of feeding (*e.g.* dabbling or pursuit diving) and site selection (*e.g.* swamps or torrents) of species are also important factors with respect to their C's and their thermoregulatory costs.

Fat has no clear relationship with C in the birds of the present study. We suggest that the subcutaneous fat deposits of our birds are too thin (0.64 cm in *Podiceps cristatus*; Piersma 1984) to allow a temperature gradient to develop that reduces the heat exchange to the surroundings as in seals and whales (*i.e.* in seals, 5 cm or more; Irving & Hart 1957). We are not saying that fat does not act as an insulator, but we stress that it only becomes effective in reducing thermoregulatory costs when the fat layer is thick enough. Irving and Hart (1957) showed that a fat layer becomes an effective insulator when it is approximately 5 cm thick. In birds, fat might therefore be more significant as an energy resource during periods of food deprivation and also when thermoregulatory costs are high.

Age and sex had no apparent effect on C in the birds of the present study. Both between and within species, m has a clear effect on C in air and water. However, in most waterfowl species m is related to sex and age. Therefore, only an indirect effect by sex and age occurs. The generally smaller male and female juveniles and adult females experience a greater heat loss per unit of m than do the larger adult males.

Intrinsic species characteristics may also further influence the level of C. Although the differences between the slopes of the regression lines for the benthivore *Aythya* and the piscivore *Podiceps* are not significant, they suggest that species characteristics linked with their way of feeding might have an effect on C. The pelagic fish-eating species in Figure 1 (b, g, i, j, k, n) have a higher C than the benthic feeders and terrestrial herbivores. We suggest that the pursuit diving technique of fish-eating species might be linked with some adverse effect on C, in the same way that we suggested it is between land and aquatic birds.

The explanation for how different-sized aquatic bird species may live in the same wintering area is not found in adaptations of their C's. The study of Goudie and Ankney (1986) with wintering sea-diving ducks showed that adjustments in behaviour and energy content of diets are involved to compensate for the thermodynamic differences associated with body size. The smaller *C. hyemalis* and *Histrionicus histrionicus* spent more time feeding and consumed food items with higher energy content than did the larger *Melanitta nigra* and *S. mollissima* wintering in the same area. But the smaller species were less capable of adjusting their time allocated to feeding to factors increasing energy expenditure such as tide level, wind speed, wind direction, and air temperature. This could become critical to survival of these diurnal feeders during periods of severe winter weather or ice conditions (Goudie & Ankney 1986). A small m in combination with a decreased flexibility in adjusting with feeding to increased energy requirements raises the question of how these two factors are related. Is leaving the water an attractive behavioural option in this process, because C in air is significantly lower than in water?

We tried to solve these questions by visualising these factors in a simple model that relates m, air and water temperature, time allocation of water contact, and the energetic costs of thermoregulation (Fig. 4). The product of C (in the present study) and difference between T_a and T_b subtracted by the value of basal metabolic rate (BMR) during the resting phase (σ) (Aschoff & Pohl 1970) gave us the cost of thermoregulation. For all m's we assumed a T_b of 39 °C. In Figure 4 the isographs of the costs of thermoregulation are expressed in multiples of resting BMR (Aschoff & Pohl 1970). The isographs relate T_a with m for five different levels of costs of thermoregulation. The relationships between m, T_a and energetic costs of thermoregulation can be summarised as follows from Figure 4: decreasing
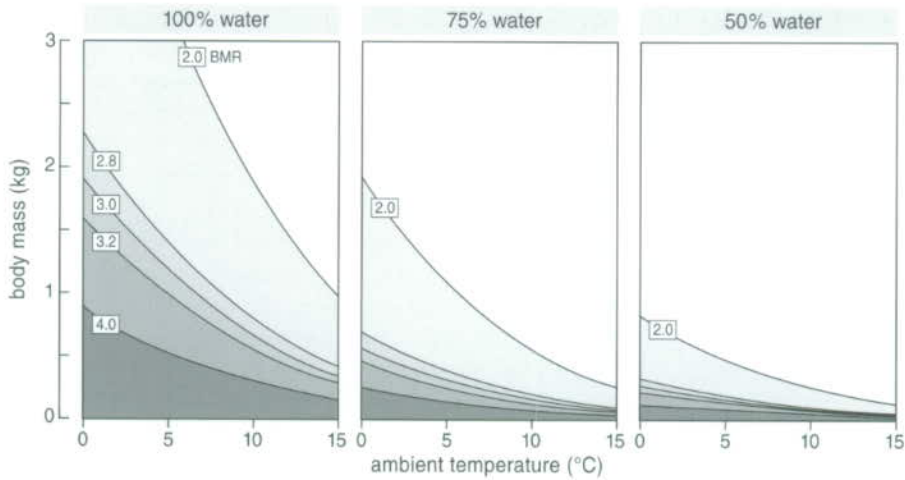
Figure 4. Relationship between time allocations in water and on land and the energetic cost of thermoregulation at various temperatures and *m*'s. The isographs represent the thermoregulatory cost expressed in multiples of the BMR of birds during the resting phase (Aschoff & Pohl 1970).

T_a and decreasing *m* increase thermoregulatory costs; that is, at the same T_a smaller birds have to spend more energy for thermoregulation than larger birds. The model also indicates that shifts in time allocation in contact with water have a considerable effect on the energetic costs of thermoregulation. In order to cope with the constraints of a higher daily energy expenditure due to thermoregulatory costs, aquatic birds have according to Figure 4 three options (1) to choose sites with high T_a's, (2) to compensate higher energetic costs of thermoregulation by increasing food intake, and (3) to reduce the energetic costs of thermoregulation by leaving the water.

We stress the importance of leaving the water as a behavioural adjustment in the corollary of Goudie and Ankney (1986), which explained why different-sized aquatic species may live in the same breeding and/or wintering area. We predict that smaller birds or birds with a diet of low energy content tend to spend more time on land. By reducing the costs of thermoregulation, birds may reduce feeding time and or accept food with less dense energy. In theory, spending time on land makes an aquatic bird more flexible in adjusting its feeding time to meet increasing energetic requirements, for example, during wintertime. In aquatic birds this flexibility may be of paramount importance on both the breeding and wintering grounds as well as in deciding when and where to go during migration.

Acknowledgements

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Appendix

Sample sizes of species obtained and used for *C* and fat determinations

Species	Age, Sex[a]	Obtained	Used Standing	Swimming	Diving	Fat
Podiceps cristatus	J, M	4	4	4	1	4
Aythya fuligula	J, M	1	1	1	1	1
Fulica atra	J, M	1	1	0	0	0
Mergus serrator	J, M	1	1	1	0	1
Mergus albellus	J, M	1	1	1	0	1
Aythya marila	J, M	1	1	1	0	1
Anas crecca	J, M	1	1	1	1	1
Somateria mollissima	J, F	1	1	1	1	1
P. cristatus	J, F	5	4	4	4	5
A. fuligula	J, F	5	5	5	1	4
M. albellus	J, F	3	3	2	0	3
Gavia stellata	J, F	1	1	1	1	1
A. crecca	J, F	1	1	1	1	1
Phalacrocorax carbo	A, M	1	1	1	0	1
Bucephala clangula	A, M	1	1	1	1	1
P. cristatus	A, M	9	9	9	6	9
Anser anser	A, M	2	2	2	0	2
Mergus merganser	A, M	1	1	1	1	1
A. fuligula	A, M	27	27	26	10	25
M. serrator	A, M	4	4	4	0	3
M. albellus	A, M	2	2	2	1	2
A. marila	A, M	6	6	6	5	5
Anas platyrhynchos	A, M	2	2	2	1	1
A. crecca	A, M	1	1	1	1	1
B. clangula	A, F	4	4	4	1	4
P. cristatus	A, F	3	3	2	2	3
A. anser	A, F	1	1	1	0	1
M. merganser	A, F	1	1	1	0	0
A. fuligula	A, F	7	7	7	2	6
M. albellus	A, F	4	4	2	0	4
A. marila	A, F	7	7	7	4	7
A. crecca	A, F	4	4	4	4	4
Total		113	112	106	50	104

[a] J = juvenile, A = adult, M = male, and F = female.

Chapter 5

Food intake of Great Crested Grebes *Podiceps cristatus* wintering on cold water as a function of various cost factors

CONSTRAINTS

Popko Wiersma, Theunis Piersma & Mennobart R. van Eerden

Food intake of Great Crested Grebes *Podiceps cristatus* wintering on cold water as a function of various cost factors

Food intake rate during the nonbreeding season of Great Crested Grebes *Podiceps cristatus* was estimated by reconstructing the stomach content of drowned birds from recognizable remains of the fish prey. Food intake by individual birds since the ejection of the last pellet (the accumulated prey mass) was assessed by estimating fresh mass of ingested fish on the basis of otoliths and pharyngeal bones. We present arguments for a constant pellet ejection rate during the winter season, which is essential for interpreting the data. The large sample sizes enabled us to analyze accumulated prey mass for monthly intervals. We show that food intake varied considerably during the season, increasing 1.8 fold from October to January. Intake rate was even lower in September than in October, but during this time most adults are undergoing wing moult which involves a strong reduction in diving activity. We explored the extent to which these variables caused the observed 1.8 fold increase in food intake from autumn to mid-winter. Changes in the air and water temperature, time spent submerged, heating up food, diving depth, fattening and buoyancy can explain a total of 55% of the observed increase in food intake. The remaining 45% must be due to higher activity costs during winter, as a result of the increased food intake.

Introduction

Few studies have examined seasonal changes in daily energy expenditure (DEE) of nonbreeding birds, since DEE is usually difficult to measure outside the reproductive phase of the annual cycle (Nagy 1987). However, the available empirical studies (Kendeigh *et al*. 1977, Olsen & Kendeigh 1980, Puttick 1980, Mugaas & King 1981, Williams & Kendeigh 1982, Wijnandts 1984, Masman *et al*. 1986, 1988, Owen *et al*. 1992) indicate that DEE within a species may vary with a factor 0.7 to 2.1 within a year. In many of these cases the thermostatic cost (*i.e.* the energy needed to sustain a constant body temperature) has been put forward as an important determinant of the observed variation. In water a bird's plumage has a high thermal conductivity (*i.e.* a poor insulation, *e.g.* Kooyman *et al*. 1976). Therefore, waterbirds spending the nonbreeding season in temperate areas, where water temperatures regularly reach the freezing point, are likely to have high thermostatic costs.

The extent to which ambient temperatures influence energy expenditure of waterbirds has been indicated by a variety of indirect measures. Daily feeding time was shown to increase with lower air temperatures in non-breeding ducks (Tufted Ducks *Aythya fuligula* and Goldeneyes *Bucephala clangula*, Nilsson 1970; Mallards *Anas platyrhynchos*, Jorde *et al*. 1984; Harlequin Ducks *Histrionicus histrionicus*, Goudie & Ankney 1986; Eiders *Somateria mollissima*, G. Nehls pers. comm.), suggesting that more food is required to balance the higher costs during colder periods. In larger-bodied birds these relationships often do not appear. Decreasing foraging activities with decreases in air temperature have been shown in Snow Geese *Anser caerulescens* (Frederick & Klaas 1982), Barnacle Geese

Branta leucopsis (Owen *et al.* 1992), Black Scoters *Melanitta nigra* and also in Eiders (Goudie & Ankney 1986). However, these birds may not be in energetic balance but temporarily rely on stored nutrients.

We tried to estimate food intake of Great Crested Grebes *Podiceps cristatus* obtained during seven successive nonbreeding seasons at lake IJsselmeer, the Netherlands. This is close to the northern boundary of their wintering distribution (Cramp & Simmons 1977). In August grebes arrive on the lake in order to moult, appearing in flocks of up to 40 000 birds (Piersma *et al.* 1986). After the moulting period, *i.e.* September until the first half of October (Piersma 1988a), the grebes disperse over the lake and total numbers decrease to 500-5000 birds (unpubl. data). On average, about 14 000 grebes winter in the Netherlands (Beintema *et al.* 1993). In February/March some 10 000 grebes concentrate at lake IJsselmeer again (unpubl. data) shortly before leaving in late March/April to breed elsewhere in the Netherlands and further north east.

The availability of a large number of Great Crested Grebes accidentally drowned in gill-nets set on the lake's bottom enabled us to make various measurements of a good series of specimens throughout the nonbreeding season. Great Crested Grebes feed on small fish, at lake IJsselmeer mainly Smelt *Osmerus eperlanus* (Piersma *et al.* 1988, Van Eerden *et al.* 1993). Due to their peculiar digestive system, the diet of the drowned grebes can be reconstructed in great detail from the gut content of the carcasses. Following maceration in their non-acid stomach (pers. obs.), fine material passes the pyloric feather plug-sieve (Piersma & Van Eerden 1989) into the intestines. Hard, bony material, however, stays behind in the stomach, trapped inside a feather ball. The stomach-feathers are actively eaten and periodically a pellet is produced, thereby casting out all remains accumulated in the stomach (Piersma & Van Eerden 1989). Remains of the fish, *i.e.* otoliths and pharyngeal bones, can be used to reconstruct the size and mass of the fish. Since pellets are produced at a constant rate (see below), the intake of the fish in the period since the last pellet can be reconstructed by examining the remains in the stomach. This offers a unique opportunity to quantify the seasonal intake of free living individuals in a species which is difficult to observe in its natural wintering habitat.

Methods

From 1978 to 1985 1331 drowned Great Crested Grebes were collected at lake IJsselmeer. The carcasses were brought ashore by fishermen and stored in tight plastic bags at -20 °C. The depth at which the grebes were found in the gill-nets, *i.e.* their drowning depth, is used as an estimator of diving depth (see Hofer 1969). Body mass was measured and corrected for the amount of water in the plumage (Piersma 1984). Body mass was much larger in males than in females (Piersma 1988b). Age was recorded as juvenile (in first winter) or adult (after first winter) using plumage characteristics (Kop 1971, Piersma 1988b) and by examination of the gonads. The oesophagus sometimes contained intact fish of which the fresh mass was measured, but usually it was empty or contained only a small amount of prey. The otoliths and pharyngeal bones found in the stomach were measured and the fresh mass of the prey was estimated (calibration curves in Piersma 1988c). Due to slight wear of the otoliths of Smelt a corrected predictive equation of fish length from otolith length was used (Van Eerden *et al.* 1993). The estimated fresh fish mass in the oesophagus and the stomach combined is called *accumulated prey mass*: this is the total intake since the stomach content was ejected last.

In order to investigate changes in body condition of the grebes, three internal measures were collected. The abdominal fat layer was excised and weighed. The thickness of the subcutaneous fat layer was measured just anterior of the breast bone and ribs. The fresh mass of the right breast muscles (*pectoralis major* plus *supracoracoideus*) was measured and multiplied by two.

Water temperatures were recorded at a depth of 1 m at various locations in lake IJsselmeer at 0900 MET. Water temperatures are very similar at different depths, due to the high level of mixing of the water layers (E. Van Duin, pers. comm.). The mean monthly water temperature was calculated by averaging all data of different locations per month per year. Average daily air temperatures at Lelystad, along the south east coast of lake IJsselmeer, were recorded by the Royal Dutch Meteorological Institute (KNMI 1978-1985).

Methodological rationale
Variation in food intake rate will only be reflected in the accumulated prey mass if the pellet ejection rate remains constant over the period under consideration. If not, variations in accumulated prey mass can also be the result of variation in pellet ejection rate. Alternatively, a bigger feather production might lead to an earlier filling of the stomach and hence to a more frequent pellet production; this would explain a lower estimated "intake" during periods when moult is heavier. The amount of fish in the stomach will not have an effect since the fish mass will pass through into the intestines, leaving only a small amount of remains behind. We can show that the amount of feathers has no effect: the feather mass in the stomach is a fixed proportion of the contour feather production rate, within individuals as well as within averages over different months (Piersma & Van Eerden 1989, and see Fig. 1). This suggests that a certain fraction of moulted feathers is eaten and that the stomach is emptied at a seasonally constant average rate.

Another indication of a constant pellet production rate is given by the proportion of grebes with empty stomachs. A change in the pellet ejection rate would change the proportion of grebes in the population having an empty stomach and thus the probability of encountering an empty stomach. However, the frequency of empty stomachs does not change during the season (Kruskal-Wallis One-way ANOVA, KW statistic $= 1.22$, $P = 0.27$; Fig. 2). The latter argument hinges on the assumption that with a pellet the complete stomach content is evacuated, which seems very likely considering the compact
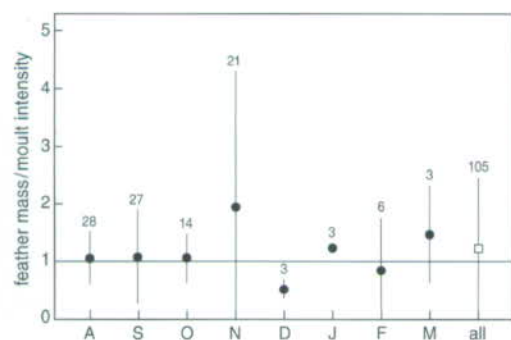

Figure 1. Amount of feathers in the stomach (g) divided by the estimated daily contour feather production rate (g d⁻¹) for all months of the season separately. Numbers in the figure give sample sizes, the bars indicate standard deviations (± 1 SD). The category 'All' gives the average value of all data combined. Data from Piersma and Van Eerden (1989) in which their Figure 2 shows feather mass in the stomach on the y-axis and moult intensity on the x-axis, both of which are here combined on the y-axis.
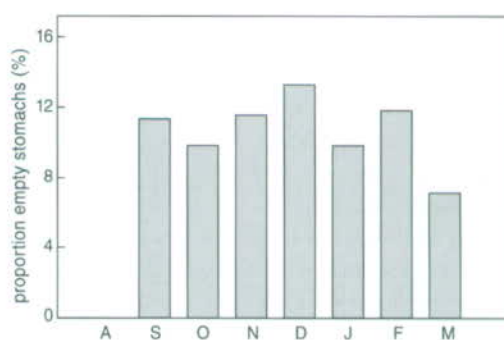
Figure 2. Proportion of Great Crested Grebes with empty stomachs of the total number collected per month.

structure of the feather ball (Geiger 1957, pers. obs.). Both arguments support the idea that pellet ejection takes place at fixed intervals, irrespective of stomach content, and justifies the use of average accumulated prey mass as an index for the food intake of a population of grebes.

The grebes probably eject a pellet every other day (Piersma & Van Eerden 1989, Kop 1972, pers. obs. on captive grebes), presumably at night or very early in the morning (Simmons 1973, Piersma *et al.* 1988). Storer (1961, 1969) and O'Donnell (1982) suggest similar systems for other grebe species. We, therefore, expect accumulated prey mass to reflect the amount of fish eaten during a period ranging from 0 to 48 hours (somewhere between two pellet ejections) and, therefore, the average of a sample to equal the daily intake rate.
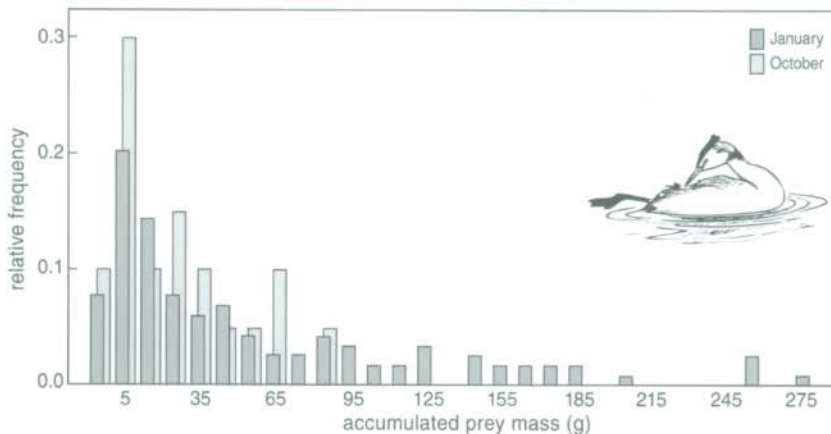

Figure 3. Frequency distributions of accumulated prey mass of adult male Great Crested Grebes for two different months of the nonbreeding season (October and January). The data are divided into 10 g classes, while empty stomachs are treated separately.

Methodological pitfalls

The frequency distribution of accumulated prey mass is truncated at the value 0, causing a positive skewness, *i.e.* a relatively long tail of high values (Fig. 3). The probability of finding a grebe with many prey in its oesophagus and stomach (more than *c.* 100 g) is very low. In addition, behavioural factors might increase this skewness. Hypothetically, grebes that have fed and had a high accumulated prey mass were diving from below a school of fish, moving consistently in a vertical direction (spot diving). This would considerably decrease the probability of drowning in a net. Grebes with a few prey in their stomach, on the other hand, might have been swimming in horizontal directions, hunting single fishes (pursuit diving) or seeking for a school of fish. Such behaviour would increase their risk to drown in a net, and independently lead to a skewed distribution. The latter scenario is supported by the findings of Ydenberg and Forbes (1988), who showed that Western Grebes *Aechmophorus occidentalis* exploit schools of fish for a while (spot diving) and then spend much time searching until another school is found and intense feeding starts. The choice between pursuit or spot diving might depend on the food situation and the experience of the grebes.

In view of the difficulties in interpreting average values of the strongly skewed distributions, we also present monthly averages of a subset of the sample; the upper 10% of the accumulated prey masses. If the seasonal pattern of these values parallel that of the overall averages, it implies that the behavioural

differences are evenly mixed among the samples. The averages of the upper 10% will represent the accumulated food intake of grebes which are about to produce a pellet, thus nearly equalling a two-daily food intake.

Results

Seasonal variation in daily food intake

The average accumulated prey mass changed considerably during the nonbreeding season (Fig. 4). In adult birds it increased threefold from August to March from 25 to 82 g (average for males plus females, $r_s = 0.88$, $P < 0.005$ and $r_s = 0.95$, $P < 0.001$, in adult males and females, respectively). Juveniles showed a similar increase from 12 to 43 g ($r_s = 0.88$, $P < 0.005$). These results are very similar to the seasonal change in number of fishes per stomach reported by Büttiker (1985) for grebes wintering on a Swiss lake. The upper 10% of accumulated prey mass showed exactly the same seasonal pattern as the average values (Fig. 4), in spite of the very small sample sizes (1 to 15 grebes per montthly average). From August to March the mean of the upper 10% of the accumulated prey masses (or the 2-daily intake) increases from 100 to 233 g in adult birds, and from 43 to 135 g in juveniles. On the basis of allometric equations of field metabolic rates given by Nagy (1987), we would expect a Great Crested Grebe of 1200 g to consume 300 g fresh fish per day (assuming an assimilation efficiency of 85% when fed on Smelt (balance study captive grebe, pers. obs.) and an energetic value of Smelt of 4.5 kJ g^{-1} fresh mass, pers. obs.). This is 2.5 to 12 times the value indicated by our data (Fig. 4).

Thus the food intake rate estimated from the accumulated prey mass seems to be underestimated for reasons we do not understand. However, since pellet ejection rate is seasonally constant, the estimated food intake rate will be a fixed percentage of the real food intake rate. We conclude from Figure 4 that food intake increases 1.8 times (range 1.6-2.3, over different age and sex classes) from autumn to mid-winter, i.e. October to January. We take October to obtain a base-line value since in August or September most grebes are moulting. Piersma (1988d) showed that during primary moult Great Crested Grebes forage less, probably to avoid the risk that their growing feathers become damaged during feeding dives.
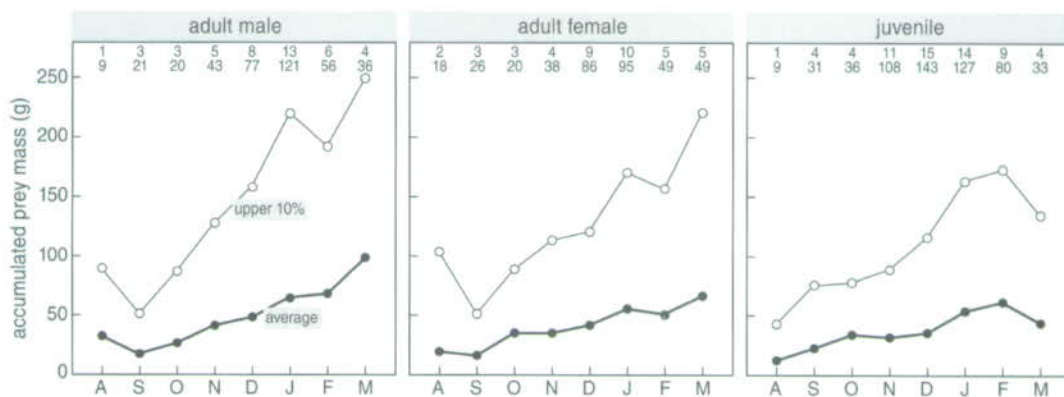

Figure 4. Seasonal changes in accumulated prey mass of adult male, adult female and juvenile grebes. The lower lines represent the overall average values, the upper lines the average values of the highest 10% of the distribution. Sample sizes, in the same order, are given in the top of each panel.

Variables affecting the daily food intake

Air temperatures decreased by *c*. 9 °C from October (11.4 °C) to January (2.6 °C) and water temperature by 12 °C (October 14.6 °C, January 2.8 °C) (Fig. 5). Temperature seems to have a strong effect on the food intake rate (Fig. 4). From August onwards the accumulated prey mass significantly increases in adult males, adult females and juveniles, the increase being almost a mirror image of the decrease in both air and water temperature (Fig. 5). The average accumulated prey mass is strongly correlated with monthly water temperature in adult males and females and in juveniles (r_s = -0.55, -0.51 and -0.44, and $P < 0.005$, 0.005 and 0.0005, respectively).

Body size possibly influences the energy requirements through the maintenance costs: a larger body will need more energy to support its basic functions (*e.g.* Daan *et al.* 1989). Therefore we expect males to have a higher food intake than females or juveniles, since males have a body mass *c*. 26% higher than females and *c*. 7% higher than juveniles (of both sexes combined). Indeed males' average prey mass was higher than the females' in 7 out of 8 months, and in 6 out of 8 months compared with juveniles (Fig. 4). Body mass also reflects the fat mass of the bird, which possibly influences the energy requirements as well. Grebes with higher fat loads are prone to have higher diving costs due to stronger upwards forces (buoyancy) when submerged (Lovvorn & Jones 1991a). In the discussion we explore and try to quantify the various ecological factors which might cause the pronounced seasonal variation in food intake.
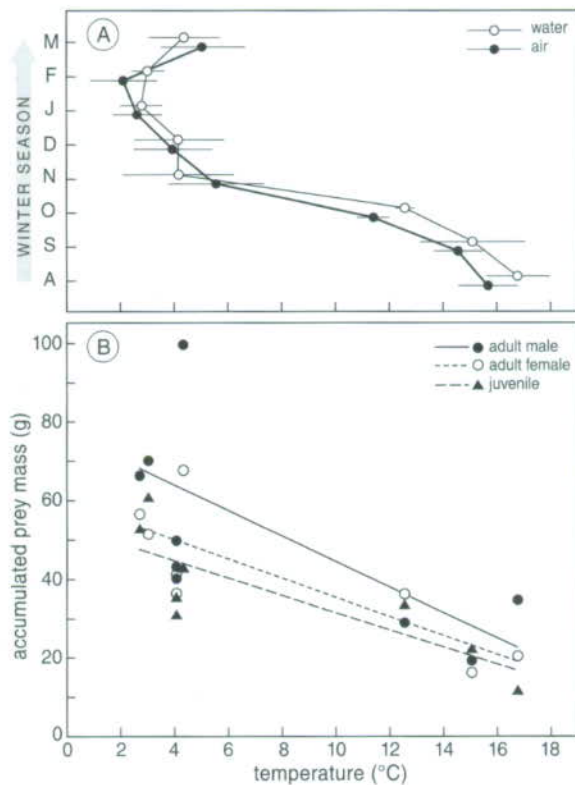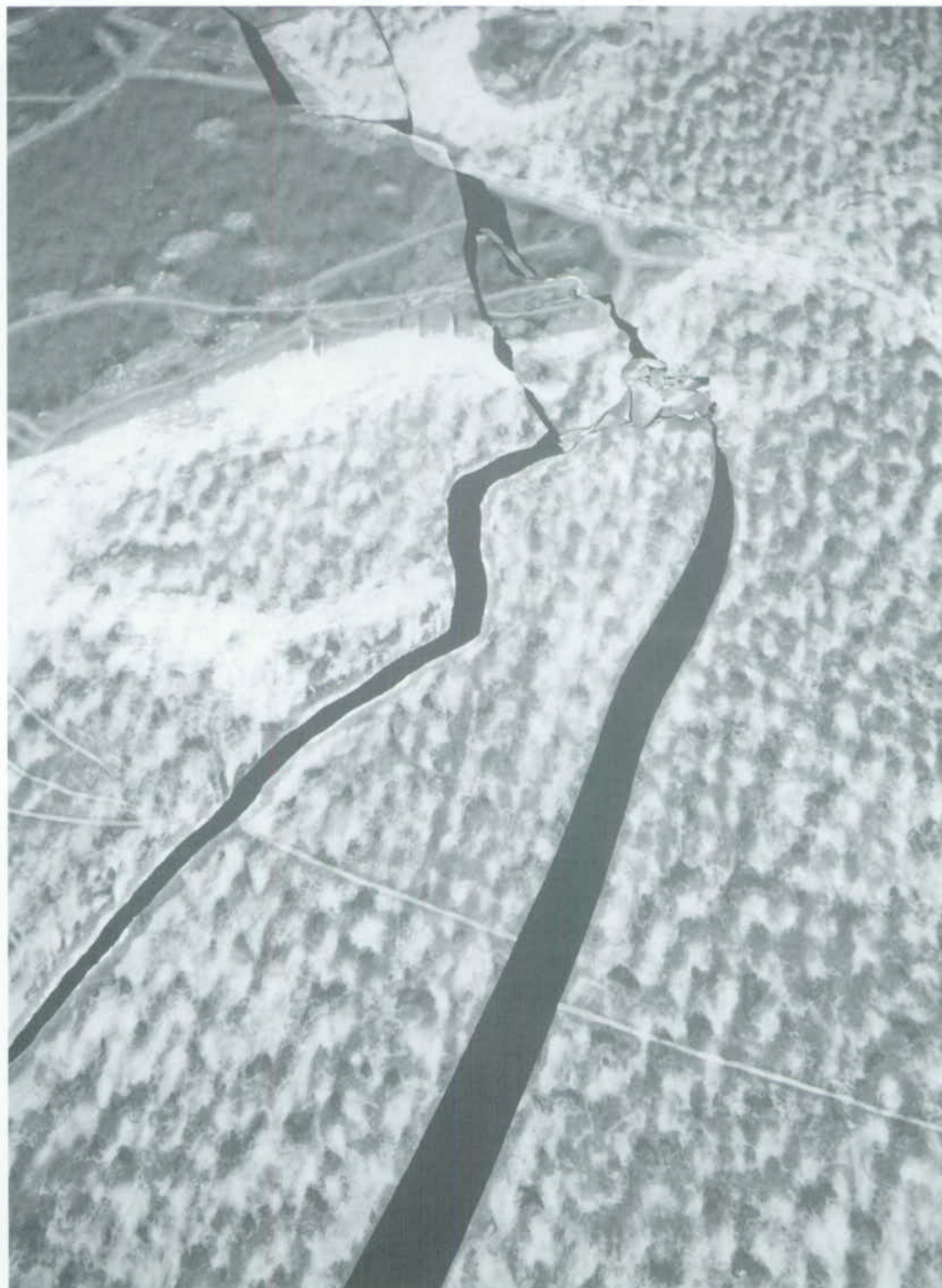

Figure 5. (A) Monthly averages with standard deviations of water temperatures (average of different locations in lake IJsselmeer) and air temperatures (Lelystad), from 1978 to 1985. (B) Monthly averaged accumulated prey mass in combination with water temperature for three categories of grebes. The different lines show the best linear fit.

Lake IJsselmeer, ice cracks serve fish-eaters a suitable habitat, February 1991.

Discussion

Daily energy expenditure

Heat loss is linearly related to the temperature difference between the environment and the body core (Scholander *et al.* 1950). With a body temperature of 40 °C, the temperature difference between body and environment would be *c.* 37 °C in January and *c.* 27 °C in October (see Fig. 5). The ratio of the two is an estimate of the increase in heat loss, here 1.4. For an absolute estimate of the maintenance metabolism, *i.e.* Basal Metabolic Rate plus thermoregulation costs, the value for the grebes' thermal conductance has to be known. From empirical data of various authors presented in Chapter 4 (De Vries & Van Eerden 1995), we calculated the allometric equation of conductance of aquatic birds, resulting in thermal conductance = $0.149 \times$ Body mass$^{-0.391}$ ($R^2 = 0.84$, $N = 12$), with conductance in W °C^{-1} kg^{-1}. For an average grebe, weighing 1.2 kg, the conductance would be 0.166 W °C^{-1}.

Carcasses of aquatic bird species in swimming position have conductance values that are 2.2 times higher than when standing on land (De Vries & Van Eerden 1995). Similar increases are shown by Stahel and Nicol (1982), Jenssen *et al.* (1989, 1990), Jenssen and Ekker (1989) and Croll and McLaren (1993). For a swimming Great Crested Grebe the conductance would therefore be 0.37 W °C^{-1}. This translates into a maintenance metabolism (thus including BMR) of 9.9 W in October and 13.5 W in January. To assess the increase of the total energy expenditure we also need an estimate of the activity costs. Only data for waders are available: net activity costs in Knots *Calidris canutus* (Piersma *et al.* 1991) and Turnstones *Arenaria interpres* (Piersma & Morrison 1994) vary from 1 to 1.5 times BMR. Let us assume that the daily activity cost in grebes equals 1 times BMR. For a non-passerine bird weighing 1.2 kg we predict a BMR of 4.6 W (Kendeigh *et al.* 1977). Further, if we assume that the activity costs do not change in the course of the season, total costs would be 14.5 W in October and 18.1 W in January, 3.1 and 3.9 times BMR, respectively. This represents an increase by a factor 1.25.

The excess costs of feeding submerged

Water is an enormous potential heat sink. Measurements on carcasses of aquatic bird species by De Vries and Van Eerden (1995) show that the overall conductance increases with a factor 4.8 when submerged, compared with the overall conductance in air (see also Barré & Roussel 1986 and Ellis 1989). Therefore, we estimate the conductance of diving Great Crested Grebes at 0.80 W °C^{-1}. In order to quantify the cost of being submerged we need an estimate of the time spend under water. We estimate it to be maximally 3-4 hours in midwinter (see below). Adding the underwater heat loss to the daily energy loss, we still only estimate an increase with a factor 1.26 from October to January (Table 1). Note that Ellis (1989) estimated actual cost of diving in Eared Grebes *Podiceps nigricollis* of 3.5 to 5.5 times the cost of floating, while Wilson *et al.* (1992) estimate activity costs for swimming underwater of more than 5 times BMR. These values are notably higher than our estimate which is based on maintenance costs alone.

The grebes, which have to eat more during the cold months, probably dive more and spend more time submerged. The extra time spent diving in winter will also have energetic repercussions. We tried to estimate the total time spent submerged by assuming that for every fish caught, the grebe had to make one extra dive. The number of fish found inside the stomach showed an increase from August to September, after which it became fairly stable and increased again in March (Fig. 6). In addition, the diving depth changed too, demonstrated by the depth at which the bird was found entangled in the net (Fig. 6). The estimated number of dives multiplied by the diving depth results in a crude index for the total time submerged (Fig. 6). From this we conclude that the time submerged may increase by a factor 1.5 from October to January, *i.e.* from roughly 2.0-2.7 hours to 3-4 hours. (From data of moulting Great Crested Grebes in mid September (Van Eerden *et al.* 1993) it was estimated that during the active

Table 1. Summary of the extent to which the various cost factors described in the text can be responsible for the observed 1.8 fold increase in food intake of Great Crested Grebes from October to January. The explained proportions are given as factors relative to October, and the total, cumulative, effect is shown in the last column. The effect of increased feeding and locomotory activity (last row) is not empirically derived, but covers the remaining, unexplained increment.

| Variable	Effect	Cumulative effect
Maintenance metabolism; not feeding	1.25	1.25
Maintenance metabolism; feeding submerged	1.01	1.26
Maintenance metabolism; divetime increment	1.03-1.04	1.30-1.32
Maintenance metabolism; diving depth increment	1.01-1.02	1.32-1.34
Body mass gain	trivial	
Increasing buoyancy through change of body mass	1.02	1.34-1.37
Heat for warming up cold prey	1.06	1.42-1.45
Increased feeding and locomotory activity in winter	1.24-1.27?	1.8
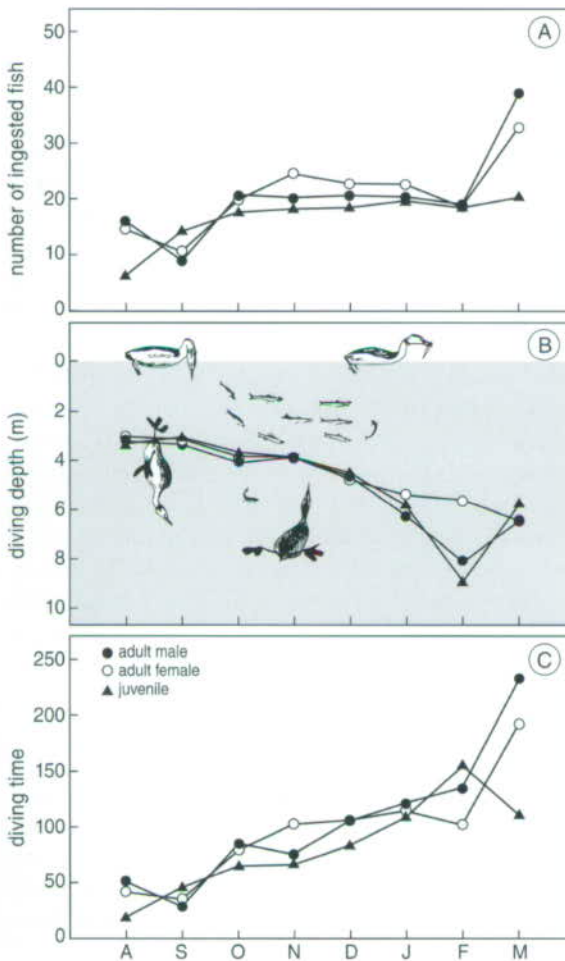
Figure 6. (A) Number of fish, reconstructed from prey remains, inside the stomach and oesophagus of drowned grebes and (B) the depth at which the grebes were found in the nets. (A) multiplied by the drowning depth (B) produces an estimate for the time spend submerged (C). For (C), the individual combinations of drowning depth and number of fish were used instead of the monthly averages.

periods at dawn and dusk the grebes spent 1.5-2.0 hours foraging under water, *i.e.* 2.5 hours active at spot with alternating 20 sec dive time and 10 sec rest.) Combining the conductances for diving and swimming Great Crested Grebes with the increase in time submerged, we arrive at a total increase in daily energy expenditure of a factor 1.30-1.32 from October to January (Table 1).

Another factor that changes the rate of heat loss is diving depth. Earlier we showed that the depth at which the grebes drowned changed through the season, with a peak in the coldest month (Fig. 6). Similar results were found for grebes on a Swiss lake (Hofer 1969). It implies that the diving depth is 1.5 times as large in January than in October. In Adelie Penguins *Pygoscelis adeliae* the conductance is up to 18% higher 10 m underwater than at the surface (Kooyman *et al.* 1976). The increased pressure compresses the insulating air layer between the feathers, raising the conductance of the plumage considerably. De Vries & Van Eerden (1995) measured the conductance of carcasses by holding them just below the water surface, so, as these authors state, this conductance value, as well as the derived maintenance costs, are likely to be underestimates. To derive a crude estimate of what the effect might be in Great Crested Grebes we assumed that thermal conductance is 18% higher at 10 m (Kooyman *et al.* 1976) and linearly decreases towards the surface to the values as presented by De Vries & Van Eerden (1995) at a depth of 0 m. Using the diving depths from Figure 6 we estimated an increase in conductance of diving grebes from October to January of 4%, that is from 7% to 11%, respectively. On a daily basis this factor explains only up to 2% extra of the overall increase (Table 1).

Effects of body mass on energy expenditure

Figure 7 shows the changes in conditional variables of the Great Crested Grebes during the season. It must be emphasised that body mass, thickness of the subcutaneous fat layer, abdominal fat mass and also pectoral muscle mass are all significantly correlated with each other (all P's < 0.001). Overall, the grebes are fattest and have the heaviest pectoral muscles during winter. Mass gain of these tissues starts already in August and reaches its peak during December/January (Fig. 7). Because the period of mass gain is spread over a period of about 5 months we do not expect it to cause a measurable increase in food intake (Table 1).

Fresh body mass of adult grebes increased by *c.* 7% (*i.e. c.* 85 g) from October to January (Fig. 7). Lovvorn & Jones (1991a) showed that in several *Aythya* duck species body volume is a linear function of body mass, resulting in higher buoyancies in heavier individuals (see also Lovvorn & Jones 1991b). This force is, however, also strongly affected by the amount of air in the plumage and in the lungs and air-sacs, which again is influenced by diving depth (Stephenson *et al.* 1989, Lovvorn & Jones 1991a). The data presented by Lovvorn and Jones (1991a) on Lesser Scaup *Aythya affinis* show that a 100 g increase in body mass results in a *c.* 10% increase in energy expenditure of ducks foraging at the bottom. Also there is more power required to descent when buoyancy increases. If we, very simplistically, assume that a Great Crested Grebe would experience 8.5% higher costs when weighing 85 g more (proportional to the earlier mentioned Lesser Scaup result), daily energy expenditure is expected to rise by maximally 2.5% from October to January (Table 1).

The cost of ingesting cold prey

The fish eaten by the grebes have the same temperature as the lake's water. This means that the ingested fish absorb heat from the grebes' much warmer bodies. The average water temperature during January was 2.8 °C and during October 14.6 °C (Fig. 5). Fish of such temperatures are heated to 40 °C. Based on a specific heat of fish of 3.7 J g^{-1} °C^{-1} (dependent on the water content, here 80% of fresh mass, Van Eerden unpubl. data), heating the prey was 2.6 times more expensive in January than in October (*i.e.* increment in food intake times the October/January ratio in temperature gradient between fish core and
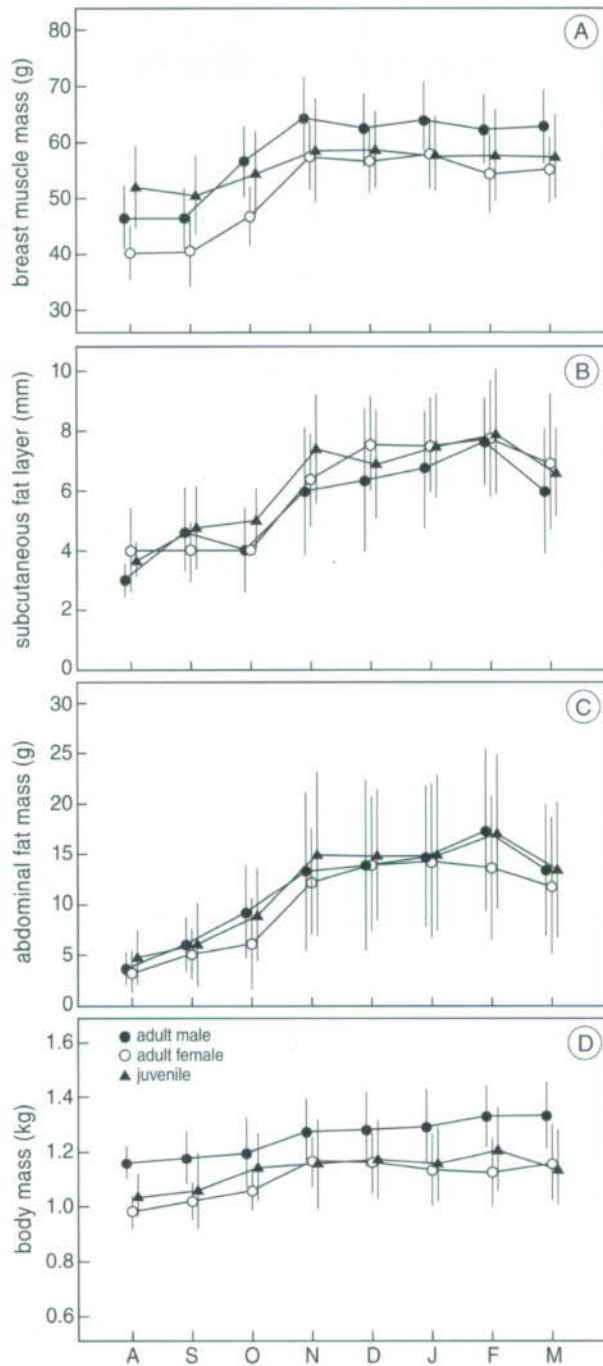
Figure 7. The seasonal changes in (A) mass of the pectoral muscle, (B) thickness of the subcutaneous fat layer, (C) fresh mass of abdominal fat and (D) fresh body mass for three categories of grebes. Shown are averages with standard deviations. Open dots represent sample sizes of 10 or less, the remaining samples contain numbers ranging from 28 to 52.

bird core: $1.8 \times (40-2.8) / (40-14.6)$). On a daily basis energy expenditure would increase by *c*. 6% from October to January (Table 1).

Unaccounted part of the seasonal variation in food intake

Food intake rates in August and September are almost 40% below the October values. This difference can not be explained by the factors described in Table 1. However, it is likely that other factors are involved because during this period most Great Crested Grebes are moulting their primary feathers. Piersma (1988d) showed that food intake was greatly reduced during moult, and suggested that the birds dived less to protect their brittle, growing primaries. The data presented by Piersma (1988d) suggest that grebes partially rely on their fat stores.

We realise that our quantitative explorations to attribute seasonal changes in food intake to different cost factors only resulted in crude estimates. We were able to explain a large part of the 1.8 fold increase in food intake, but not all potential cost factors could be quantitatively evaluated. At least part of the remaining unexplained energetic costs may be covered by a higher level of activity; foraging activity has to be more intense during winter when more fish has to be caught. And, as mentioned earlier, Ellis (1989) and Wilson *et al.* (1992) estimated very high locomotory costs during diving. Travel distances (*e.g.* flight and diving path) could also vary during the season. Although we do not have the data to test this, it seems reasonable to suggest that altered activity costs explain the remaining 45% of the increasing food intake.

Our estimate of the daily energy expenditure during October (including all factors discussed and shown in Table 1) equals 15.6 to 16 W, *i.e.* almost 3.5 times BMR, and since we estimated that costs in January were 1.8 times higher, we would expect the costs in January to equal more than 6 times BMR. This value is extremely high with respect to DEE values published sofar. Only during chick rearing such high levels of DEE are reported (Nagy 1987). Even a minimum estimate of the costs in January (maintenance metabolism of a floating bird plus activity costs equalling 1 times BMR) adds to 4 times BMR already. Great Crested Grebes wintering at lake IJsselmeer may therefore live rather close to a "metabolic ceiling" of *c.* 4 times BMR (Drent & Daan 1980, Karasov 1990, note that Weiner (1992) concluded that 7 times BMR is probably closer to the maximum level of sustainable energy expenditure). Our analysis is in accordance with the statement by De Vries and Van Eerden (1995) that wintering aquatic birds have rather limited energetic leeway due to high maintenance costs. Only a rich and harvestable supply of fish allows such diving birds to survive the winter in temperate Europe.

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Chapter 6

Scaling metabolisable energy intake and daily energy expenditure in relation to the size of herbivorous waterfowl: limits set by available foraging time and digestive performance

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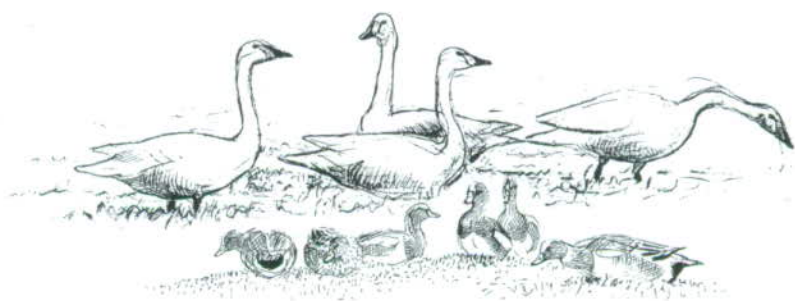
CONSTRAINTS

Scaling metabolisable energy intake and daily energy expenditure in relation to the size of herbivorous waterfowl: limits set by available foraging time and digestive performance

For various herbivorous water birds, wintering or staging in the Netherlands and ranging in size from Teal *Anas crecca* (body mass 0.3 kg) to Mute Swan *Cygnus olor* (body mass 11 kg), digestive efficiency was estimated for three major components in their food, *i.e.* protein, hemicellulose and soluble carbohydrates. Metabolisable Energy Intake (MEI, in W) was estimated in free ranging wild birds using composition of food and droppings, dropping mass and dropping intervals and Acid Detergent Fibre (ADF) as a natural marker. MEI of diets consisting of either foliage, seeds, or roots and tubers is compared with the energetic requirements of the birds (Basal Metabolic Rate, BMR and Daily Energy Expenditure, DEE).

Retention times varied significantly with body mass, larger species retaining food for longer periods. This contrasted to the passage rate, which did not vary with body mass, estimated as being *c.* 0.2 mm s^{-1} in all species. Larger birds thus have longer retention times because their digestive tract is longer, not because food is transported through their intestines at a lower speed. Digestibility was significantly affected by the plant species for all three nutritional components, and only the digestion of hemicellulose was clearly affected by the body mass of the consumer. A separate analysis of the digestibility of foliage and seeds also showed significant effects of body mass on protein digestibility, but with opposite trends in each of the two diets. Digestibility of hemicellulose differed among plant leaves but not among different seeds, as was also the case for the digestibility of soluble carbohydrates. Generally the larger avian herbivores digested both protein and hemicellulose in seeds to a greater extent than the smaller ones.

MEI increased with body mass with an exponent of 0.78-0.86 (for birds foraging on seeds and foliage respectively), and was roughly twice as high on seeds compared to foliage. The contributions of the three nutritional components to the energy intake were significantly different in diets of seeds or roots and tubers compared to diets of foliage, but for none of the components was a significant relation with body mass found. For seeds the contribution of protein, soluble carbohydrates and hemicellulose to the energy intake was 23, 64 and 13% respectively, and for plant storage material these values were 16, 69 and 15% respectively. Leaves, however, were significantly different, 42, 32 and 26% respectively. Energy metabolism in seeds depended largely on the digestion of carbohydrates, while in a foliage diet most energy was obtained from the digestion of protein.

Allometric equations were derived relating BMR to body mass (4.59 $M^{0.69}$, $N = 19$ species) and DEE (8.24 $M^{0.68}$, $N = 33$ species) in herbivorous *Anseriformes*. These equations showed that daily energy expenditure in herbivorous water birds was remarkably low, being about 1.8 times the resting level. This low level of energy expenditure is probably an evolutionary adaptation related to the low dietary quality of their food. In line with theoretical predictions and empirical results on mammals, metabolisable energy intake scales to body mass with a higher exponent (range 0.78 - 0.86) than the exponent relating BMR or DEE to body mass (range 0.68 - 0.69). So larger herbivorous water birds achieved higher intake rates in

both a relative and absolute sense, which was not caused by the selection of better food items, on the contrary, larger herbivores usually took food of a lower quality. However, the longer digestive tract enables larger herbivores to digest their food more efficiently. The smaller species can increase their energy intake by selecting high quality food plants, or by increasing their foraging time within the available time window set by ecological factors (time of day or night) or physiological factors (digestive bottle-neck).

Introduction

The amount of energy herbivores obtain from their food is determined by the content of potentially digestible components, the rate of digestion and the retention time of food in the gut (Prop & Vulink 1992).

Herbivory is relatively rare among birds. In a recent review Sedinger (1997) summarised the avian taxa in which it occurred, and tabulated results for the two best known orders, the *Tetraonidae* (grouse species) and the *Anseriformes* (geese, swans and some ducks). The main reason why herbivory is not widespread among bird species is that the edible parts of green plants contain relatively few nutrients, are relatively difficult to digest (Robbins 1993) and contain a large amount of fibres, which can easily lead to a digestive bottle-neck (Kenward & Sibly 1977). The high degree of specialisation necessary to cope with such a diet has important consequences for the ecology of the different species. Spatial selection of wintering sites (Prins & Ydenberg 1985, Owen 1980, Chapter 8, Van Eerden 1984), breeding areas (Prop *et al.* 1984) and moulting sites (Loonen *et al.* 1991, Loonen 1997), and timing of migration (Prop & Deerenberg 1991), but also life history traits, such as breeding success (Prop *et al.* 1984), onset of incubation (Sedinger & Raveling 1986, Sedinger & Flint 1991) and growth of the young (Cooch *et al.* 1991, Loonen *et al.* 1997), are all largely determined by the quality of the food plants. This strong affiliation to the quality of their food is a general feature of all herbivores, and condemns them to become "prisoners of their food supply" (Drent & Prins 1987).

Folivory (eating leaves) is in the avian kingdom restricted to flightless birds, or to birds which spend only a very limited amount of time on flying. Dudley and Vermeij (1992) hypothesised that daily expensive flights cannot coexist with folivory, since the weight imposed by the full guts would be too heavy for the animals. The relatively large gut system as found in folivorous mammals would probably interfere with the ability to fly in birds. Indeed, restricted flyers such as grouse *Tetraonidae* have larger *caecae* than geese (Sedinger 1997). The Hoatzin *Opisthocomus hoatzin,* a neo-tropical leaf eating bird species, has a well-developed crop and oesophagus, which allows foregut fermentation, but restricts room for flight muscle attachment to the sternum (Grajal *et al.* 1989) and is therefore probably better equipped to digest cellulose than *e.g.* geese (Sedinger 1997).

In herbivorous mammals, the relation between body mass and both energy expenditure and digestive efficiency (and hence diet choice), has received much attention, especially among African herbivores (see Demment & Van Soest 1985, Owen-Smith 1988). In the African savannahs, 20 mammalian herbivore species can easily be simultaneously encountered, ranging in size from a Dikdik *Madoqua kirkii* (5 kg) to an African Elephant *Loxodonta africana* (5000 kg), all having a different diet choice. Jarman (1974) and Bell (1971) explained this coexistence by differences in diet and energy expenditure. Energy expenditure increases with a fractional power of body mass (usually an exponent of around 0.7), while gut capacity scales with a constant fraction of body mass. Larger herbivores should therefore be able to cope with a diet of lower quality, leading to specific food choices related to body size. This concept was labelled the "Jarman-Bell" principle (Owen-Smith 1988).

Among avian herbivores this "Jarman-Bell" principle has so far not been demonstrated. Although

the allometry of energy expenditure has received sufficient attention (Zar 1969, Nagy 1987, Bennett & Harvey 1987, Nagy & Obst 1991) to cover one side of the story, data on metabolisable energy intake in relation to body mass of free living *Anseriformes* have scarcely been published.

In this paper we try to fill the gap by analysing the metabolisable energy intake, digestive efficiency and retention time for free ranging ducks, geese and swans. Our primary data refer to wildfowl in the Netherlands outside the breeding season. These data include intestine morphology and are related to a literature review on Basal Metabolic Rate (BMR) and Daily Energy Expenditure (DEE). We tested the hypothesis that small avian herbivores face relatively high levels of energy expenditure compared to the energy intake over time, thus spending a large proportion of the day (and night) actively foraging on a diet which is considerably and necessarily of higher quality, compared to the food of their larger family members.

Methods

Sampling of data
During various field trips in the Netherlands in autumn, winter and early spring, groups of foraging water birds were located in single food type situations of natural origin as well as in pastures. Vegetation samples were taken here, complete droppings collected and dropping intervals recorded where possible. Most data were obtained at the same time (*i.e.* the collection of food plants and droppings and records of dropping intervals), but in some cases this was not possible. In these (few) cases data from different sources had to be combined.

Dropping intervals were determined by three different methods: first, by focusing on individual birds and measuring the exact time between two consecutive droppings, second, by randomly watching birds and measuring the time until a dropping was produced, averaging these values and multiplying the average by two, which gives an estimate for the group average dropping interval, and third, by meticulously registering the time spent by the birds in a certain area in terms of bird-hours and collecting all droppings in this area over the elapsed period. The latter procedure was the only possibility in night-foraging *Anatidae*, and was carried out with the aid of an infrared telescope from a watchtower in the foraging area.

Chemical analyses
The chemical analyses of food and droppings included the following parameters: dry mass (dried at 70 °C), Ash Free Dry Weight (AFDW, determined by incineration at 400 °C), Neutral Detergent Fibre (NDF), Acid Detergent Fibre (ADF, Goering & Van Soest 1970), total Kjeldahl-nitrogen and partly indigestible protein. Energy content of plants and droppings was determined by adiabatic bomb-calorimetry using benzoic acid as a reference. All determinations were performed in duplo. Total nitrogen was multiplied by 6.25 to obtain an estimate of total crude protein. Hemicellulose was estimated as the difference between NDF and ADF. The fat content was not measured, since fat was not assumed to be a major component in the energy metabolism of herbivorous birds (Prop & Vulink 1992). The fat content of all plant parts was assumed to be 5% (AFDW basis), of which 30% is digested. The fraction of soluble carbohydrates was determined by subtraction: (100%-protein % - fat (fixed at 5%) - NDF %).

Droppings contain matter of faecal origin and urinary waste products. To distinguish between these two, the urinary compound in the droppings was determined following Terpstra and De Hart (1974), since urinary nitrogen does not originate directly from the food, like faecal nitrogen, but from protein turnover in the body pool. Urinary nitrogen was subtracted from the total nitrogen in the faeces and the

remaining fraction was multiplied by 6.25 to obtain the crude protein content of the faeces. Digestibility (D) of component c (D_c) was calculated according to Prop and Vulink (1992):

$$D_c = (CF_c - (CD_c \times R)) / CF_c \times 100\%$$

CF_c is the concentration of component c in the food (%), CD_c is the concentration of component c in the droppings, R is the ratio of a natural marker (in our case ADF) in the droppings and in the food (ADF droppings/ADF food). The Metabolisable Energy of component c (ME_c) was calculated following Prop and Vulink (1992) as:

$$ME_c = (D_c \times CF_c \times J_c) \times 10^{-4} \text{ (kJ g}^{-1})$$

J_c is the energetic value of component c. The physiological energy contents of protein (17.8 kJ g^{-1}), carbohydrates (17.6 kJ g^{-1}) and fat (39.3 kJ g^{-1}) were based on Schmidt-Nielsen (1975). The value of cell walls (13.2 kJ g^{-1}) was based on Hungate (1966). The metabolisable energy of the food was obtained by summing the ME_c values of the different components (protein, soluble carbohydrates, fat and cell walls, ME_{tot}). Metabolisable Energy Intake during foraging (MEI, in W) was calculated from dropping mass M_d (AFDW, in g) dropping rate R_d (s) and total digestibility (D_{tot}). Total digestibility was defined as the sum of all digestibilities of the components multiplied by the fraction of these components in the food:

$$D_{tot} = S(D_c \times CF_c)$$

Metabolisable Energy Intake was calculated by multiplying the dropping mass (M_d, in g) by the dropping rate (R_d, in s), giving the intake of undigested material in grams per second. This value was then divided by 1 minus the total digestibility (dimensionless) and multiplied by the total metabolisable energy content of the food to obtain Metabolisable Energy Intake. The latter value was divided by 1000 to obtain estimates in Joules per unit of time:

$$MEI = M_d \times R_d / (1-D_{tot}) \times ME_{tot} \times 10^{-3}$$

Dropping intervals were measured prior to or after the collection of food and faecal samples. Care was taken in selecting cases where the species under focus was foraging for at least one hour in the field. In some cases the intervals could not be determined directly, the dropping intervals were then reconstructed according to the relation between body mass and dropping interval. However, this was only necessary for three species (see Appendix 1).

The length of the digestive tract (LDT, in mm) was determined in dissected birds collected in the field. For most species the length of the droppings in the field (LD, in mm) was measured. For the remaining species an estimation was made according to the allometric relation shown in Appendix 1. Using these variables and dropping interval I, the retention time (R, in s) was calculated (Prop & Vulink 1992):

$$R = LDT \times I / LD$$

Since all values were converted into SI units, the foraging time per day (F) for each species could be calculated by dividing DEE by MEI, multiplied by 24 hours.

$$F = DEE / MEI \times 24 \text{ hours}$$

Results

Retention time and intestine morphology

For all species the body mass, dropping interval, length of the dropping and length of the digestive tract are given in Appendix 1. From these parameters the passage rate through the digestive tract (mm s^{-1}) and the retention time (s) have been calculated. Regression analysis showed that retention time increased significantly with body mass ($P < 0.05$, $R^2 = 0.42$, $N = 11$). When excluding the two species for which both dropping length and dropping interval were reconstructed based on allometric relations (see Appendix 1), the same result was apparent ($P < 0.05$, $R^2 = 0.39$, $N = 9$). Retention time (R, in s) is a function of body mass (M, in kg) according to the equation:

$$R = 8427 \ M^{0.22}$$

In contrast to the retention time, the passage rate through the digestive tract (mm s^{-1}) is not significantly related to body mass ($P = 0.13$). Consequently, as the retention time increases with body mass, a particular food particle remains longer inside the intestine of a Mute Swan *Cygnus olor* than a comparable food particle inside the intestine of a Teal *Anas crecca,* but both food particles are transported inside the intestines with an identical rate of *c.* 0.2 mm s^{-1}.

Data on the length of different parts of the digestive tract (all in cm) in herbivorous *Anseriformes* have been summarised in Appendix 2. In general, the different parts of the digestive tract scale to body mass with an exponent ranging between 0.23 - 0.42 (Table 1). This is only one dimension which determines the total gut volume. If the two other dimensions of the total gut scale with an identical exponent to body mass, gut volume scales to body mass with an exponent ranging between 0.8 - 1.2. We hypothesise therefore that larger birds can simultaneously digest relatively larger amounts of food compared to small birds.

Table 1. Regression equations relating the length of different parts of the intestinal tract (cm) to body mass (M, in kg) and also the total length of the two *caecae* (cm) as a function of the total length of the digestive tract (LDT, in cm).

Tractus:	regression equation:	
Duodenum	25.4 M$^{0.239}$	($N = 19$, $R^2 = 0.74$, $F = 47.8$, $P < 0.0001$)
Ilium	138.4 M$^{0.233}$	($N = 19$, $R^2 = 0.48$, $F = 15.4$, $P < 0.005$)
Rectum	9.0 M$^{0.312}$	($N = 19$, $R^2 = 0.79$, $F = 64.8$, $P < 0.0001$)
Total	176.8 M$^{0.241}$	($N = 17$, $R^2 = 0.57$, $F = 19.6$, $P < 0.0005$)
Caecae (M)	30.7 M$^{0.413}$	($N = 19$, $R^2 = 0.54$, $F = 20.3$, $P < 0.0005$)
Caecae (LDT)	0.124 LDT$^{1.08}$	($N = 17$, $R^2 = 0.38$, $F = 9.4$, $P < 0.01$)

Digestion

To test the assumption that larger herbivorous water birds digest their food more efficiently, the digestive efficiencies of small and large birds foraging on identical food sources have been analysed. For this analysis the data were categorised in plant leaves, seeds, and stolons and other below ground storage parts. In Figure 1 protein digestibility in diets on leaves and seeds has been plotted as a function of body mass. The lines connect the same plant species. Protein digestibility was not related to body mass (ANCOVA, $P = 0.8$), but differed significantly among plant species (ANCOVA, $P < 0.001$). The
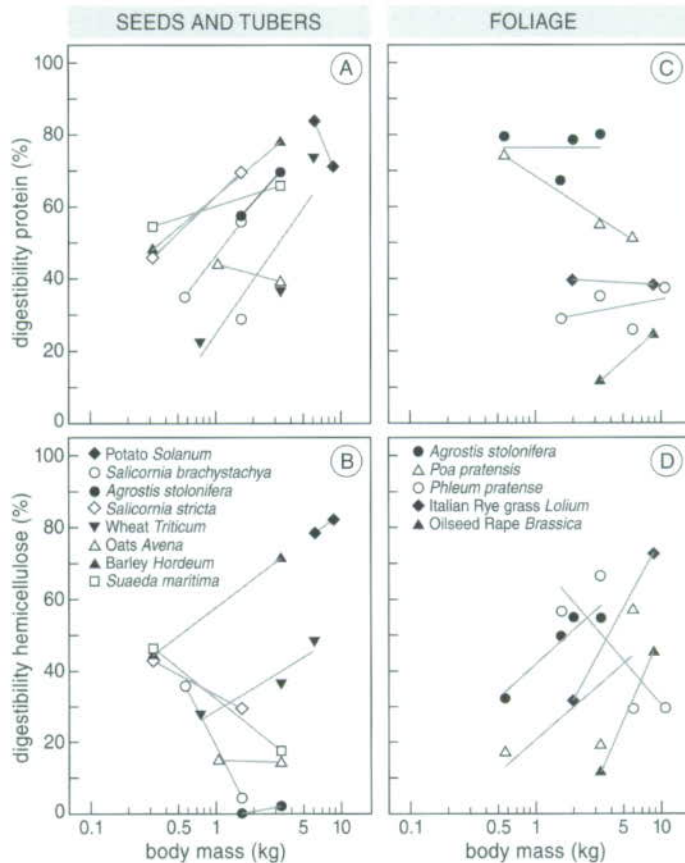
Figure 1. (A) Digestibility in seeds of protein (% of protein in food digested) and (B) of hemicellulose as a function of body mass (kg). (C) Digestibility in plant leaves of protein and (D) of hemicellulose as a function of body mass (kg). The different plants species are for seeds and tubers: *Agrostis stolonifera, Salicornia brachystachya, Salicornia stricta, Suaeda maritima* and the field food crops: Barley seeds *Hordeum vulgare,* Oats *Avena sativa,* Wheat *Triticum aestivum* and Potato tubers *Solanum tuberosum.* For foliage: *Agrostis stolonifera, Poa pratensis, Phleum pratense* and the field crops: Italian Rye-Grass *Lolium multiflorum* and Oilseed Rape *Brassica napus.*

digestibility of protein in leaves varied significantly both between plant species (ANCOVA, $P < 0.001$) and with logarithmic body mass (ANCOVA, $P < 0.001$). However, the latter correlation is caused by an unequal distribution of the different plant species over the consumers, the small herbivores choosing highly digestible foliage. Connecting the different plant species suggested a slight trend for a more efficient protein digestibility in larger birds, but the effect of bird mass on protein digestibility was by far less pronounced than the differences between the plant species. Concerning the digestibility of protein in seeds, no significant differences between plants species were found (ANCOVA, $P = 0.13$), but logarithmic body mass explained a significant part of the variance (ANCOVA, $P < 0.01$), larger consumers digesting the protein in the seeds more efficiently. Comparing protein digestibility between diets of leaves and seeds, a great difference in digestibility among plant leaves was apparent, in contrast to seeds of different plant species, which showed less variation.

Digestibility of hemicellulose significantly correlated with body mass (ANCOVA, $P < 0.05$) and varied also between different plant species (ANCOVA, $P < 0.05$, Fig. 1B, D). Separate analyses for seeds and leaves showed a significant effect of the plant species on hemicellulose digestibility in the case of seeds (ANCOVA, $P < 0.01$), but in neither of the two diets a significant effect of body mass was apparent.

Digestibility of soluble carbohydrates in general was not affected by body mass (ANCOVA, $P = 0.9$), but varied significantly among the different plant species (ANCOVA, $P < 0.005$). Separate analyses for seeds and leaves showed a significant effect of the plant species on carbohydrate digestibility for seed diets only (ANCOVA, $P < 0.01$), and in neither of the two diets a significant effect of body mass.
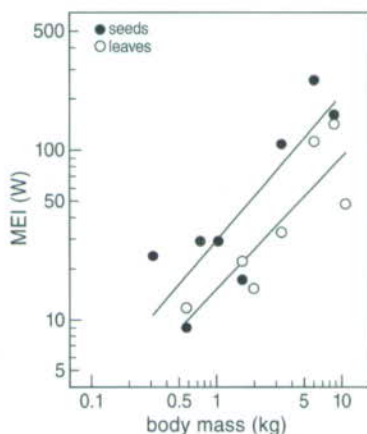

Figure 2. Metabolisable Energy Intake (MEI, in W) for various water birds on different plant species; closed dots refer to diets of seeds and open dots to diets of leaves. For equations see text.

Metabolisable energy intake, general body mass pattern

In Figure 2 the metabolisable energy intake (MEI, in W) as a function of body mass (M, in kg) is shown for diets consisting of foliage and diets consisting of seeds. Metabolisable energy intake was significantly related to body mass (ANCOVA, $P < 0.0001$) and differed significantly between foliage and seeds (ANCOVA, $P < 0.05$). Regression of MEI on body mass (both log transformed) resulted in the following allometric relations:

$$\text{MEI}_{\text{foliage}} = 15.2 \ M^{0.78} \ (R^2 = 0.67, F = 13.1, N = 6, P < 0.05) \tag{Eq. 1}$$

$$\text{MEI}_{\text{seeds}} = 29.5 \ M^{0.86} \ (R^2 = 0.69, F = 16.9, N = 8, P < 0.01) \tag{Eq. 2}$$

MEI increased with body mass with an exponent of 0.78-0.86 for foliage and seed respectively, and was roughly twice as high for birds feeding on seeds than on leaves.

The analysis above has shown that larger birds obtained more energy per unit foraging time than small birds (and that this value was higher while foraging on seeds than on leaves). These results might have been biased, however, because differently sized birds may choose different food plants as their food source. To investigate this possibility, the relationship between MEI and body mass was compared
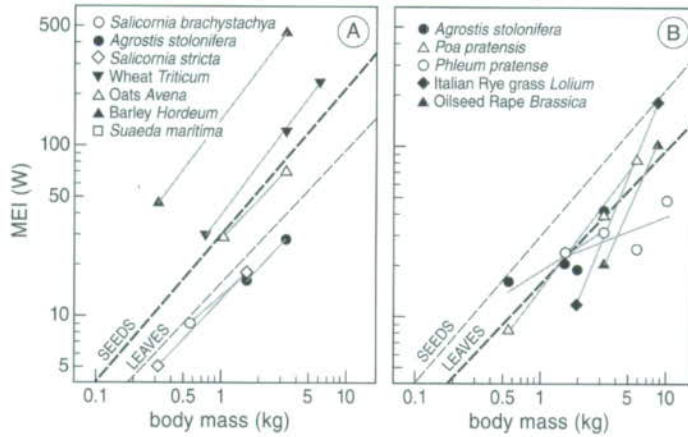
Figure 3. Metabolisable Energy Intake (MEI, in W) plotted against body mass (kg) for avian herbivores foraging on (A) seeds, (B) leaves of different plant species. For reasons of comparison the allometric relation between MEI and body mass for avian herbivores foraging on seeds and leaves has been plotted both.

among different bird species, foraging on *identical* plant species under field conditions. In Figure 3A this is shown for birds feeding on seeds and in Figure 3B for birds foraging on leaves. All seeds of different plant species corroborated the general pattern (note the enormous energy intake on Barley, five times the average intake!). MEI on the grass species *Agrostis stolonifera* and *Phleum pratense* showed slightly depressed slopes, while slightly elevated slopes were apparent in birds foraging on foliage of Oilseed Rape *Brassica napus* and leaves of Italian Rye-Grass *Lolium multiflorum*, but in general the average trend was followed.

Energy can be obtained by digestion of any of the three components studied: protein, carbohydrates and hemicellulose. For each bird species we partitioned the energy obtained from the food in components attributable to protein, soluble carbohydrate and hemicellulose digestion. Analysis of covariance with logarithmic body mass as covariate showed in neither of the three components a significant contribution of the covariate, but for all components a significant difference between the diets (seeds, plant storage material or foliage) was found (protein ANOVA, $P < 0.005$, soluble carbohydrates ANOVA, $P < 0.0001$ and hemicellulose ANOVA, $P < 0.05$). The average values of the contribution of the three major components to the energy intake are given in Table 2. Energy metabolism on seeds and root components largely depended on the digestion of carbohydrates, whereas on leaves a major part of the energy was obtained from the digestion of protein.

Table 2. Relative contribution (percentage and standard error) of the three major nutritional components (protein, soluble carbohydrates and hemicellulose) to the total metabolisable energy intake. Data are given separately for diets consisting of seeds, storage material (bulbils, stolons and tubers) and green foliage.

Diet	Protein	Soluble carbohydrates	Hemicellulose
Seeds	23 ± 3	64 ± 5	13 ± 3
Storage	16 ± 2	69 ± 5	15 ± 4
Foliage	42 ± 4	32 ± 6	26 ± 4

Energy expenditure, DEE and BMR.

In order to obtain a reliable estimate of Basal Metabolic Rate in relation to body mass of herbivorous water birds, the data collected in this study were combined with some unpublished data. In Appendix 3 values of BMR (W) and body mass (kg) for different species are given. Beside values of the energy expenditure of resting birds, values of daily energy expenditure in herbivorous water birds were also calculated. The estimates of Daily Energy Expenditure (DEE, see Appendix 4) were based (1) on Existence Metabolism in a cage (EM_c), (2) on total daily food consumption (DMEI, Daily Metabolisable Energy Intake), (3) on one value obtained with Doubly Labelled Water (DLWc) on caged birds (Brunckhorst 1995) and (4) on Time Energy Budgets (TEB). In Figure 4, BMR and the different DEE estimates are given as a function of body mass. The three different methods for obtaining DEE estimates (EM, DMEI and a pooled group of TEB and DLW estimates) were not significantly different (ANCOVA, $P > 0.4$), but body mass as covariate was highly significant (ANCOVA, $R^2 = 0.88$, $N = 33$, $F = 232.9$, $P < 0.0001$). The relationship describing BMR (W) as a function of body mass (kg) in water birds could be formulated as:

$$BMR = 4.59\, M^{0.69}\ (R^2 = 0.91, N = 19, F = 173.8, P < 0.0001) \tag{Eq. 3}$$

and the relationship describing DEE (W) in herbivorous water birds as a function of body mass (kg) as:

$$DEE = 8.24\, M^{0.68}\ (R^2 = 0.88, N = 33, F = 232.9, P < 0.0001) \tag{Eq. 4}$$

In general, the workload for *Anseriformes* under field conditions is roughly 1.8 times the energy expenditure at rest. Since we know how energy expenditure depends on body mass (equation 4) and how the energy intake depends on body mass for birds foraging on foliage (equation 1) or on seeds (equation 2), for each bird species the foraging time needed to cover the daily energy expenditure could be estimated on both of the two different diets. To achieve this, for each species the estimated DEE (equation 4) was divided by the estimated MEI (equations 1 or 2) which gave a dimensionless estimate of the
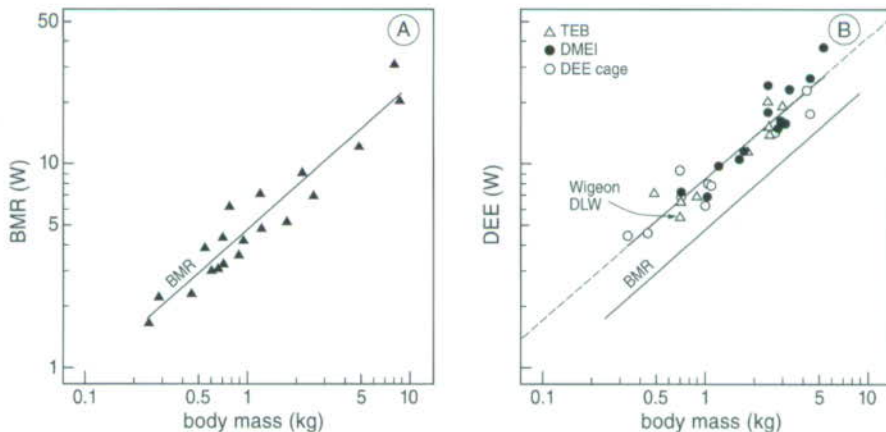

Figure 4. (A) Basal Metabolic Rate (BMR, in W) as a function of body mass (kg) for *Anseriformes*. (B) Daily Energy Expenditure (DEE, in W) measured by different methods as a function of body mass. The different methods are: Daily Metabolisable Energy Intake (DMEI), Existence Metabolism in caged birds (DEE_{cage}) and Time Energy Budgets (TEB). One study used the Doubly Labelled Water technique (DLW) in Wigeon (Bronckhorst 1995).
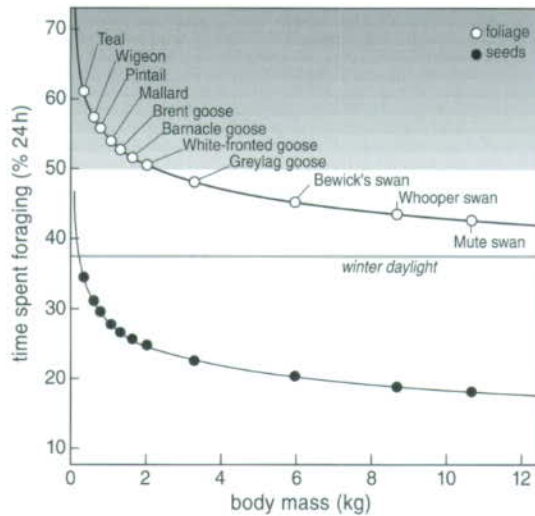
Figure 5. Calculated percentage of the total time (24 hours) spent on foraging to meet the daily energy demands for 11 herbivorous water birds foraging on foliage (upper line) or seeds (lower line). The shaded zone indicates the boundaries set by different periods of time available for foraging (10-14h).

As indicated, the period of daylight during midwinter in the Netherlands is not sufficient to provide the species enough energy on a diet of leaves. To overcome this bottle-neck birds can either extend their foraging period into the night (as is common in ducks), switch to a more energy rich diet consisting of seeds and tubers, or use their fat reserves.

fraction of the total time spent foraging (Fig. 5). Time spent on foraging increases rapidly with decreasing body mass. The mathematical relation describing the fraction of a 24 hour period necessary to spend foraging (F) in order to cover the daily energetic needs on a diet of leaves or seeds as a function of body mass (kg) is given by equation 5 and 6, respectively.

$$F_{foliage} = 0.54 \; M^{-0.10} \quad\quad\quad\quad\quad\quad\text{(Eq. 5)}$$

$$F_{seeds} = 0.28 \; M^{-0.18} \quad\quad\quad\quad\quad\quad\text{(Eq. 6)}$$

Fibre content beside body mass as a predictor of energy intake

Figure 6 shows metabolisable energy intake as a function of fibre content (NDF) of the food (note the log-scale on both axes). Sufficient data were available for Greylag Goose, Teal, Wigeon and a combination of Bewick's Swan and Whooper Swan. For all groups a significant negative relationship existed between NDF content in food and MEI, body mass acting as an important covariate. In Figure 7 the same relation between NDF and MEI is illustrated, but now on an arithmic scale. When DEE was calculated for Wigeon, Greylag Goose and Bewick's Swan (equation 4), all foraging on a foliage diet of similar composition, it could be ascertained that larger birds achieved higher intake rates. One of the most important features of the energy metabolism of an animal is how the energy intake is related to the energy expenditure. For each of the three species three points were indicated in the graphs of Figure 7, representing the energy intake which counterbalanced foraging efforts of 10, 12 and 14 hours respectively. When the potential daily foraging periods are becoming shorter, birds have to increase their energy intake to remain in energy balance. This increase in energy intake can be achieved by either an increase in foraging effort, or by selecting a grass species of higher quality (lower fibre con-
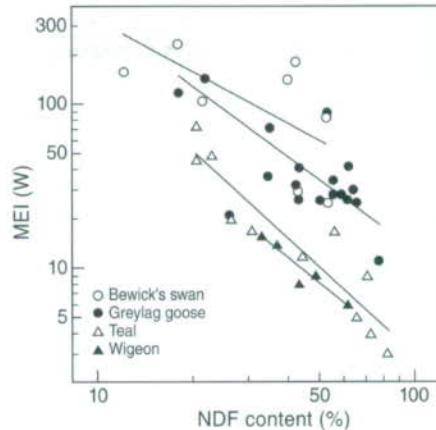
Figure 6. Double logarithmic plot of Metabolisable Energy Intake (MEI, in W) plotted against NDF content of the food (in % on AFDW basis) for Bewick's Swan *Cygnus c. bewickii* (6 kg), Greylag Goose *Anser anser* (3 kg), Wigeon *Anas penelope* (0.6 kg) and Teal *Anas crecca* (0.3 kg).
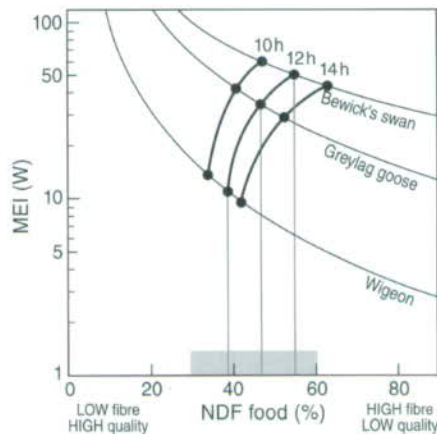

Figure 7. MEI (W, logarithmic scale) plotted against NDF content of the food (in % on AFDW basis, arithmic scale) for Bewick's Swan *Cygnus c. bewickii*, Greylag Goose *Anser anser* and Wigeon *Anas penelope*. The curves represent the regression line of Figure 6. The dots indicate the minimal food quality (in terms of NDF) necessary to counterbalance the energy expenditure under daily foraging regimes ranging from 10 to 18 hours, foraging on leaves (grasses). The box indicates the natural range of fibre content of different grasses. Under similar foraging regimes, the small Wigeon needs food with a lower fibre content (higher nutritional value) than the large Bewick's Swan. A small change in dietary quality of the food has to be compensated by a larger shift in daily foraging time in a smaller species than in a larger species.

tent). It is clear that for Wigeon diet composition is very important; a small change in dietary quality of the grass strongly affects the total time needed to spend on foraging. For Wigeon the chances of encountering grass which is better in quality becomes critical, given the natural range of fibre content in grass species (box in Fig. 7), while on the other hand opportunities to expand the total foraging effort are limited. It is clear from Figure 7 that, on a diet of leaves, neither species can afford only foraging during daylight hours during the period of the shortest days in midwinter.

Discussion

Digestibility patterns and BMR

We have demonstrated that larger avian herbivores retained food for longer periods in their intestines, with marked consequences for their digestive capacities. Both protein digestion on a diet of seeds and hemicellulose digestion on the combined diets increased with body mass of the consumer. For the digestion of easily metabolisable soluble carbohydrates no effect of body mass was apparent. Protein digestion of grass leaves showed an opposite trend with body mass, but this was probably caused by an unequal distribution of grass species over the consumers. Prop and Vulink (1992) showed that within a single species, the Barnacle Goose *Branta leucopsis,* retention times were adjusted to the quality of their food plants (mainly grasses and Bryophytes). On summer diets of low quality, Barnacle Geese achieved relatively high intake rates by retaining the food up to four times longer in their digestive tracts, which was possible because of the continuous daylight during arctic summer. The effect of longer retention times was most profound in the digestion of hemicellulose which roughly doubled, while the digestion of the cell contents (protein and soluble carbohydrates) only slightly improved (see Table 4 in Prop & Vulink 1992). This intraspecific trend was also apparent in our interspecific data set on the digestion of grass leaves. Due to longer retention times, larger species could digest hemicellulose more efficiently than the smaller ones. However, in the digestion of cell contents such an effect of body size was not visible. Mattocks (1971) did not find any cellulolytic bacteria, necessary for the degradation of cell walls, in the intestines of domestic geese, but Vulink (1980, in Prop & Vulink 1992) provided evidence for the presence of bacteria capable of fermenting hemicellulose and cellulose in the intestines of both domestic geese and White-fronted Goose *Anser albifrons.* We should, however, keep in mind that the methods used to determine digestibility are based on gravimetrical assessment of fiber fractions in food and droppings. The high quality of foods of avian herbivores means, in comparison with large mammals, a relative large error due to sampling and subsampling procedures. Especially the detailed level of digestion of different compounds therefore has to be considered with some caution.

Van Soest *et al.* (1983) derived an allometric relation predicting cellulose digestion by herbivorous animals based on body mass. Their predictions for herbivores of 4.0 and 1.6 kg would be 22.1 and 20.6 % respectively (in Buchsbaum *et al.* 1986), which agrees well with empirical data of Buchsbaum *et al.* (1986) on Canada Goose *Branta canadensis* and Brent Goose *Branta b. nigricans,* indicating that cellulose digestion in geese is similar to or somewhat higher than the values predicted by Van Soest and co-workers. Our values for hemicellulose digestion on a foliage diet range between 10 - 40% for a 1 kg animal, and between 10 - 60% for a 4 kg animal. The contribution of hemicellulose digestion in the energy intake of the birds under study was *c.* 13% and 15% on seeds and storage material respectively, and 26% on foliage, which is in fair agreement with the values reported by Buchsbaum *et al.* (1986), ranging between 2 and 17%.

Energy expenditure in *Anseriformes* at rest does not deviate from other birds, and the exponent upon body mass found in this study (0.687 based on 19 species), is indistinguishable from the exponent Zar (1969) derived for waterfowl (0.685, based on 9 species). The daily energy expenditure in water birds proved to be remarkably low; an average working level of 1.8 times Basal Metabolic Rate was found. Bennett and Harvey (1987) pointed out that not only *Anseriformes* are having low levels of activity metabolism, as herons *Ciconiiformes,* gamebirds *Galliformes,* raptors *Falconiformes* and owls *Strigiformes* show similar low working levels. However, in waders and gulls *Charadriiformes* and passerines *Passeriformes* relatively high working loads were found (Bennett & Harvey 1987). The low working level in water birds can be explained by low thermoregulation costs (see Bech 1980, but see Chapter 4) and low activity levels, in particular a limited amount of time spent on flying. If this is the case, one would expect to find no profound differences in the estimates of daily energy expenditure between

caged and free-living birds. Indeed, estimates of existence metabolism do not deviate from the daily metabolisable energy intake estimates and from the time energy budget estimates (Fig. 4).

The herbivorous water birds are in this respect on the leisurely side of the avian spectrum, but they combine this low energy expenditure with remarkably long periods of activity. Food plants in the diet of herbivorous water birds can be categorised as a rather stable and predictable source of energy, but relatively poor in quality. The only way these food sources can be utilised is by an animal which can devote long periods to foraging (in the proximity of safe roosts), doing so at a low daily cost (further discussion in Chapter 20).

Balancing energy intake and energy expenditure; time spent foraging
In order to balance its energy intake and energy expenditure, a bird has to spend a certain amount of time on foraging. Using the equations 5 and 6 this critical amount of time spent on foraging could be estimated. In Table 3 estimates of the critical time spent foraging are given for a variety of birds, listed in sequence of body mass. These estimates are compared with empirical data on foraging time taken from literature. Empirical values higher than predicted indicate birds depositing fat, values lower than predicted indicate a possibly negative energy balance. The estimated times spent foraging and the empirical data are in general agreement $(R^2 = 0.46, N = 14, P < 0.01)$. However, note that not every individual or population is necessarily in energy balance over a certain time. Especially for larger birds which carry relatively more fat, a daily basis is a relatively small time span to balance energy intake and expenditure. Beside this factor, differences in the quality of the food are also affecting the time spent on foraging. The latter may explain that six studies reported shorter foraging times than predicted (all on grass), whereas only two showed a longer foraging time (on seeds).

Table 3. Empirical data from literature on the time spent on foraging on a 24 h basis, compared to our estimates of the critical foraging time needed to maintain energy balance (derived by equations 5 and 6).

species	diet	M (kg)	observed foraging time (h)	ref.	predicted foraging time (h)
Teal *Anas crecca*	seeds	0.31	11.0	1	8.2
Wigeon *Anas penelope*	grass	0.57	13.9	2	13.7
Ring-necked Duck *Aythya collaris*	tuber	0.72	7.2/9.6	3	7.2
Gadwall *Anas strepera*	grass	0.79	14.9	4	13.4
Pochard *Aythya ferina*	seeds	0.82	7.0	5	7.0
Barnacle Goose *Branta leucopsis*	grass	1.80	7.0/8.9	6	12.2
Barnacle Goose *Branta leucopsis*	grass	1.80	7.7	7	12.2
White-fronted Goose *Anser albifrons*	grass	2.00	7.4	8	12.0
White-fronted Goose *Anser albifrons*	grass	2.00	13.2	9	12.0
Pink-footed Goose *Anser brachyrhynchus*	grass	2.50	9.4	10	11.8
Lesser Snow Goose *Chen c. caerulescens*	seeds	2.50	3.1	11	5.8
Greater Snow Goose *Chen c. atlanticus*	grass	3.00	11.5/13.0	12	11.5
Andean Goose *Chloëphaga melanoptera*	grass	3.18	8.9	13	11.5
Bewick's Swan *Cygnus c. bewickii*	seeds	6.00	6.0	14	4.8

References

1 Tamisier in Mayhew (1988), 2 Mayhew (1988), 3 Jeske & Percival (1995), 4 Paulus in Mayhew (1988), 5 Klima in Mayhew (1988), 6 Prop & Vulink (1992), 7 Owen *et al.* (1992), 8 Ebbinge *et al.* (1975), 9 Mooij (1992), 10 Madsen (1985), 11 Frederick & Klaas (1982), 12 Gauthier *et al.* (1984), 13 Summers & Castro (1988), 14 Rees & Bowler (1991).

The concept of the herbivore as a "prisoner of its food supply" as proposed by Drent and Prins (1987), is further worked out by the data described above and illustrated in Figure 7. Metabolisable energy intake, body mass and time spent on foraging have been plotted against the fibre content of grass leaves, being a measure of the quality of the food plants. Three important conclusions can be drawn from this graph:

1. A small herbivore has to select high quality food in order to maintain its energy balance.
2. A change in fibre content (quality) of the food plants has much more implications for a small herbivore than for a larger one.
3. A limit imposed on the daily time spent on foraging is easily reached for a small herbivore, but is unlikely to be commonly reached for a large avian herbivore, unless the energy expenditure increases dramatically (*e.g.* due to disturbance or degree of water contact, *cf.* Chapter 4) and/or food quality decreases drastically (*e.g.* severe cold). In this scenario a bird can increase its energy intake by spending more time on foraging (unless the digestive capacity of the gut is not surpassed) or selecting food plants of a higher quality (lower fibre content).

For the individual species, size of the body has consequences for the dietary options that are open. Our model correctly predicts that Teal, at the lower end of the range in mass, is an obligate seed-eater (or may switch to energy-dense animal prey), for which grass leaves provide insufficient food per unit of time. Also, the habit of rooting up below ground storage organs of plants is open only to the larger species such as geese and swans, which in turn have difficulties in exploiting small natural seeds as ducks can.

Again, the paramount role of agricultural crops and leftovers after harvest as food for waterfowl was highlighted. Both kernels of cereals and maize, root crops such as sugar beet and potato as well as fertilised leaves of grass and cereals provide a highly digestible food. As has been outlined elsehere, the result of the presence of these resources was a tremendous increase of the number of herbivorous *Anatidae* (Chapter 3, Van Eerden *et al.* 1996).

On a large scale, the time-energy paradigm in avian herbivores, which has its basis in digestive (in)capability, also has consequences for the migration system. Migratory waterfowl choose their route in spring such that they follow the "green wave" of emerging new growth to the North, thereby encountering at higher latitudes food plants of higher quality and longer daylight periods which allow extended foraging. This strategy provides extra time to store surplus energy as fat, a necessary prerequisite for successful breeding (Prop *et al.* 1984, Loonen 1997, Ebbinge *et al.* 1982).

Acknowledgements

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Appendix 1.

Retention time

Body mass (M), dropping interval (I), dropping length (LD), digestive tract length (LDT) and the calculated variables, passage rate (V = LD/I) and retention time (R = LDT x I/LD). Values for dropping interval (I) or dropping length (LD) in bold are extrapolated from body mass, see equation [1]) and [2]) below.

Species	M (kg)	I (s)	LD (mm)	LDT (mm)	V (mm/s)	R (s)
Teal *Anas crecca*	0.315	196	24.9	1220	0.13	9600
Wigeon *Anas penelope*	0.575	168	35.1	1280	0.21	6130
Pintail *Anas acuta*	0.75	**211**	44.1	1730	**0.21**	**8277**
Mallard *Anas platyrhynchos*	1.05	**239**	**46.3**	1430	**0.19**	**7382**
Brent Goose *Branta b. bernicla*	1.3	243	**51.0**	1980	**0.21**	**9434**
Barnacle Goose *Branta leucopsis*	1.6	280	54.5	1910	0.19	9810
White-fronted Goose *Anser albifrons*	2.0	**303**	**62.1**	1730	**0.20**	**8441**
Greylag Goose *Anser anser*	3.3	266	81.4	2040	0.31	6670
Bewick's Swan *Cygnus c. bewickii*	6.0	523	100.7	2770	0.19	14390
Whooper Swan *Cygnus cygnus*	8.7	451	118.0	3170	0.26	12120
Mute Swan *Cygnus olor*	10.7	718	**133.3**	4030	**0.19**	**21707**

[1]) Regression of log-transformed dropping interval on log body mass was highly significant and body mass explained 84% of the variance. The relation describing dropping interval I (s) as a function of body mass M (kg): I = 235.3 $M^{0.363}$ (R^2 = 0.84, N = 8, P < 0.005)

[2]) Regression of log-transformed dropping length on log body mass was highly significant and body mass explained 99% of the variance. The relation describing length of a dropping LD (mm) as a function of body mass M (kg): LD = 45.27 $M^{0.456}$ (R^2 = 0.99, N = 7, P < 0.0001)

Appendix 2.

Length of digestive tract

Length of the digestive tract in *Anseriformes* of the western Palearctic. Species have been arranged according to body size. *Caecum* length has been measured separately.

Body mass M, duodenum length (D, in cm), ileum length (I), rectum length (R) and caecum length (C) and the total intestine length , excluding *caecae* (Tot).

Species:	M (kg)	D (cm)	I (cm)	R (cm)	Tot. (cm)	C. (cm)
Garganey *Anas querquedula*	0.29	14	105	4	123	3
Teal *Anas crecca*	0.31	21	93	8	122	10
Shoveler *Anas clypeata*	0.42	24	257	8	289	11
Wigeon *Anas penelope*	0.57	23	102	8	128	19
Ferruginous Duck *Aythya nyroca*	0.61	19	94	7	120	10
Gadwall *Anas strepera*	0.75	31	172	10	214	27
Pintail *Anas acuta*	0.75	29	131	8	173	17
Pochard *Aythya ferina*	0.80	28	124	-	-	15
Mallard *Anas platyrhynchos*	1.05	25	106	7	143	12
Brent Goose *Branta b. bernicla*	1.30	28	159	11	198	22
Red-breasted Goose *Branta ruficollis*	1.30	21	123	-	-	12
Barnacle Goose *Branta leucopsis*	1.60	26	153	11	191	32
White-fronted Goose *Anser albifrons*	2.00	26	134	12	173	24
Pink-footed Goose *Anser brachyrhynchus*	2.50	30	162	1	205	28
Greylag Goose *Anser anser*	3.30	36	156	12	204	23
Bean Goose *Anser fabalis*	2.70	33	155	12	200	26
Bewick's Swan *Cygnus c. bewickii*	6.00	35	197	18	277	23
Whooper Swan *Cygnus cygnus*	8.70	45	253	19	317	28
Mute Swan *Cygnus olor*	10.70	48	340	15	403	38

Appendix 3.

Basal Metabolic Rate

Basal Metabolic Rate (BMR, in W) of *Anseriformes*, arranged in sequence of body mass. Body mass according to original data supplied by the authors of the studies cited.

Species:	M (kg)	BMR (W)	ref.
Teal *Anas crecca*	0.250	1.67	1
Garganey *Anas querquedula*	0.289	2.23	1
Wood Duck *Aix sponsa*	0.460	2.31	2
Shoveler *Anas clypeata*	0.554	3.88	1
Ferruginous Duck *Aythya nyroca*	0.610	3.03	1
Wigeon *Anas penelope*	0.672	3.05	2,3
Ring-necked Duck *Aythya collaris*	0.719	3.27	4
Pintail *Anas acuta*	0.721	4.37	1
Gadwall *Anas strepera*	0.791	6.21	1
Black Duck *Anas rubripes*	0.904	3.57	5
Mallard *Anas platyrhynchos*	0.967	4.20	2,6
Brent Goose *Branta bernicla*	1.242	4.81	6,7
Red-crested Pochard *Netta rufina*	1.237	7.10	1
Barnacle Goose *Branta leucopsis*	1.812	5.18	7,8
Northern Screamer *Chauna chavaria*	2.62	6.88	9
Greylag Goose *Anser anser*	3.236	9.02	7,10
Bewick's Swan *Cygnus c. bewickii*	5.007	12.16	7
Trumpeter Swan *Cygnus buccinator*	8.88	20.26	9
Mute Swan *Cygnus olor*	8.3	30.29	11

References

1 Bennett & Harvey (1987), 2 Gavrilov in Pinowski & Kendeigh (1977), 3 Brunckhorst (1995), 4 Jeske & Percival (1995), 5 Hartung (1967), 6 Daan *et al.* (1990), 7 M.J.J.E. Loonen unpubl. data, 8 Nolet *et al.* (1992), 9 Benedict & Fox (1927) in Lasiewski & Dawson (1967), 10 Gavrilov & Dol'nik in Pinowski & Kendeigh (1977), 11 Bech (1980).

Appendix 4.

Daily Energy Expenditure

Body mass (M, in kg) and Daily Energy Expenditure (DEE, in W) of *Anseriformes*. The methods on which the values are based are indicated: caged Existence Metabolism (EM_c), Doubly Labelled Water caged birds (DLW_c), Daily Metabolisable Energy Intake (DMEI) or Time Energy Budgets (TEB).

| species:	M (kg)	EMc (W)	DMEI (W)	TEB (W)	ref.
Blue-winged Teal *Anas discors*	0.34	4.41			1
Wood Duck *Aix sponsa*	0.45	4.56			2
Baikal Teal *Anas formosa*	0.50			7.22	3
Black-bellied Tree Duck *Dendrocygna autumnalis*	0.71	9.16			4
Ring-necked Duck *Aythya collaris*	0.72			6.36	5
Wigeon *Anas penelope*	0.72	6.85	7.19	5.52 [1]	2,6,7,8
Black Duck *Anas rubidiceps*	0.90			6.87	9
Red-crested Pochard *Netta rufina*	1.02	6.16			10
Mallard *Anas plathyrhynchos*	1.07	7.84	6.83		2,11
Red-breasted Goose *Branta ruficollis*	1.12	7.72			10
Brent Goose *Branta b. bernicla*	1.25		9.69		12
Ruddy-headed Goose *Chloëphaga rubidiceps*	1.65		10.4		13
Barnacle Goose *Branta leucopsis*	1.80		11.4	11.3	15, 25
White-fronted Goose *Anser albifrons*	2.50		17.5	14.9	14
Pink-footed Goose *Anser brachyrhynchus*	2.50		23.7	13.7	16
Lesser Snow Goose *Chen c. caerulescens*	2.50			20.0	17
Magellan Goose *Chloëphaga leucoptera*	2.72	14.2			10
Spur winged Goose *Plectropterus gambensis*	2.90		14.8		18
Greater Snow Goose *Chen c. atlanticus*	3.00		16.0	19.1	19, 20
Greylag Goose *Anser anser*	3.251	15.7			10
Upland Goose *Chloëphaga picta leucoptera*	3.40		22.6		13
Andean Goose *Chloëphaga melanoptera*	3.18		15.6		24
Canada Goose *Branta canadensis*	4.30	22.8			22
Cape Barren Goose *Cereopsis novaehollandia*	4.50	17.1	25.6		10,21
Bewick's Swan *Cygnus c. bewickii*	5.50		36.2		23

[1] DLW caged.

References: 1 Owen (1970), 2 Gavrilov in Pinowski & Kendeigh (1977), 3 Allport *et al.* (1991), 4 Cain (1973), 5 Jeske & Percival (1995), 6 Brunckhorst (1995), 7 Madsen (1988) in Brunckhorst (1995), 8 Mayhew (1988), 9 Owen (1970) in Pinowski & Kendeigh (1977), 10 Gavrilov & Dol'nik in Pinowski & Kendeigh (1977), 11 Sugden in Halse (1984), 12 Drent *et al.* (1979), 13 Summers & Grieve (1982), 14 Mayes (1991), 15 Ebbinge *et al.* (1975), 16 Madsen (1985), 17 Frederick & Klaas (1982), 18 Halse (1984), 19 Gauthier *et al.* (1984), 20 Bédard & Gauthier (1989), 21 Mariott & Forbes (1970), 22 Williams (1965) in Pinowski & Kendeigh (1977), 23 Beekman *et al.* (1991), 24 Summers & Castro (1988), 25 Owen *et al.* (1992).

Chapter 7

Simultaneous mass starvation of wintering diving ducks in Switzerland and the Netherlands: A wrong decision in the right strategy?

Werner Suter & Mennobart R. van Eerden
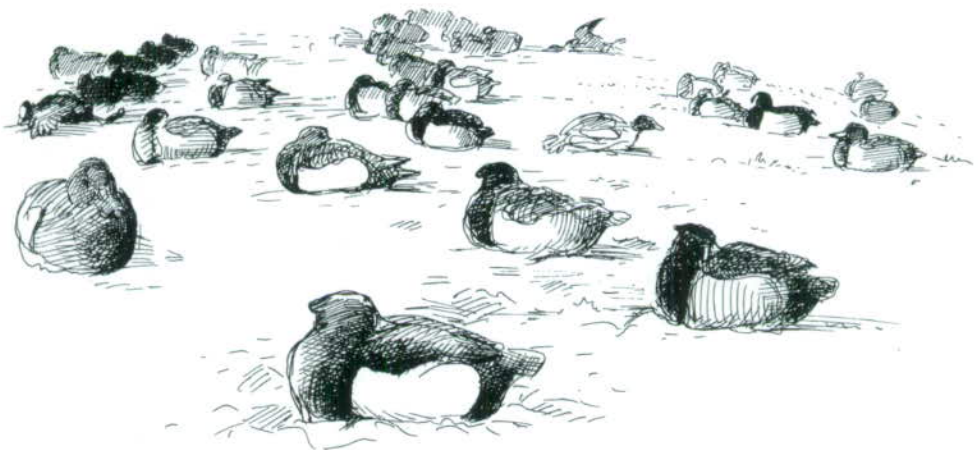
CONSTRAINTS

Simultaneous mass starvation of wintering diving ducks in Switzerland and the Netherlands: A wrong decision in the right strategy?

On an important wintering site for waterfowl along the river Rhine, Switzerland, between 2700 and 6200 diving ducks died from starvation in March 1986. At the same time, mass starvation occurred in the western part of the Dutch Wadden Sea with at least 18 000 water birds involved of which over 14 000 were diving ducks. In Switzerland, only Pochard and Tufted Duck were affected. Both species are dependent on the Zebra Mussel *Dreissena polymorpha*. Mussel stocks are annually depleted by the birds towards late winter, around the onset of home migration. In 1986 however, when the available mussel biomass was probably below average, a month-long cold spell occurred in February. In the Netherlands the diving ducks faced equally harsh weather conditions when available *Mytilus edulis* food stocks were low. In both areas, many birds remained and starved, instead of moving away. The inadequate reaction may be explained by a waterfowl migration strategy which does not account for extremely long cold spells in late winter, since the probability of such events is very low.

Introduction

Although starvation is generally considered the main natural mortality factor in waterfowl (Owen 1977, Reinecke *et al*. 1982), mass mortality is more often associated with the outbreak of diseases, such as botulism (Smith 1976, Stout & Cornwell 1976). Mass starvation seems to be uncommon and restricted to unusually severe weather conditions. Wrånes (1988) and Mørner (1982) report some 14 000 Eider *Somateria mollissima* having starved to death in the Skagerrak area in the winter 1981/82, due to a combination of food shortage and low ambient temperatures. But even in the extremely cold winter of 1962/63, reported casualties for England and Wales numbered less than 3000 waterfowl (Boyd 1964). The impact of cold winters on waterfowl populations is sometimes easier to detect indirectly through the analysis of population statistics or ringing recoveries (Andersen-Harild 1981, Nilsson 1984, Cavé & Visser 1985), than by finding dead birds. Predators and scavengers remove most corpses within 24 hours after death (Meile 1991). Only in large incidents, when predatory animals are swamped by dead waterfowl, the corpses persist for several days and become noticed. Since deaths from starvation are more evenly spread in space and time than from the outbreak of a disease, and since not all species are affected to the same degree, accumulations of starved cadavers are unusual. This paper reports two cases of mass starvation in diving ducks, one on the river Rhine near lake Constance, an important Swiss wintering site, the other in the western part of the Dutch Wadden Sea. The incidents occurred simultaneously in late winter 1985/86, just after an unusually long cold spell. The inadequate reaction of the ducks is discussed with respect to migration strategies and energetics in late winter.

Numbers and distribution

Normal situation, upper Rhine

The river Rhine below lake Constance provides some of the best habitat in Switzerland for wintering diving ducks, particularly for Pochard *Aythya ferina*, Tufted Duck *A. fuligula* and Goldeneye *Bucephala clangula*. Numbers of Little Grebe *Tachybaptus ruficollis*, Mallard *Anas platyrhynchos* and Coot *Fulica atra* are also high (Table 1). The upper part of sector A (Fig. 1) is classified as a wetland of international importance for waterfowl, and the rest of sector A, as well as B and parts of C are also listed as important areas (Marti & Schifferli 1987).

At the western end of lake Constance and on the adjacent part of the river Rhine (upper half of sec-

Table 1. Numbers of the main waterfowl species on the river Rhine between lake Constance and Rheinsfelden barrage (sectors A - C).

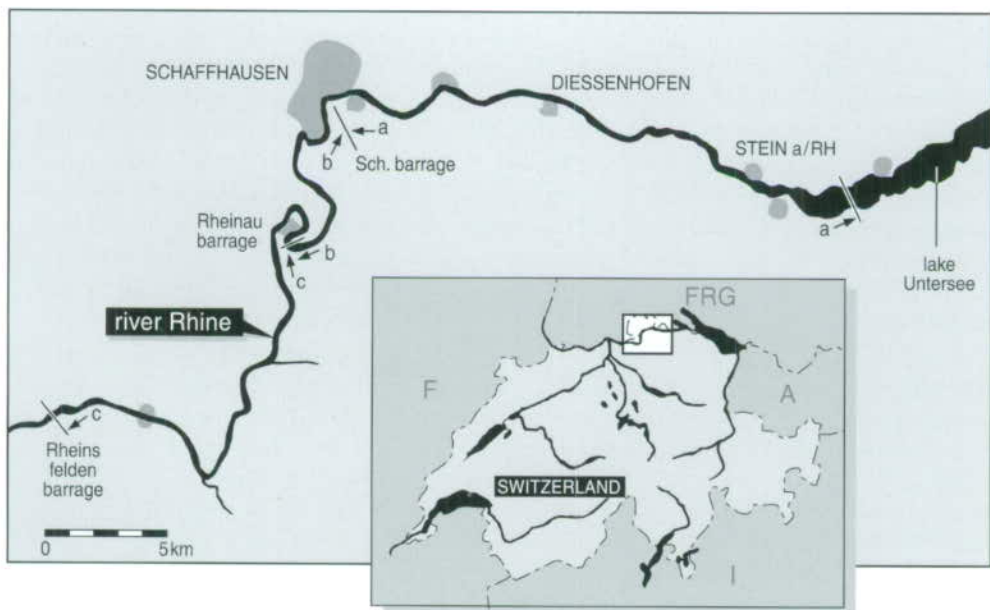|	January		March	
	1976 - 1989 mean ± SD	1986 mean ± SD	1976 - 1989	1986
Little Grebe	648 ± 216	927	781 ± 143	835
Mallard	3101 ± 995	2636	1346 ± 782	1559
Pochard	14573 ± 5340	11693	2145 ± 1664	854
Tufted Duck	24593 ± 8779	19974	5265 ± 4233	3376
Goldeneye	1813 ± 334	1514	791 ± 486	1573
Coot	10686 ± 4237	6469	7819 ± 3477	6458

Figure 1. The river Rhine in northeastern Switzerland (inset), with sectors A, B and C.

tor A), numbers of Pochard, Tufted Duck and Coot are highest in late autumn or early winter and dwindle between December and March. The remaining birds shift downstream as they deplete the banks of Zebra Mussels *Dreissena polymorpha*, their main food. Coots proceed fastest, Tufted Ducks slowest, and Pochards at intermediate speed, according to different diving abilities. Tufted Ducks are more efficient in exploiting a given area and can therefore stay longer. Goldeneye and Little Grebe mainly feed on Caddisfly larvae *Hydropsyche* sp. and do not participate in the movements (Suter 1982a-c). Figure 3 suggests that Coots, Pochards and Tufted Ducks do not only shift within sector A, but that their movements extend further downstream, since the percentage of birds in sectors B and C is higher in March than in January.

The situation in late winter 1985/86, upper Rhine

Waterfowl numbers in January 1986 were slightly below the 14-year mean, but well within the normal range (Table 1). Little Grebes were more numerous whereas Coot numbers were exceptionally low. By March 1986, populations of Little Grebe, Mallard, Goldeneye and Coot had remained at the January level or slightly below and thus were similar to the long-term mean, except in the Goldeneye where they were much higher. Numbers of Pochard and Tufted Duck, however, were much below average.

The mussel-feeding species also shifted downstream earlier and faster than usual. In both January and March, sector A held a much smaller percentage of Pochard and Tufted Duck than usual, while the percentages were 1.5 to 3 times higher in sectors B and C (Fig. 3). The same applied to the Coot in March. The distribution of Little Grebe, Goldeneye and Mallard was similar to the long-term mean in both months.
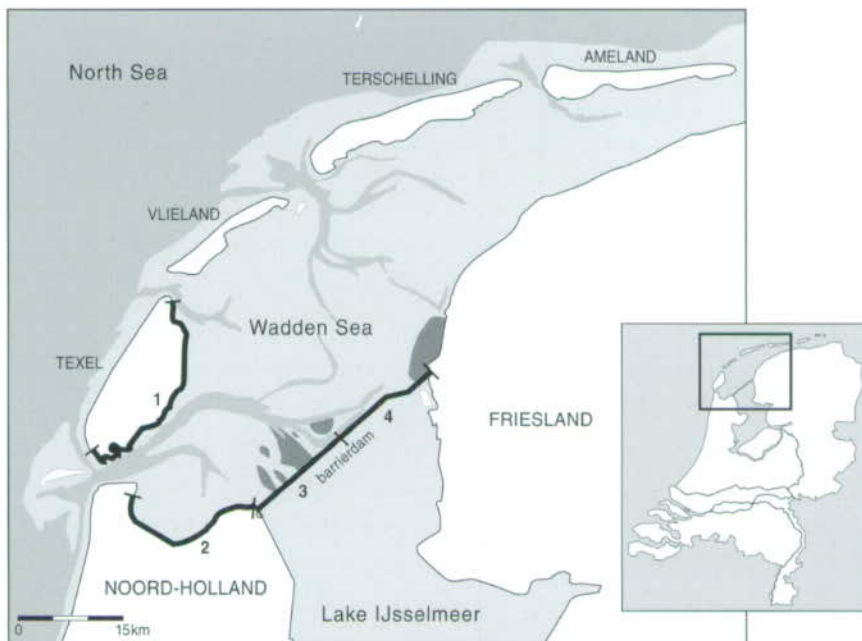

Figure 2. Western Wadden Sea and lake IJsselmeer. Transects counted (1 - 4, *cf*. Table 4) and important feeding grounds for Scaup (hatched areas) are indicated. Noorderhaaks is the sand bar southwest of the island of Texel.
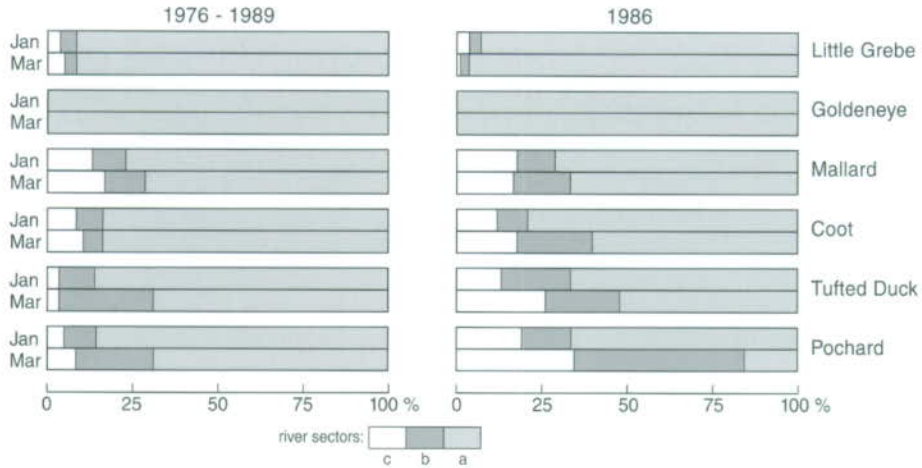
Figure 3. Percentages of the most common waterfowl species in the upper Rhine sectors A, B and C, given as mean values for January and March 1976-89, respectively, and for January and March 1986.

Normal situation, Wadden Sea

The area of lake IJsselmeer and the western part of the Wadden Sea is among the most important European sites for diving ducks (Fig. 2). It may hold up to 163 000 Tufted Duck, 85 000-150 000 Scaup *Aythya marila*, 51 000 Pochard, 11 000 Goldeneye and 67 000 Coot (Van Eerden & Bij de Vaate 1984, Monval & Pirot 1989). Eider numbers inshore fluctuate more strongly between 600 and 45 000 (Swennen 1985, Swennen *et al.* 1989, pers. obs.). Except for Scaup and Eider most species of diving ducks are largely confined to the freshwater conditions of lake IJsselmeer (2000 km², 2-4 m water depth). Here the ducks forage on *Dreissena* which is abundant over large areas (Van Eerden & Bij de Vaate 1984, Bij de Vaate 1991). The part of the Wadden Sea north of the barrier dam holds important concentrations of the bivalves *Mytilus edulis* and *Cerastoderma edule* some of which are used as shellfish cultures. Especially *Mytilus* spat is supposed to be the food source for Scaup. During frost the shallow lake IJsselmeer readily freezes within a few days. Open water remains at the river IJssel, the Amsterdam harbours and some large canals (Noordzeekanaal, Amsterdam-Rijnkanaal). Due to the currents the western part of the Wadden Sea normally also stays open. In the periods of frost Tufted Duck, Pochard and most Coots keep to their freshwater habitat, partly moving away to the large rivers and the delta area in the province of Zeeland (Van den Bergh 1988). Scaup concentrate in the western Wadden Sea, joined by Goldeneyes and smaller numbers of the other species (Smit & Wolff 1981).

The situation in late winter 1985/86, Wadden Sea

Only 13 100 Scaup were counted during an aerial survey of the western part of lake IJsselmeer and the western Wadden Sea on 17 January 1986, prior to the cold spell. Virtually no Scaup and only 1500 Eider were present at the usual feeding grounds north of the barrier dam (Fig. 2), indicating poor feeding conditions. Fish-eating species such as Goosander *Mergus merganser* (32 800) and Red-breasted Merganser *M. serrator* (10 300) were more abundant than on average. During the period of frost many birds moved away from the lake. Open water remained especially north of the barrier dam and in the deep gullies between the islands. About half of the shallower areas of the western part of the Wadden Sea was frozen or blocked by ice dams. The aerial survey of 18 February 1986 showed a total of 31 500

Table 2. Numbers of waterfowl found dead along the upper river Rhine at Schaffhausen barrage (1), Rheinsfelden barrage (2) and along the shore near Diessenhofen (3), and species percentages (N = 805).

species	(1)[1]	(2)	(3)	%[2]
Little Grebe	(4)	1	1	0.7
Mallard	(-)	3	2	0.6
Pochard	76	318	6	41.0
Tufted Duck	342	321	71	53.3
Goldeneye	(-)	1	-	0.1
Coot	88	21	9	4.0
unidentified	-	-	10	-

[1]   Number of birds other than Pochard, Tufted Duck and Coot known for only 1 out of 11 days when corpses were examined.

[2]   Excludes those samples from (1) where numbers of only three species are known. Single casualties of Great Crested Grebe and Scaup are included in the calculation, but not listed.

Table 3. Waterfowl counts in the Wadden Sea-IJsselmeer area on both sides of the barrier dam Afsluitdijk (cf. Fig. 2). The number of birds washed ashore is expressed as percentage of the February count (mortality index). B = benthivore, P = piscivore. The mortality index for Coot refers to birds feeding in the water.

species	normal		17 Jan 1986	18 Feb 1986	N died Afsluitdijk	mortality index	food
Great Crested Grebe	250 -	1000	400	390	73	18.7	P
Pochard	200 -	1000	15	200	155	77.5	B
Tufted Duck	1500 -	3500	1520	2550	951	37.3	B
Scaup	10 000 -	40 000	-	31 500	9817	31.2	B
Eider	1000 -	10 000	6000	12 800	70	0.5	B
Goldeneye	500 -	1500	475	1050	785	74.8	B
Smew	50 -	100	-	200	1	0.5	P
Red-breasted Merganser	250 -	2500	-	840	6	0.7	P
Goosander	1000 -	5000	175	3950	0	0	P
Coot	250 -	1500	475	800	184	92.0	B

Scaup here. Apparently birds from further NE had been joining the Scaup already present. However, numbers still stayed well behind those of other years. Numbers of other diving ducks increased as a result of the complete freezing of lake IJsselmeer. Only Tufted Duck (2550) and Goosander (3950) were present in fair numbers along the Afsluitdijk although they represent only a small proportion of the numbers counted at lake IJsselmeer during the January census (Table 3).

Mass mortality

Numbers

After the mild January 1986, a very unusual and long-lasting cold spell occurred in western Europe. In early February, mean temperatures dropped sharply to around -10 °C and remained between -5 °C and -10°C for much of the month (Fig. 4). From 7 February to 4 March, they were up to 10 °C below the long-term mean. At the river Rhine, mortality set in briskly around 1 March, i.e. 21 days after the onset
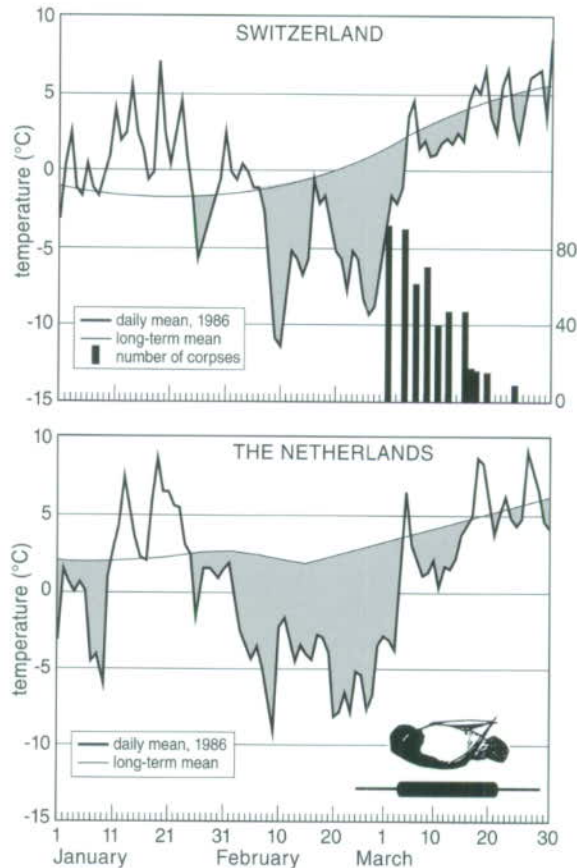
Figure 4. Daily mean temperatures (1986 and long-term) at Schaffhausen, Switzerland, and Lelystad, the Netherlands, and the die-off period. For Switzerland numbers of corpses of Tufted Ducks, Pochards and Coots collected at Schaffhausen barrage are given, for the Netherlands the period when dead birds were washed ashore in the barrier dam region (line: total period, bar: mass numbers; T. Peper pers. comm.)

of the cold spell. Until about 20 March 1986, waterfowl died on a 45-50 km long stretch of the river below lake Constance (Fig. 1). At least 1177 corpses were collected in the barrages of the sectors A and C (Table 2), and some 50 were removed from the barrage at Rheinau in sector B (estimation by the staff). In the middle of the period, 99 corpses washed up along the shore near Diessenhofen (sector A) were counted on a sample of 2.2 km of shoreline, *i.e.* 90 birds km^{-1} for both shores. Estimates of the total number of perished birds rely on the figure used when extrapolating the numbers of beached birds over the entire area. The total losses may have numbered between 2700 and 6200 (> 1200 birds collected at the barrages plus between 30 and 100 corpses ashore km^{-1}, for 50 km).

In the western part of the Wadden Sea area counting of dead birds was conducted on the islands of Texel, Noorderhaaks and Ameland, along the barrier dam Afsluitdijk and along the mainland coasts of Noordholland and Friesland (Fig. 2). Out of a total of 187 km suitable shoreline in the region, 99 km were searched and a total number of 17 810 beached corpses was estimated for the entire area (all waterbirds excluding waders, gulls, and seabirds). The mean number was 207 birds km^{-1}, and highest

numbers were counted along the barrier dam between Den Helder and Den Oever (255 birds km⁻¹) and between Den Oever and Breezanddijk (296 birds km⁻¹). The first beached birds were found on 24 February, but most victims were washed ashore between 3 and 20 March.

Species-specific mortality

The dead waterfowl examined along the upper Rhine belonged to 8 species, six of them common in the area (Tables 1, 2), and included one Great Crested Grebe *Podiceps cristatus* and one Scaup. These two species and those without losses are excluded from further analysis. Pochard and Tufted Duck account for 94.4% of the dead birds (Table 2), and Coot for another 4.0%. Frequency distributions of birds present at the mid-March waterfowl count (although many birds had already died by this time) and of victims differed significantly ($P < 0.001$, df = 5, chi-square = 2532 for absolute values). The ratio observed : expected is 7.1 for Pochard and 2.3 for Tufted Duck, but 0.01-0.13 for the other four species. Pochard and Tufted Duck therefore suffered most, while the other species were barely affected. However, a mortality index (number of dead birds expressed as a percentage of the nearest waterfowl count) cannot be estimated since a too small proportion of the shoreline was surveyed for beached birds. But the samples collected at the barrages allow interspecific comparisons. Pochard suffered higher losses than Tufted Duck. The difference is highly significant with both March and January counts for reference ($P < 0.001$, χ^2 with Yeates' correction, df = 1). Pochard also suffered significantly more than Tufted Ducks during the second half of the period in sector C, with the March count as the reference ($P < 0.01$), but slightly less than Tufted Duck at the same time in sector A ($P < 0.05$). Moreover, Pochards died earlier than Tufted Ducks. There were relatively more Pochards in the samples of the first half-period, but relatively more Tufted Ducks in the second half, both in sector A ($P < 0.001$) and sector C ($P < 0.05$).

In the Wadden Sea 23 species of waterbirds were recorded dead (Table 4). Most casualties were benthivorous ducks (96.8%). Herbivorous waterfowl accounted for 2.4%, piscivorous waterfowl for 0.7% and planktivorous ducks for 0.04%. Most victims were Scaup (82.3%) followed by Tufted Duck (5.7%) and Goldeneye (5.8%). Unlike for the Swiss incident, a mortality index may be computed, since a much higher proportion of the beachline was checked for corpses. The mortality index is an estimate for the mortality since the mortality rate in the strict sense is unknown. There are no data on the turnover in bird numbers between the February count as a reference for the population size and the die-off, and there is no information about possible interspecific differences in recovery rates. Compared to the February count the fish-eaters had few casualties. The three *Mergus* species lost less than 1%, while losses in the Great Crested Grebe were significantly higher with 18.7% ($\chi^2 = 839.6$, df = 1, $P < 0.0001$). Benthivorous ducks were affected more strongly than fisheaters ($\chi^2 = 2313.1$, df = 1, $P < 0.0001$). Within the group of benthos feeders the sequence of mortality index was Scaup (31.2%), Tufted Duck (37.3%), Goldeneye (74.8%), Pochard (77.5%) and Coot (92.0%). The latter figure was derived by excluding those Coot foraging on the vegetated dike. All interspecific differences except between Goldeneye and Pochard are significant at $P < 0.001$ (χ^2 for absolute values).

Sex-specific mortality

For the Dutch case data are available on the sex ratio in the Scaup population before mortality set in. The proportion of males was 60.7% in the February count ($N = 2107$ birds sexed out of a flock of 31 500) but significantly lower among the dead birds (52.1%, $N = 4496$, $\chi^2 = 37.9$, df = 1, $P < 0.001$). Thus more female Scaup died than males. The percentage of dead females was also higher in the eastern (marginal) part than in the western (central) part of the region ($\chi^2 = 6.30$, df = 1, $P < 0.02$; Table 5).

Table 4. Corpses of beached waterfowl in the western part of the Dutch Wadden Sea. Data for transect 1 from Leopold *et al.* 1986. Numbers of transects 2, 3 and 4 derived by extrapolation. 1: Texel, 2: Den Helder-Den Oever. 3: Den Oever-Breezanddijk, 4: Breezanddijk-Kornwerderzand (see Fig. 2).

species	transect				total	%
	1	2	3	4		
Red-throated Diver *Gavia stellata*	5	5	-	1	11	0.06
Black-throated Diver *G. arctica*	1	-	-	-	1	0.01
Great Crested Grebe *Podiceps cristatus*	16	10	22	41	89	0.50
Red-necked Grebe *P. grisegena*	5	-	-	1	6	0.03
Slavonian Grebe *P. auritus*	5	-	-	-	5	0.03
Greylag Goose *Anser anser*	1	-	-	-	1	0.01
Brent Goose *Branta bernicla*	5	-	-	-	5	0.03
Shelduck *Tadorna tadorna*	155	40	12	4	211	1.18
Wigeon *Anas penelope*	4	5	-	1	10	0.06
Teal *A. crecca*	-	10	10	6	26	0.15
Mallard *A. platyrhynchos*	35	10	4	-	49	0.27
Pintail *A. acuta*	95	20	4	-	119	0.67
Shoveler *A. clypeata*	3	5	-	-	8	0.04
Pochard *Aythya ferina*	8	15	78	62	163	0.91
Tufted Duck *A. fuligula*	60	400	380	171	1011	5.67
Scaup *A. marila*	4850	5445	3172	1200	14 667	82.26
Eider *Somateria mollissima*	22	30	34	6	92	0.52
Common Scoter *Melanitta nigra*	20	20	18	20	78	0.44
Velvet Scoter *M. fusca*	3	10	2	2	17·	0.10
Goldeneye *Bucephala clangula*	240	315	340	130	1025	5.75
Smew *Mergus albellus*	1	-	-	-	1	0.01
Red-breasted Merganser *M. serrator*	5	-	4	2	11	0.06
Coot *Fulica atra*	40	35	68	81	224	1.26
Total	5579	6375	4148	1728	17 830	
N km^{-1}	174	255	296	115		

Table 5. Sex ratio of Scaup washed ashore in the western part of the Wadden Sea, March 1986. Sex ratio counts in combination with total numbers result in a weighted mean of 52.1% of males which died.

transect	females	males	% males	source
Ameland	28	19	40.4	E. v. Hijum
Kornwerd - Sexbierum	9	7	(43.8)	E. v. Hijum
Kornwerderzand - Breezanddijk	105	89	45.9	E. v. Hijum, M.R. v. Eerden
Breezanddijk - Den Oever	571	698	55.0	M.R. v. Eerden
Den Oever - Den Helder	470	502	51.7	M.R. v. Eerden
Texel	951	1047	52.4	M. Leopold *et al.* 1986

Condition of the birds

All diving ducks found dead were completely emaciated and had apparently starved. Loss of body mass averaged 29-41% in the Swiss birds and 48-54% in the Dutch birds, when compared to healthy birds from the same area (Table 6). Only one male Pochard from the Rhine with 930 grams was within the normal mass range of the species (not included in Table 6). The body composition of 9 Swiss Pochards and 11 Tufted Ducks was analysed by Jenni-Eiermann and Schifferli (1989), who found the fat content in various organs to be only 1-13% of that in healthy birds, and the breast muscle to be reduced to 26-38% of the normal mass.

Table 6. Body mass in grams (mean, standard deviation, range and sample size) of diving ducks found dead in March 1986, and of normal weight birds from the same area (Rhine: shot or caught for ringing, January-February 1977-1981, from Suter 1982b; Dutch data of birds freshly drowned in gill-nets in lake IJsselmeer, February 1980-1989, M.R. Van Eerden unpubl.).

species	1986 mass	range	N	reference mass	range	N	% mass loss
Upper Rhine							
Pochard, male	640 ± 46	580 - 720	12	952 ± 124	735 - 1095	11	33
Pochard, female	660 ± 63	600 - 760	5	924 ± 70	805 - 1029	14	29
Tufted Duck, male	488 ± 26	455 - 520	8	801 ± 154	595 - 1025	11	39
Tufted Duck, female	454 ± 56	390 - 540	9	773 ± 78	625 - 880	22	41
Wadden Sea							
Pochard, male	606 ± 37	545 - 685	19	1160 ± 196	866 - 1320	19	48
Pochard, female	564 ± 40	495 - 615	26	1116 ± 103	1087 - 1223	8	49
Tufted Duck, male	453 ± 62	427 - 525	27	987 ± 140	842 - 1120	82	54
Tufted Duck, female	426 ± 27	385 - 500	25	899 ± 121	853 - 1052	53	53
Scaup, male	641 ± 43	580 - 731	27	1351 ± 150	1140 - 1513	251	53
Scaup, female	571 ± 22	512 - 618	30	1238 ± 155	1165 - 1476	135	54
Goldeneye, male	599 ± 33	502 - 641	19	1167 ± 136	1035 - 1290	27	49
Goldeneye, female	399 ± 12	379 - 418	14	862 ± 160	880 - 1250	54	54

Another 3 Pochards and 12 Tufted Ducks from the Rhine were examined for diseases and parasites (Christine Lobsiger *in litt.*). All birds were moderately to heavily infested by intestinal parasites (mainly the trematode family *Echinostomidae* and the cestode *Hymenolepis anatina*, but also the cestode *Fimbriaria fasciolaris*, the trematode family *Plagiorchidae* and others). In half of the birds, caeca were found to contain high numbers of the trematode *Notocotylus attenuatus* and moderate numbers of nematodes of the family *Trichuridae*, and single birds also carried other parasites. In all Pochards a latent infection by *Salmonella typhimurium* was diagnosed. However, no signs of Duck Plague (Duck Virus *Enteritis*), Avian Cholera (*Pasteurellosis*) or any other disease known to cause mass mortality in waterfowl were found. Botulism, Duck Plague and Avian Cholera cause quick death without weight loss, and birds usually die with spastic movements, leaving the body in a cramped position (L. Leibovitz, N. Rosen in Davies *et al.* 1971, Kronberger & Schüppel in Kolbe 1984, Friend 1987). Dying birds were seen sitting motionless at the shore, on ice edges or on logs. Dead birds were found frozen in sleeping positions, the head turned with the bill in the back feathers. There were also no signs of blood-dripping, excretions or untidy plumages typical of such diseases, and species were affected selectively.

Discussion

Diseases, parasites and body condition

The lack of evidence for disease and the poor body condition in the diving ducks suggests that the birds had starved. Except one Pochard, all birds weighed had lost on average 30-50% of the normal weight. Only 1-13% of the original fat remained, probably being non-metabolizable, and breast muscle atrophy was very prominent (Jenni-Eiermann & Schifferli 1989). Mean losses of 34-49% of the winter weight were also found to be lethal in Mallard (Jordan 1953), Coot (Visser 1978), Redshank *Tringa totanus* and Oystercatcher *Haematopus ostralegus* (Davidson & Evans 1982, Hulscher 1989). Wrånes (1988) reports a mass loss of 35-39% in starved Eiders in winter, while fat pre-breeding Eiders can lose up to 35% of their weight during incubation (Kuresoo & Paakspuu 1983). The parasite infestation may also have contributed to death, as it has been shown in other diving ducks, *e.g.* Eiders (Persson *et al.* 1974). Nevertheless, parasites do not seem to have caused the starvation, and thus were not the ultimate reason for death. In a sample of starved Pochard, Tufted Duck and Coot collected at the same time near the upper Rhine on lake Constance, the ducks were similarly affected by parasites, while 13 of 28 Coot were free of endoparasites and the others much less affected than the ducks (Christine Lobsiger *in litt.*). More likely, the weakness of the birds enabled the parasites to multiply.

Food shortage and starvation

There is strong evidence that food shortage was responsible for the mass mortality. As on many Swiss lakes and rivers, both Pochard and Tufted Duck rely almost completely on Zebra Mussels in the lake Constance and upper Rhine area, as do Coot to a lesser extent. Every winter 95-99% of the standing crop is taken (Suter 1982c). After depletion of the huge mussel banks at the outlet of lake Constance, the birds shift downstream where mussel densities are lower. The speed depends on the mollusc biomass available and varies from year to year (Suter 1982a-c). In the winter 1985/86, the birds reached the lower sectors earlier and were present in sectors B and C in much higher percentages, though in smaller numbers than usual (Fig. 3). This indicates that the amount of food available in 1985/86 was below average and had been largely depleted by late February in sector A, but also in sector B and C. The inferior diving ability of Pochard in comparison to Tufted Duck (Willi 1970), does not only influence local distribution patterns (Suter 1982a,b), but was also apparent in the catastrophe: Pochard suffered higher mortality and died earlier than Tufted Duck. Species not depending on Zebra Mussels, such as Mallard and other dabbling ducks, Mute Swan *Cygnus olor*, or Great Crested Grebe and Goosander, did neither show unusual distribution patterns nor increased mortality. Goldeneyes were also unaffected; their diet on the river Rhine consists mainly of Caddisfly larvae and small mussels unavailable to other diving ducks (Suter 1982a,b). Some Coot also starved, but their mortality was apparently lower than in Pochard and Tufted Duck despite their limited diving performance. Coot may supplement or even replace their mussel diet with water plants (especially Long-leaved Water-Crowfoot *Ranunculus fluitans*), algae and by grazing, or are fed by people (Hurter 1979, Suter 1982a).

The Wadden Sea case is largely comparable to the Swiss situation. Prior to the cold spell of 29 days few Scaup attended the *Mytilus* banks north of the Afsluitdijk barrier dam indicating a poor food supply. This was confirmed by the administration of the shellfish exploitation (Mosselkantoor Yerseke). Scaup preying on *Dreissena* at lake IJsselmeer moved towards the Wadden Sea where open waters remained. Many other Scaup from further NE as well as other diving ducks joined the Scaup. Neither the fish-eating ducks nor the herbivorous waterfowl suffered great losses. Within the group of benthic feeders Goldeneye, Pochard and Tufted Duck, *i.e.* the freshwater species were more severely affected than the Scaup. This may be explained by their lesser diving ability as compared to Scaup (and other sea ducks) in combination with possible competition with the larger species. In contrast to the Swiss

incident, Goldeneye had the second highest mortality in spite of its diving performance being superior to that of Pochard. This may be related to a shortage of their preferred small mollusc sizes (Pehrsson 1976), their energetically more expensive foraging behaviour (Suter 1982b) and the absence of alternative food types.

Weather, migration strategies and energetics

Food shortage alone does not explain the mass starvation. Waterfowl in northern latitudes often meet situations when food is either depleted or unavailable in harsh weather conditions. Unlike some wader species (Davidson & Evans 1982), ducks usually react quickly by moving to more favourable areas (Ogilvie 1982, Saint-Gérand 1982, Van Eerden 1984, Ridgill & Fox 1990), although there are interspecific differences in the response patterns. At the river Rhine, depletion of the mussel banks by the diving ducks is a regular phenomenon (Suter 1982c). Many birds, especially Pochard, leave before the end of the winter, and the final depletion normally coincides with the onset of spring migration. In 1986 however, the Pochards and Tufted Ducks that were still present in the area by early February did not move away but stayed until starvation.

The failure to leave the area in time may be explained by a combination of the weather situation and its timing. 1986 was characterised by a rather mild January, followed by the coldest February since 30 years and the fourth-coldest ever recorded (Fig. 4). This was due to a continuous arrival of extremely cold continental air from northeastern Europe. Had such a cold spell occurred in January, the ducks would probably have moved south-west as the food situation had become precarious. In February however, when the ducks are ready to start spring migration, movements in the opposite direction might not normally be a good option, given the uncertainty of the food and weather situation in prospective refuge areas (see Ridgill & Fox 1990). The tendency to winter as close as possible to the breeding grounds and to return early has been shown to be part of the migration strategy of many northern waterfowl species, particularly in males and older individuals (Sayler & Afton 1981). Conroy *et al.* (1989) noticed that Black Ducks *Anas rubripes* were more dispersive and undertook more long-distance migration when freeze-up occurred earlier in the season (December) than later (January). The decision to stay in spite of the food limitation and "sit out" the cold spell, must generally be appropriate in late winter. Although body weights of many northern hemisphere waterfowl decline during winter and lipid reserves of diving ducks at lake IJsselmeer are about 20% lower in February than in January (M.R. Van Eerden unpubl.), the probability that a cold spell in February lasts for longer than the survival time allowed by the fat stores is probably low, especially if the ducks are not completely deprived from any food resources. This time, however, temperatures remained below freezing point for 29 days, and the birds apparently became "trapped".

Although domestic geese are able to fast more than 40 days under experimental conditions (Le Maho *et al.* 1981) and Mallards up to 25 days (Jordan 1953), the survival time for ducks under free-living conditions is shorter. Ambient temperatures below zero markedly increase the energetic demands of diving ducks (Nilsson 1970, Smith & Prince 1973). In Pochard the standard metabolic rate (SMR) at -20 °C has been found to be 2.6 times higher than the basal metabolic rate (BMR) at 15 °C (Galhoff 1987). Preliminary analysis of lipid percentage in carcasses of normal-weight February birds from lake IJsselmeer produced values of 14.4-19.5% of fresh body mass (Table 7), slightly less than the 20% found by Serie and Sharp (1989) in adult winter male Canvasbacks *Aythya valisineria*. Survival times (Table 7) from the metabolism of lipid reserves alone can be calculated using either allometric equations (Kendeigh *et al.* 1977) or measurements of SMR in Pochard at -5 °C (Galhoff 1987). The difference in the results (5.2-6.9 *versus* 6.5-8.8 days of survival) is mainly due to the ratio applied between field and basal or standard metabolic rate. $FMR = 3 \times BMR$ is more appropriate for birds showing normal activitity but is probably too high for starving ducks that may be sitting around motionless for long

Table 7. Fresh mass, body fat, metabolisable energy content of fat, estimated daily energy expenditure (basal, field, and standard metabolic rates), and survival time for Pochard, Tufted Duck, Scaup and Goldeneye, based on Dutch body weights from Table 6.

	mass	fat	fat	metabolisable[1] energy	BMR[2]	FMR[3] 3xBMR	survival time	SMR[4]	FMR 1.5xSMR	survival time
	(g)	(%)	(g)	(kJ)	(kJ d⁻1)	(kJ d⁻¹)	(d)	(kJ d⁻¹)	(kJ d⁻¹)	(d)
Pochard, male	1160	14.8	172	6130	384	1152	5.3	612	918	6.7
Pochard, female	1116	19.5	218	7770	373	1119	6.9	589	884	8.8
Tufted Duck, male	987	17.6	174	6201	343	1029	6.0	521	782	7.9
Tufted Duck, female	899	15.6	140	4990	321	963	5.2	475	713	7.0
Scaup, male	1351	14.4	195	6950	427	1281	5.4	713	1070	6.5
Scaup, female	1238	15.2	188	6700	402	1206	5.6	654	981	6.8
Goldeneye, male	1167	16.1	188	6700	385	1155	5.8	616	924	7.3
Goldeneye, female	862	17.1	147	5239	312	936	5.6	455	683	7.7

[1] 1 g fat equivalent to 39.6 kJ (Ricklefs 1974); assimilation rate assumed to be 90%.

[2] Basal metabolic rate calculated from Kendeigh *et al.* (1977): equation 5.4.

[3] Ratio field metabolic rate : BMR = 3, according to Suter (1982b), Nagy (1987) and unpublished data for diving Tufted Duck (J. De Leeuw & M.R. Van Eerden).

[4] Standard metabolic rate measured at -5 °C for Pochard (Galhoff 1987): 0.022 kJ g⁻¹ h⁻¹.

periods. In addition to fat mobilization, protein may also be catabolized. According to Jenni-Eiermann and Schifferli (1989: tables 7, 8), starved Swiss birds had lost at least 39 g (Tufted Duck) to 52 g (Pochard) of protein. These values correspond to 702-936 kJ of metabolizable energy (Ricklefs 1974) and would provide the birds with another day of survival. Total survival time of diving ducks relying on body reserves only may therefore be estimated at 8.5-10 days. This is consistent with the 8-9 days obtained by Reinecke *et al.* (1982) for Black Ducks but higher than the calculations of 4-7 days for Mallards by White and Bolen (1984). In any case, the time span is much shorter than the interval of 20-23 days between the onset of the cold spell and the discovery of the first victims around 1st March, both at the Rhine and in the Wadden Sea. The ducks therefore must have been able to obtain food in the beginning of the cold period, perhaps enough to account for some 80% of daily requirements. Then probably both food intake and energy expenditure gradually decreased before most locomotory activity finally ceased. As suggested by Serie and Sharp (1989), relative lipid reserves are smaller in females and immatures than in males which implies a shorter survival time. However, among the IJsselmeer birds no sex-related difference in survival time was noticed. The higher mortality in female than in male Scaup in the Wadden Sea can neither be explained simply by differences in fat reserves, but may be related to diving performance as we have argued before in the case of Pochard and Tufted Duck on the Upper Rhine. We suggest that competitive performance at a specific and often reduced food resource has much more influence on sex-related and interspecific differences in vulnerability to starvation than fat reserves built up prior to cold spells. This supports the earlier arguing that the mass starvation was mostly the result of the reluctance of the birds to leave those areas with insufficient food stocks rather than a consequence of widespread poor body condition when the cold spell set in.

Although mass starvation did not occur on a large scale in Central and Northwestern Europe in March 1986, it was still more than a local phenomenon of the upper Rhine and the western Wadden Sea. East of the river Rhine at lake Untersee, losses of Coot, Pochard and Tufted Duck were estimated at 600 birds (Meile 1991). Considerable mortality occurred also among *Aythya* ducks at the refuge area

Amsterdam harbours and Noordzeekanaal but details are not available (C.J. Camphuijsen pers. comm.), while among waterfowl in the Delta area, SW Netherlands, Shelduck *Tadorna tadorna* was the main species to suffer (Meininger *et al.* 1991).

Acknowledgements

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Chapter 8

Waterfowl movements in relation to food stocks

Mennobart R. van Eerden

CASE STUDIES

Waterfowl movements in relation to food stocks

Introduction

Many species of waterfowl that winter along the shores of western Europe breed at northern latitudes. In autumn they migrate towards the wintering areas which, according to the species concerned, coincide with, or lie south of, the zone free of snow and ice. In spring some species move north again, following the retreating ice edge (*e.g. Mergus* spp.), whereas others build up fat reserves at lower latitudes before migrating by a few long-distance flights to the breeding grounds (*e.g.* species of geese of the genus *Branta*). Radar studies have revealed the often massive flights of waterfowl that occur between staging areas (Bellrose & Sieh 1960, Bergman & Donner 1964, Blokpoel & Richardson 1978, Bergman 1978) and much attention has been paid to the modifying influences of weather conditions upon the timing of migration.

However, little is known of other influences on waterfowl movements and on the duration of use of possible wintering sites. We believe that the amount of available food at a given site plays an important role. For some arctic-nesting geese, the timing of spring migration normally coincides with the start of plant growth along a primarily south to north climatological gradient. Plants are most digestible during their first flush of growth, and, while on migration, the geese seem to "ride the crests of the digestibility waves of their food plants" (Drent *et al.* 1978). In contrast, those waterfowl that are dependent upon highly mobile animal food may react to seasonal shifts in prey availability.

The patterns of use of a stop-over site described here are more or less typical for many other species of waterfowl. This chapter summarises some of the work in progress in Lauwersmeer, northern Netherlands.

Being a former estuary, Lauwersmeer borders the Dutch Wadden Sea and its enclosure by a dike, built in 1969, caused marked changes in the food supply for waterfowl. The prime question we addressed was to what extent food supply influences bird numbers on a given staging area. We report here on the situation in autumn (August-December) as it refers mainly to three herbivorous species, Wigeon *Anas penelope*, Barnacle Goose *Branta leucopsis* and Teal *Anas crecca*. After some introductory remarks on each species we concentrate on the role of food depletion in affecting bird behaviour. If it is important, we would expect to observe, in parallel with changes in food, one or several of the following events (*cf.* Newton 1980): (1) shifts in bird numbers; (2) shifts in diets; (3) shifts in foraging speed; (4) competition or related phenomena. We look first at food depletion in the area as a whole and then at the level of individual plants to assess which cues might be used by birds in deciding whether or not to feed there.

The study area and its vegetation

Following enclosure in May 1969, Lauwersmeer provided over 5000 ha of tidal sandflats where the vegetation was allowed to develop naturally; another 2000 ha of heavier soils were allocated to agri-

cultural purposes and the original system of creeks and gullies made up the remaining 2000 ha. According to detailed studies by Joenje (1978), plant colonisation started mainly from a seed bank on the former sea bottom. Within a few years the lowest parts of the vast sandflats were covered by an almost pure stand of glasswort (*Salicornia* spp.), at one time with an extent of about 3500 ha. Desalination of the fine-grained sandflats was slow and it required more than 10 years for plant succession to reach a stage no longer dominated by halophytes. At intermediate stages other species increased, at first members of the goosefoot family *Chenopodiaceae* (Seablite *Suaeda maritima*, Sea Purslane *Halimione portulacoides* and Saltwort *Salsola kali*). Later these were invaded by Sea Spurrey *Spergularia maritima*, Sea Aster *Aster tripolium*, and grasses (*Puccinellia* spp. and *Agrostis* spp.). Because the area was not managed by Man by grazing or mowing, each autumn a huge food stock for waterfowl was present in the form of seeds. After the growing season, the standing crop was not renewed and autumnal grazing by waterfowl could be studied rather easily.

Only a few food plants were common, *Salicornia europaea* being the most important, with a seed production peaking at over 340 tons of dry weight in 1972. Within one year after enclosure the approximately 2000 ha of water in the central part of Lauwersmeer became fresh. Sandflats suitable for wildfowl roosts and shallow freshwater areas for drinking remained available throughout the period of study (1969-81) and no hunting took place. So the main factor that varied between years was food abundance.

The methods of study of the birds and their foods

In the first six years detailed descriptions of plant colonisation were made by Joenje (1978) and in the seventh by J. Prop and M.R. Van Eerden. Assessment of total food stocks on Lauwersmeer required measurement of the extent, the density and the size of the food plants. After the first four years, changes in the total food stock of *Salicornia* mostly depended on shrinkage of the area covered. Annual mapping of vegetation was verified twice by aerial photography (1978, 1980, J. Slager & H.J. Drost).

More extensive measurements were carried out on a 44 ha tract of the area called Schildhoek. Grazing of seeds by wildfowl occurred predominantly at night and was measured directly by counting the seed heads lost, since the whitish stalks remaining at the base of the ear after grazing were very obvious. Because of the regular shape of the plants the number of seed heads grazed could be converted to estimates of the absolute amount of food removed.

Counts of droppings each morning indicated foraging patterns in the previous night. Droppings of *Anas penelope, A. crecca, A. acuta, A. platyrhynchos, Branta leucopsis* and *Anser anser* could be distinguished by their appearance (see Chapter 6). They are produced at a fairly constant rate and therefore indicate the time spent by a bird at a given spot. Thus when feeding on *Salicornia*, Wigeon produce a dropping about every 3 min and Barnacle Geese every 4.25 min on average.

Also, direct observations were made of foraging behaviour (time spent feeding, intake rate and flock density) from a 4 m tall tower hide during the daytime by telescope and at night by infra-red telescope. The 44 ha study area was divided into 1 ha cells, each watched continuously by a team of enthusiastic observers.

To calculate the number of bird-days spent by each species, 5-10 total bird counts were organised in the period August to December each year.

The annual cycles of the waterfowl species

The Barnacle Goose is a high-arctic breeder, spending four summer months there and the other parts of the year along the coasts of western Europe. Three distinct populations exist, the largest breeding in the Novaya Zemlya/Vaigach region and wintering in the Netherlands (54 000 birds in the 1970s, Rooth *et al.* 1981). The migration route of the Russian population is well known through direct and radar observations. Figure 1 depicts flyways and known staging areas *en route* (Bauer & Glutz von Blotzheim 1968, Kumari 1971, Owen 1980). On a European scale only a few places are known where flocks of more than one thousand birds can be seen and between which the birds distribute themselves in the winter.

In a mild winter several thousands of birds tend to stay along the coast of north-west Germany (*cf.* Busche 1977); in a severe one almost all the geese concentrate into the Delta area of the Netherlands, the most south-western part of the range. Our study area is one of the staging areas, shown in more

Figure 1. Migratory flyway of the Barnacle Goose *Branta leucopsis* (inset at top) with indication of principal autumn and winter haunts of the Novaya Zemlya population (centre) and location of Lauwersmeer study area (inset bottom).
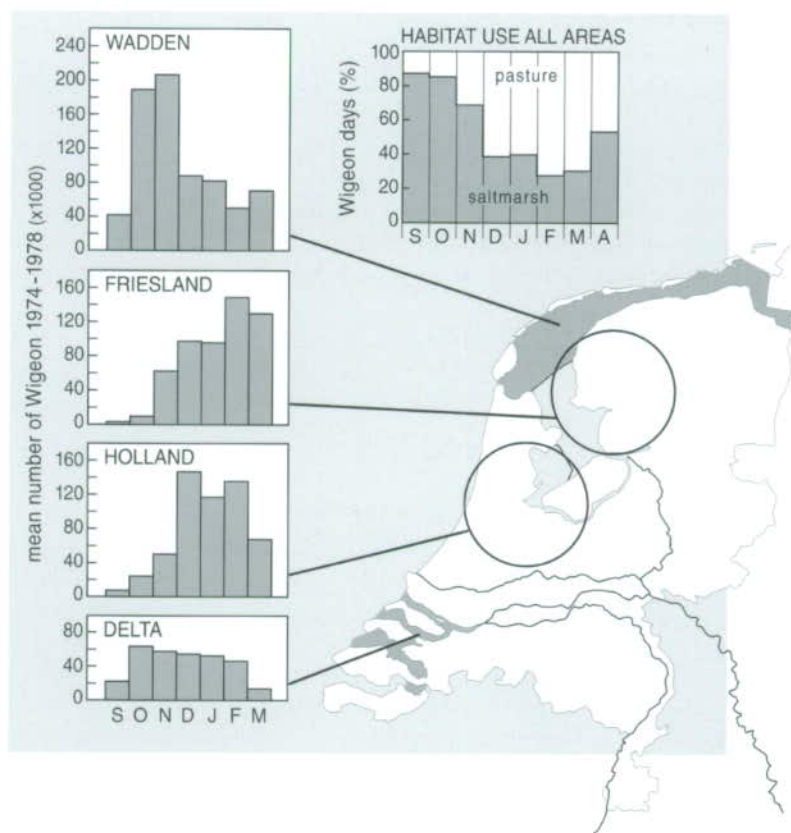
Figure 2. Distributional shift of Wigeon *Anas penelope* wintering in the Netherlands (5-year means of regional counts). Inset shows habitat use through the season on the basis of bird-days (all areas combined) emphasising the heavy usage of saltmarsh in autumn.

detail in the bottom corner of Figure 1. As many as 50 000 Barnacle Geese have been counted together at this site, representing over 95% of the total flyway population at that time.

A less discrete pattern of halting places is observed in Wigeon. As a grazing species, it is one of the most numerous wintering ducks in the Netherlands. Over 350 000 birds occurred in a series of mild winters (1974-78) (J. Rijnsdorp, unpubl.). Some Wigeon feed on pastures, others on saltmarsh. The relative proportions of all Wigeon present in the Netherlands that feed in the two habitats change throughout the autumn and winter (Fig. 2). From September through to November most are found close to the sea in both the Wadden and Delta regions.

From December to March mainly inland foraging sites are used, chiefly in the provinces of Friesland, Noord Holland, Zuid Holland and Utrecht. Total numbers present in the Netherlands change rather little, however, suggesting a mass shift from salt- to freshwater plant foods. The use of the Lauwersmeer area closely follows that of the Wadden Sea (Fig. 2) with up to 64 000 birds present in October. The major shift in habitat is related to a shift in the types of plants eaten, the saltmarsh plant species and algae being highly preferred in autumn.

Analysis of the diet (see Stewart 1967) of Wigeon in our study area also showed this shift, although both food types occurred in the same area. At the times of peak numbers in early autumn, *Salicornia*

spp. is eaten in preference to the nearby grasses, whereas after most of the birds have gone the remaining Wigeon shift to a diet comprised almost totally of grasses. These findings could be explained if Wigeon obtain calorific returns from their foods similar to those measured for the *Branta* species of geese by Drent *et al.* (1978). They found the following values of energy assimilated (in kcal g⁻¹ food taken): *Salicornia* 1.85 (October), *Enteromorpha* 1.84 (November), *Zostera* 1.60 (October), *Festuca* 1.57 (December), *Poa, Lolium* 1.42-1.58 (December-February). From a calorific point of view, birds should prefer to graze the foods highest on this energy gradient, if they are available. Apparently Wigeon do so. Whether it is really the number of calories or some other "quality" factor in the food to which the birds respond is unknown but further investigation along these lines seems worthwhile. Clearly, colonisation of vast areas of Lauwersmeer by *Salicornia* was of great importance to the birds. With the presence of large stocks of a highly preferred food the "new" area competed easily with others on the flyway to attract birds.

The annual cycle and breeding areas of Teal largely overlap those of Wigeon (Bauer & Glutz von Blotzheim 1968). Most Teal that migrate to the North Sea area originate from the boreal zone of northwest Russia, west of the Urals (*cf.* ringing results, Speek 1975). These ducks use a highly specialised technique of sieving out food particles (Chapter 9). The habitats they can use are thus restricted to those with a thin layer of water covering the feeding grounds. On migration their food consists mainly of vegetable matter. In western Europe no clearly defined halting places exist where feeding conditions are predictable and optimal year after year.

After September, large numbers appear suddenly soon after conditions become favourable at a given place, usually a result of flooding. Lauwersmeer area attracted up to 60 000 Teal in November 1974, the species being overall the third most common consumer of the seed stock present.

The impact of waterfowl on their food supplies, and *vice versa*

As mentioned above, one of the major food plants for waterfowl in the area during the years of our study was *Salicornia europaea*. After germination in May from seeds lying in the bare mud, the next seed crop of this annual species ripens during October with a change in colour from green to deep red. Waterfowl begin to eat the crop soon after the period of ripening. Only plants bordering the water's edge and close to the roosts are consumed in the green stage.
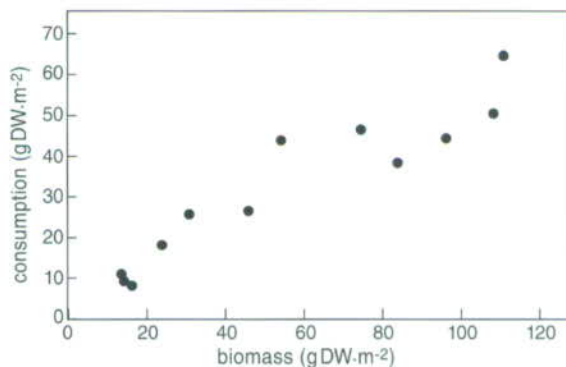

Figure 3. Grazing impact (dry mass of seeds removed m⁻²) in relation to food supply at the onset of autumn (biomass dry mass m⁻² of seeds on offer) for Wigeon *Anas penelope* feeding on *Salicornia* in Lauwersmeer.

Figure 3 shows the relationship between standing stock and total food consumption by Wigeon and Barnacle Geese in the autumn of 1975. It is clear that the areas holding higher densities of food received higher grazing pressures (measured as biomass removed), but that the highest percentage of food was removed from the lower end of the food density gradient. A maximum of c. 70% was grazed at biomasses of between 20-50 g dry mass m^{-2}, but only about 50% at higher food densities. Each dot in the graph represents the value for a single area, the areas scattered over the total feeding grounds. So even at places where food was scarce, it was exploited by grazing Wigeon and Barnacle Geese, provided that the plants formed an integral part of the vegetation sward of the flats (isolated patches of suitable plant foods were underexploited).

Compared to Wigeon, much lower proportions of seed stocks were eaten by Teal: 7% of *Salicornia*, 8% of *Spergularia* in 1975. This arises in part because the season during which Teal can exploit the seed stocks is short. Their specialised way of feeding is very much dependent upon suitable weather conditions (rainfall, inundation, and no ice). In addition we investigated whether Teal might require higher food densities for successful feeding than do other species, since, unlike their grazing allies, Teal filter individual seeds from a shallow layer of water rather than stripping whole seed heads.
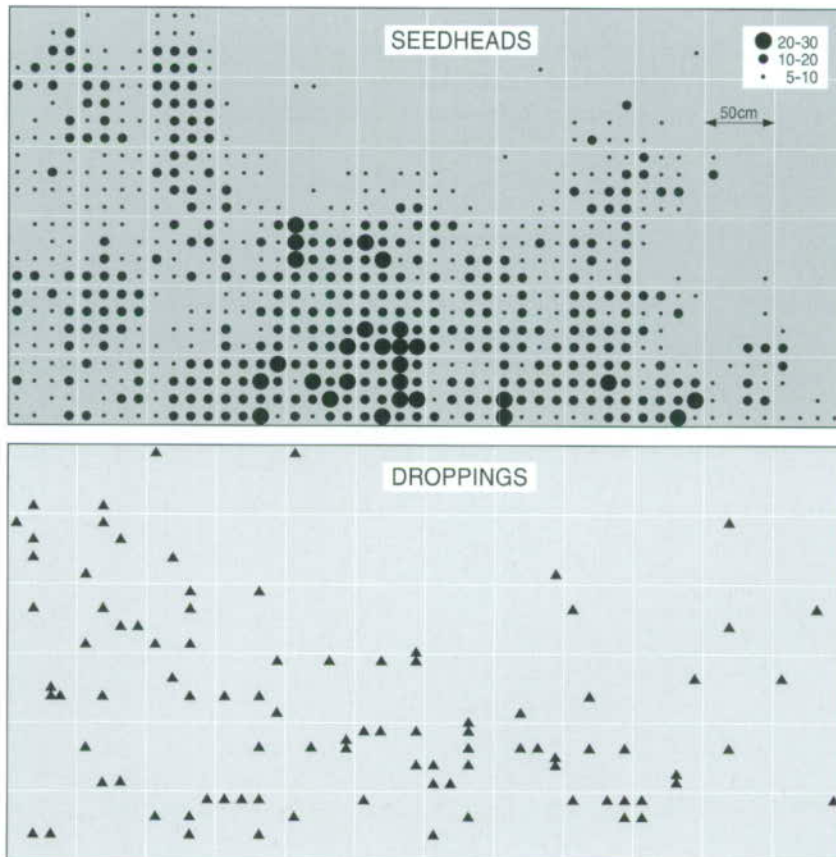

Figure 4. Grazing of Teal *Anas crecca* in relation to food stocks in Lauwersmeer. Upper panel shows food on offer (see text for methods), lower panel grazing activity of Teal as revealed by droppings (note that grid is 50 x 50 cm).

We examined the grazing intensity of Teal on seeds of the grass *Agrostis stolonifera* by searching for droppings left in areas with a high cover of vegetation, where floating plant leaves saved them from being washed away. Figure 4 shows part of such a heavily vegetated area where the Teal used to forage at night. The patchy distribution of the food source is shown by the results of 1152 sampling quadrants and the cumulative location of the individual droppings is shown in the lower panel for comparison. Figure 5 summarises these results over a somewhat larger area and indicates the presence of a certain threshold level of food density, below which the birds did not respond to differences in the density of food present. Thus the small size of the seed particles ingested by Teal does seem to lead to the requirement of a high minimum seed density before exploitation occurs.
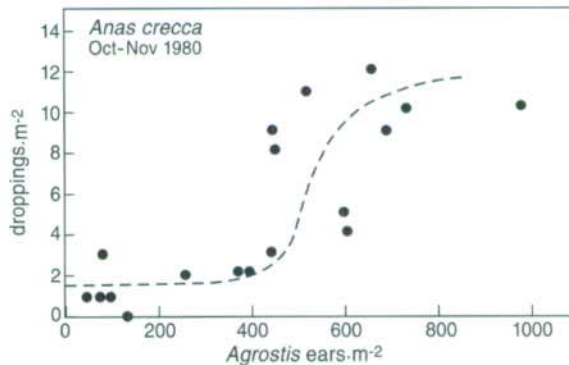

Figure 5. Grazing pressure (as measured by droppings deposited m^{-2}) in relation to food stocks (density of seedheads) for Teal *Anas crecca* feeding on *Agrostis* seed in Lauwersmeer during October-November 1980 (constructed from Fig. 4).

We then investigated the question of why not all the food potentially available is eaten by waterfowl, using Wigeon to examine in more detail the sequence of grazing events. By counting the droppings over the 44 ha study area we determined changes in foraging from night to night. Figure 6 shows the total number of droppings found in 184 sampling quadrants (of 4 m^2 each) which were cleared each day in the autumn of 1977 for 37 consecutive days. The pattern that emerged has been confirmed in other years and clearly shows that harvesting of seed crops by waterfowl is an intensive activity. It may be calculated that 500 droppings found correspond to about 4500 Wigeon foraging continuously for 10 hours at night. During a total of only 11 nights, 80% of the total annual grazing pressure was exerted.

The most important features illustrated in Figure 6 are the discontinuities in exploitation of the seed crops. Grazing periods of several successive nights alternated with periods of little grazing, when the huge flocks of birds were feeding on neighbouring areas. This regular shifting of feeding grounds resulted in a gradual lowering of the food stocks over the whole area. Associated with this, the diet of the birds changed. The proportion of *Salicornia* dropped from 90% in the first two grazing periods to only 30% in the last period, when it was replaced chiefly by perennial grasses. During the first grazing period the birds removed only 10-20% of the total amount of *Salicornia* seeds available to them. These almost always proved to be only the uppermost ears of each plant. Subsequent grazing resulted in the harvest of the remaining (lower) parts of the plants, until between 50 and 70% of the initial stock was removed, as mentioned earlier. Substantial differences in weight and protein content exist amongst the ears of *Salicornia* occurring at different heights above the ground (Fig. 7). In a sample of plants of 12 to 15 cm in height, there was a six-fold increase in mean dry mass from the lowest to the topmost ears

and a threefold increase in weight of protein and in energy content. These quality gradients within single plants explain why Wigeon strongly prefer to graze the uppermost ears. They also imply that, if grazing at a constant speed, a foraging bird would achieve a progressively lower rate of intake as the total remaining food stocks decline. We might expect them to compensate for this by increasing peck frequency, a phenomenon well known in geese grazing on progressively shorter grass swards during winter (Owen 1972).
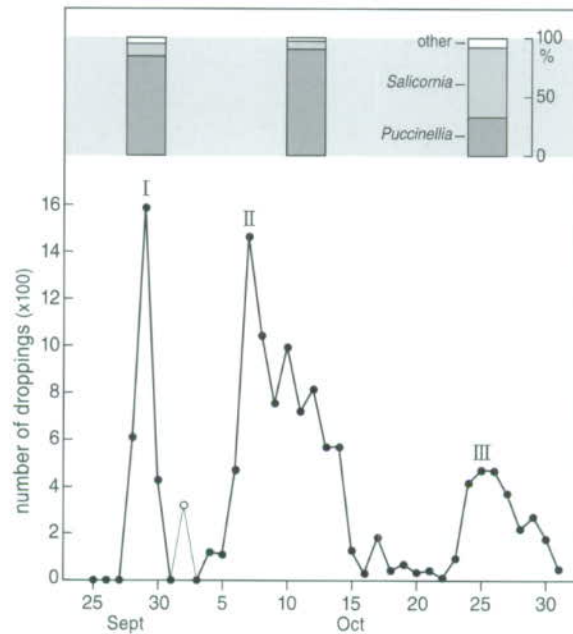

Figure 6. Grazing rhythm in Wigeon *Anas penelope* utilising pioneer vegetation in Lauwersmeer. Three waves can be distinguished, and as the seed stock was depleted a shift in diet occurred (see bar graphs).
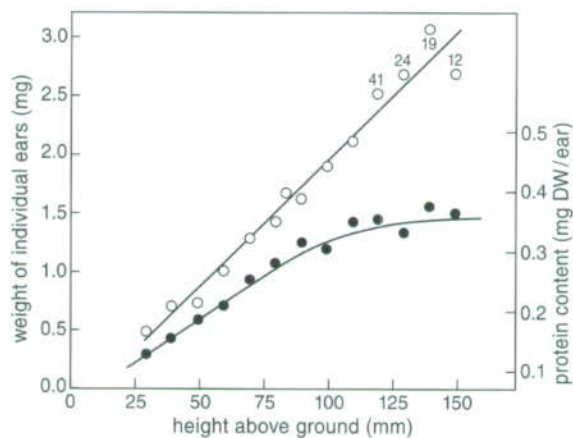

Figure 7. *Salicornia* seedhead quality in relation to height of ear above ground. Note that the protein content (solid circles) shows a maximum plateau.

Nocturnal observations on foraging Wigeon, however, showed in fact that they decreased the number of bites made per minute. If we assume that each peck resulted in the removal of a single ear (as seems probable because of the spacing of the ears on the plant), the birds did not compensate for the lowering of intake rate. Despite the higher densities of ears lower down the plants, the ducks apparently are hindered while foraging by the increasing density of empty stalks. Except by trampling, they do not alter the vegetation structure while they are grazing but merely remove the edible fraction, as if they were giants picking fruits from an orchard whilst standing above the tree canopy. Since they do not feed faster as they graze down the plants, they must feed for a longer period if they are to balance their daily energy expenditure (DEE) later in the autumn. We have calculated that the birds taking part in the first grazing period (Fig. 6) could balance their DEE by less than five hours foraging per night. During the second period the time needed should be only seven hours, but in the third period they would have needed 20 hours of foraging on *Salicornia* alone. In fact, the ducks then shifted their diet towards the more abundant but less preferred grasses, with only one third of their food intake still being *Salicornia* (Fig. 6). Since Wigeon are completing their post-nuptial moult in October and may be laying down fat reserves for the winter (Bauer & Glutz von Blotzheim 1968), it is not surprising that they should change their diet to increase their rate of intake. Apparently fewer birds were involved in the last grazing period and at the same time many Wigeon left Lauwersmeer.

The combined effects of grazing by several waterfowl species

So far we have discussed several aspects of the complex relationship between birds and their food, for each species separately, and the question now arises of whether competition between species might play a role when several tens of thousands of birds are present together. The species most likely to compete with each other for food are Barnacle Goose and Wigeon, both grazing species. As noted earlier, Wigeon tend to arrive in autumn at least one month before Barnacle Geese (Wadden Sea area, Joensen 1974, Busche 1971, P. Zegers, pers. comm.). When the geese arrived at Lauwersmeer, the *Salicornia* sward was already being harvested by Wigeon. The geese foraged by day and thereby alternated use of the area with the ducks, which fed at night. Often they foraged in places overlooked by the ducks. In such places, the intact sward still showed as a reddish purple colour, easily spotted from the air by the geese during daylight.

Extensive counts of droppings of both species on our study areas supported the idea of complementary feeding by the ducks and geese. Figure 8 shows the relative grazing pressure of both species in a number of sites. Those spots heavily grazed by Wigeon received little attention from geese, and *vice versa*. The inset in Figure 8 shows the total impact on the vegetation of the whole Lauwersmeer by the grazing birds in 1975. Wigeon consumed 46%, Barnacle Geese 24% and the highly specialised Teal only 7 % of the total seed crop of 200 tonnes dry weight of *Salicornia*. In other years this pattern was repeated, Wigeon always taking the greater part of the annual harvest. In Figure 9 the total food consumption by grazing birds is shown to follow a pattern set by annual changes in seed stocks, caused by plant succession. In 1971 the mudflats were totally covered by *Salicornia* for the first time (Joenje 1978). In that year Barnacle Geese managed to eat a greater proportion of the seeds than usual since many of the plants were of the tall (*stricta*) type, partly out of reach of Wigeon. The next year, 1972, plant height was considerably lower (*brachystachya* type); total production reached a peak value, and so did total consumption, that by Wigeon by far exceeding that by Barnacle Geese. From 1972 onwards, the Barnacle Geese gradually advanced their date of first arrival in the area, by about three weeks over a period of eight years. As a result they took an increasing proportion of the total seed harvest (Fig. 9) removed by the two species. In 1979 this trend was broken but in 1980 the geese again
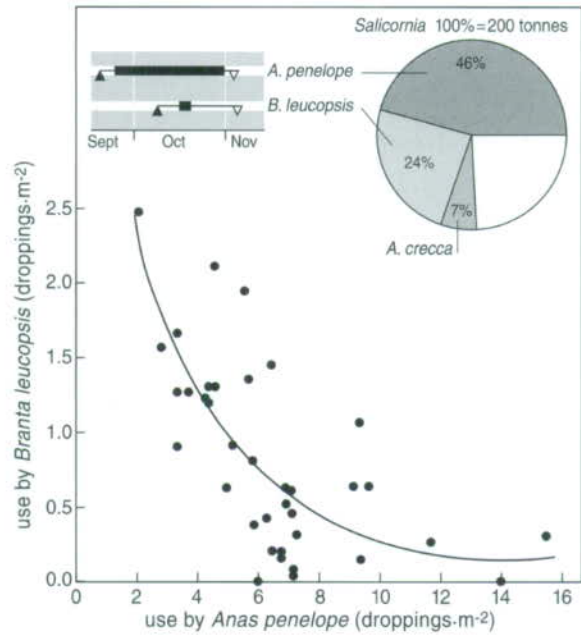
Figure 8. Barnacle Goose *Branta leucopsis* visitation (*y* axis, as measured by number of droppings deposited m⁻²) in relation to prior usage by Wigeon of the same *Salicornia* vegetation (*x* axis, again in droppings m⁻²). Inset shows proportion of seed crop of *Salicornia* removed by waterfowl in the 1979 season (23% ungrazed remaining) and arrival and departure dates for the study area (black bars indicate mean *Salicornia* feeding periods).
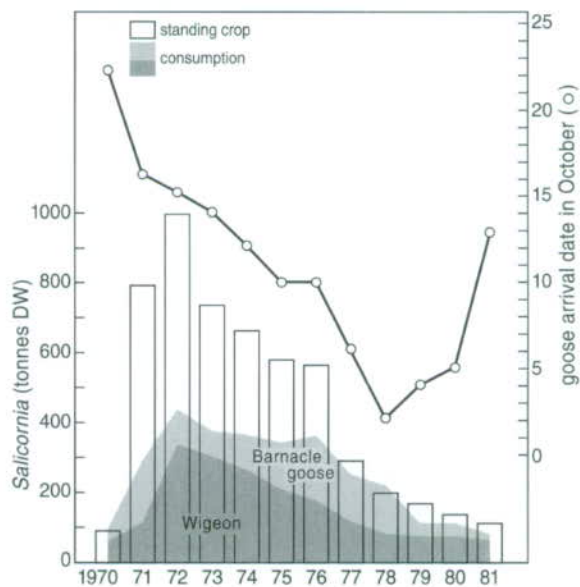

Figure 9. *Salicornia* seed consumption by Wigeon and Barnacle Goose (metric tonnes dry weight) in relation to total crop in Lauwersmeer following closure in 1969. Open circles show the arrival date (in October) of geese in each year.

arrived early. However, they were not "rewarded" in this year by gaining more food (because total stocks were lower) and we expect in the years to come that geese will no longer overfly other possible halting places on their way south as they did in the 1970s.[A]

Lauwersmeer provided huge amounts of food for waterfowl during the early plant succession. In the early 1980s, more than 10 years after enclosure, the *Salicornia* swards had been replaced by perennial grasses. In autumn the seed heads of *Agrostis stolonifera* provided food for Greylag Geese *Anser anser*. Again the birds were highly selective, stripping the seed heads but leaving the grass blades untouched. In about four weeks during September, 3500 geese were able to harvest up to 75% of the total seed crop on offer. Experiments with captive Greylags in small enclosures in the field are underway to see whether the observed sequence of food plants taken can be explained in terms of decreasing profitability. Preliminary results indicate that, by seed stripping, geese might reduce the time needed for foraging to about half that required for foraging on the less preferred grass blades. Indeed, many of the wild geese leave the area and fly to their Iberian wintering sites once the seed stocks have been depleted in Lauwersmeer (see Chapter 11).

During the 1970s the shallow fresh water of Lauwersmeer has been colonised by macrophytes, predominantly the Sago Pondweed *Potamogeton pectinatus*. The leaves and seeds of this submerged vegetation are consumed by Coots *Fulica atra*, Wigeon and Gadwall *Anas strepera*. The numbers of these species present in late summer vary roughly in proportion to the extent of the areas with a high surface cover of *Potamogeton*. Following this period of exploitation, the floating plant material dies off and another consumer, Bewick's Swan *Cygnus columbianus bewickii* arrives (see Chapter 10). *Potamogeton* tubers lie hidden in the mud but are within reach of the trampling and digging swans in water depths up to 0.6 m. As in the case of Teal, the swans cannot see their food but have to locate the better feeding areas by touch. Detailed observations at night, when most feeding occurred, showed that the swans did indeed concentrate in areas of the highest tuber biomass. Once again, a relatively short period of harvest was observed, lasting only four weeks from mid-October, by up to 700 birds. In 1980 an apparent threshold density for tuber exploitation was determined as being *c.* 7 g dry mass m^{-2}, and in areas above this density level, 43% of the tuber stock was removed by the swans. Together with other avenues of loss, almost 70% of the tuber biomass was depleted in the better areas, resulting in a low and almost uniform tuber density at the close of exploitation. At this point many swans leave the area, and the remainder shift to field-feeding where remnants of sugar beet and potatoes, left behind after the harvest, can be found. A calculation of the daily ration (tubers disappearing from the study plot, corrected for non-grazing losses and divided by the number of swan-nights determined by direct observation) gave an estimate of 283 g dry mass per swan-night (see Beekman *et al.* 1992). McKelvey (1980) estimated for the Trumpeter Swan *C. cygnus buccinator* a daily intake of 332 g dry mass of tubers. Based on body mass of the two species, respectively 6050 g and 10 000 g (Johnsgaard 1975), the Bewick's Swans in Lauwersmeer would have consumed about 20% more than the Trumpeter Swans in Canada did (but see Chapter 10 for later estimates).

One of the main conclusions regarding the effects of vegetation density on grazing waterfowl must be that although not all the plant food available was eaten, when translated into an amount of energy that the birds could extract profitably, probably the upper limit was reached in most years. The number of bird days of use of a given area therefore largely depends on the amount of food available in that area, but is also influenced by that in other areas along the migration flyway. The use made of a given area may therefore be set both by internal (food within the area) as well as by external factors (food between areas, specific needs other than energy and protein).

[A] P.S. The trend that has set in during the 1980s continued, most Barnacle Geese arriving after 20 October (M.R. Van Eerden unpubl. data).

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Chapter 9

Patch use upon touch: filter-feeding European Teal *Anas crecca* have environmentally and socially determined foraging goals

Mennobart R. van Eerden & Marjolein J. Munsterman

CASE STUDIES

Patch use upon touch: filter-feeding European Teal *Anas crecca* have environmentally and socially determined foraging goals

In water, mud and sandy clay, Teal constitute an important predator of seeds. They can refine 80-100% of the seeds present in the substrate. Teal are highly selective foragers that can discriminate between seeds upon touch.

In this study we examined the foraging techniques and patch use of five captive Teal in an experimental set-up, where the seeds on offer were not visible, but could be reached by inserting the bill in a slit (perforated lid covering a water containing petri dish). Commercial and natural seeds were both offered in varying quantities on a plateau containing 25 patches. Intake rate and patch depletion were measured by regular counts of the seeds left over, related to Patch Residence Time (PRT) and total time in patch. Handling times and intake rate varied in relation to seed density, seed size and morphology. Morphological characters of seeds could be used by Teal as a reliable estimator of digestibility.

Debris particles reduced intake rate and patch harvesting level. Corrected for other variables, Teal increased PRT as foraging effort (debris density) increased. We conclude that Teal possess two filter systems, one used in water, which enables to discriminate between objects outside the bill cavity, the other in soils which is used to discriminate between objects inside the bill. Both techniques set different goals for optimal seed size, adjusting to smaller than average particle size for organic debris when foraging in water but larger than average for soil particles in mud.

Social dominance was related to structural size, as larger birds were dominant. Subordinate birds were forced into low quality patches and had to compensate their foraging when the dominant birds had left the food-tray.

Concerning patch use, two foraging strategies were applied. When entering a new set of patches, unknown to the birds, Teal tended to use a Fixed Time Strategy, devoting their time equally to rich and poor patches. We interpret this as an effective patch sampling behaviour in an unknown and uncertain environment. In later stages of patch depletion, Teal were considered Bayesian Foragers which underused rich patches, but still achieved a positive density dependent patch harvest.

By manipulating the gain curves per patch, in the course of the experiment the location of the most profitable patch changed position. Associated with the stable situation of differences in patch quality during the second half of patch depletion, PRT increased strongly in the formerly poorest patches. By responding with increased PRT to increased stability of the environment, the dominant Teal were able to monopolise patches with the highest expected future gain, thereby applying a simple Rate Assessing rule. The lower ranking Teal continued to forage on the tableau as well, but responded with short PRT's to the remaining, heavily depleted patches.

The experiments show how Teal continually adapt their foraging goal to the rapidly changing environment, not applying a single tactic, both on the level of seed selection and foraging strategy.

Social status of birds in the flock strongly affects patch exploitation patterns and thereby final Giving Up Densities (GUD) of individual patches.

Introduction

Seed ecology and the role of predation

Many plant species which grow in freshwater and coastal wetlands are monocarpic annuals *i.e.* produce seeds only once in their lifetime. The strategy of producing many small seeds is characteristic for plant species of large-scale, open habitats where wind and water dispersal is important (Fenner 1985). Moreover, small seeds are often found in species which have persistent dormant seed banks in the soil. The probability of becoming buried by soil particles is inversely related to size (Thompson & Grime 1979). Seed banks form an important feature of the life cycle of wetland annuals, because it may take many years before water tables are such as to allow germination. Also predation pressure is supposed to have led to a selection for plants that produced smaller seeds (Janzen 1969). In the pre-dispersal phase, many predators, especially insects, may cause severe losses, even before the ripening of the seeds (Janzen 1971).

However, as seed predators often contribute substantially to the dispersal of their food plants, natural selection has not led to the overall presence of resistant seed coats which would depress digestibility (Fenner 1985). Seeds are therefore an important food source for many animals. The post-dispersal predation of seeds depends on the capability of the predator to find and collect them. Harvest rates depend on the distribution and attainability of the seeds, which, according to foraging theory, attribute to patch quality. Seed predation in nature may be substantial, as has been described for several species of waterfowl (*e.g.* Chapter 8, Van Eerden 1984, Chapter 11). The harvestability of seeds has consequences for both the vegetation dynamics (see Crawley 1997) and the carrying capacity of wetlands for seed-eating ducks. In this study we concentrate on patch depletion in Teal *Anas crecca*, provided with a variety of natural and commercially available seeds, in an experimental multi-patch situation. We will explore the mechanisms of seed uptake in relation to morphological characteristics of seeds that occur naturally in the different habitats exploited by Teal.

Teal as a seed predator and patch use theory

European Teal forage mainly on seeds in autumn and winter (Olney 1963, Bauer & Glutz von Blotzheim 1968, Tamisier 1971b). Seeds are either strained from mud with a high clay content (Zwarts 1974), or directly from a shallow water layer of several cm (pers. obs.). Lüttschwager (1955) already mentioned the high number of lamellae present in the bill of Teal and even more so in Shoveler *Anas clypeata* compared to other *Anatidae*. Among palearctic waterfowl, these species are the most specialised in filtering small particles from the habitat they are exploiting. Teal always use the shallowest parts in wetlands, preferably by walking but occasionally through up-ending. The ducks can utilise 25 cm water depth at maximum (Pöysä 1983). In the Rhone delta, Tamisier (1971a) found that Teal exploited zones with seed densities varying on average between 5 and 20 g m^{-2}. As a nocturnal forager Teal sample and exploit patches upon touch. In natural situations they will have little or no cue as to estimate patch quality. Only general information about the average quality of the habitat is available to the foragers. Teal forage in flocks, and in rich habitats several ducks per m^2 may occur at night (pers. obs.). Earlier field work in the freshwater marsh Lauwersmeer pointed to a strong positive density dependent harvest of grass seeds *Agrostis stolonifera* (Chapter 8, Van Eerden 1984). A threshold in seed density was observed, below which foraging Teal did not respond to differences in seed density.

Foraging theory has provided a general concept to explain the decisions animals make regarding their food uptake in a certain habitat (Stephens & Krebs 1986). A forager should leave a patch when the benefits from foraging (including energy, water and nutrients) balance the costs (including metabolic costs, risk of predation and missed opportunity costs from not engaging in other activities (Brown 1988)). Patch use is always related to the average quality of the environment. Food intake rate,

Patch Residence Time (PRT) and food density at the time of leaving the patch (GUD = Giving Up Density) are important parameters to describe patch use. Many tests have elucidated the general validity of the marginal value theorem (MVT, Charnov 1976), but refining remarks have been as numerous (Ydenberg 1984, Brunner *et al.* 1992). An important development in the original theory was the realisation that many predators feeding under natural conditions lack complete knowledge of their patchy environment. Sampling information about patch quality by touch feeders such as Teal is limited, and foraging Teal are therefore also likely to deviate from the perfect MVT model. Having imperfect information, these predators are likely to leave patches at different quitting rates (Valone & Brown 1989). Moreover, patch depletion, re-visitation of patches and competition with other foragers, phenomena that are everyday occurrences in flock-feeding Teal, further complicate the extension of the original theory (Mitchell 1990, Possingham & Houston 1990). Six tactics have been defined to explain how animals could decide how long they will attend a certain patch. (1) Fixed Time and (2) Fixed Number Strategies use time, respectively number of food items collected as a fixed criterion to leave the patch. (3) Giving-up Time Foragers use harvest rate in the current patch in relation to the average for the environment while (4) Bayesian Foragers use a strategy in which a so-called prior distribution of harvest rate (based on previous experience) is compared with actual harvest in the patch (Iwasa *et al.* 1981, McNair 1983, Stephens & Krebs 1986, Valone & Brown 1989). (5) For predators which feed on discrete items which they search and handle individually, a Catching Probability Model was put forward recently by Roche (1996). This compares the probability of finding a prey in the current patch with that of an alternative patch. Recent information is also weighted in this type of model (Roche 1996). These models contrast with (6) the Rate Assessor Strategy, in which an animal bases its decision to leave a patch simply on the intake rate of the current patch. It leaves when intake rate falls below a certain threshold which has no relation with the other patches in the environment.

When foraging together with many competitors on patchily distributed and depletable food, an individual forager has little control over the future densities of resources (Mitchell 1990), but can, on the other hand, profit from the pooled experience of the flock members in locating the best areas to forage. This flock habit, which is often part of the real world, rarely is considered in experimental set-ups.

Aims of the study

We used an experimental approach to detect foraging abilities of Teal in a situation with multiple patches on offer. The experimental design was made to resemble the natural situation as closely as possible. There, seeds are present in a vast continuum of patches adjacent to each other. Using different seeds, varying seed density and variable amounts of debris particles, we analysed the straining efficiency in different situations. In general, the trials were set up to describe the process of depletion of food density, relative to other patches within short range. Observations as regards foraging time and sequence of patch exploitation were conducted in order to analyse which foraging decisions were used. Because we wanted to study the outcome of patch use in terms of GUD and PRT as a result of multi-bird use, as is the case in nature, we allowed five Teal to forage simultaneously on the experimental tray. Both natural seeds and commercially available varieties were applied in order to offer different seed sizes and seed quality. The experiment was set up in order to test the following questions from the field situation and predictions from foraging theory:

1. Whether Teal are able to detect differences in seed quality and whether they can discriminate among seeds by touch,
2. Whether the intake rate in this suction feeder is positively related to seed size, seed density and seed availability in a patch,

Teal *Anas crecca* feeding on seeds offered in different densities in a multiple choice experiment.

3. To what extent Teal are able to deplete patches, and whether foraging birds experience a decelerating intake rate,
4. How time in patch varies according to the relative gain experienced,
5. Whether or not a positive density dependent harvest occurs, and how rich patches are used relative to poor ones,
6. How social interactions among flock members affect patch attendance and exploitation.

Methods

Experiments

Five Teal *Anas crecca* were captured as adult migrants in the freshwater marsh Oostvaardersplassen in September. For two years they stayed in a large aviary around a meso-cosm of 30×15 m^2 in which they could fly together with other ducks and waders (*Haematopus*, *Philomachus*). This cage was constructed around a pool of 20×10 m^2 in which the ducks could forage freely, partly on natural foods. The environment comprised wet meadow and exposed bare soil. The ducks were fed during this period with commercially available mixed seeds (Millet) and cereal grains. Additionally, fattening fodder and vitamins were supplied.

During the feeding trials, the ducks (four males and one female) were kept indoors and had a constant regime of 12 h light and 12 h darkness. Room temperature varied between 18 °C at daytime and 13 °C at night. Food, water and grit were available *ad libitum* until an hour before an experiment started. The bottom of the experimental room was covered with coated tiles, which allowed droppings

to be collected intact and easily. This room was carefully cleaned each day. Trials were conducted over a period of 20 successive days, in December and before pair formation had started.

Ripe, natural seeds were collected in the field in Teal habitat, both from saline and freshwater marshes. Ripe seeds were sampled, threshed and purified. The coastal species were collected in the Wadden Sea from the islands of Griend and Schiermonnikoog. In lake Lauwersmeer (Groningen) and Oostvaardersplassen (Flevoland), seeds from eutrophicated freshwater marshes were found, whereas Lunsveen near Borger (Drenthe) provided the species characteristic for mesotrophic conditions. In all these sites, Teal had been observed foraging on the seeds which were collected. Seeds were stored dry and cool in dark bottles until the experiment started. Seeds were offered in water in petri dishes (58 cm²) covered with a cap in which a circular hole was made (3 cm diameter). In total 25 petri dishes were put in a regular grid on a food tray (c. 50 × 50 × 4 cm³). The grid was fixed by PVC ridges, which prevented the dishes from moving. This set-up allowed the birds to walk across the patches without interfering with the aqueous feeds on offer. By inserting their bill through the hole of the cap, the Teal could sieve the water in the petri dish. Expelled water was able to flow back into the petri dish and the water level averaged 0.6 (range 0.4 - 0.8) cm. The diameter of the hole was large enough to allow the ducks to reach the entire patch bottom, and to choose the requisite angle between the bill and the water's surface (Kooloos et al. 1989). The cap over the patches also ensured that ducks could not assess patch quality other than by sampling. This is important because Teal forage under natural conditions mostly at night (Tamisier 1972, pers. obs.), whereas our experiments were undertaken during light conditions to allow us to make observations.

An experiment was started with the preparation of the 25 patches. Each patch contained a known number of seeds, sometimes accompanied by matter to deter the process of retaining seeds by sieving. As debris we used matter of both organic (non-preferred seeds) and inorganic (soil) origin, also of a known quantity. A tray thus varied in patch quality according to seed density and debris density. When the tray was offered in the experimental room, the Teal moved behind a cloth curtain and quickly returned after the experimenter had left and had positioned himself behind the door which was fitted with a slit in order to observe the birds. Birds were allowed to forage on the tray all together to imitate multi-bird use of patches. Patch use was recorded by direct observation using an event-recorder. Cumulative foraging time per patch (= time with bill submersed) and sequence of patch allocation could thus be related to the number of seeds present. Intervals of different length (several minutes to 24 hours) were chosen to monitor the outcome of seed density in different patches over time, by which the process of patch depletion could be followed. Seeds were counted with the aid of tally-counters, and, if necessary, the water level was restored between trials. Intake rate could be reconstructed by combining the results of foraging time and number of seeds eaten per patch.

The seeds were characterised by their mass, volume, greatest length, morphology and digestibility (see chemical analysis).

Chemical analysis

Samples of the food and the droppings were prepared for analysis by oven-drying at 60 °C to constant weight. Droppings and food samples were finely ground (0.5 mm sieve). Very small seeds (*Juncus* spp.) were crushed in a mortar. The chemical analyses consisted of ash, Kjeldahl-nitrogen and cell wall components (neutral detergent fibre (NDF) and acid detergent fibre (ADF), Van Soest & Wine 1967). Hemicellulose was obtained by the difference between NDF and ADF. Protein content was estimated as 6.25 × Kjeldahl-nitrogen. Additionally, droppings were analysed for non-precipitable nitrogen (Terpstra & De Hart 1974) to differentiate between nitrogen from urinary and faecal origin. A constant fat content of 5% was assumed (Owen 1976, Thomas & Prevett 1982, Sedinger & Raveling 1984). Soluble carbohydrate content was calculated as 100%-fat%-protein%-NDF%. Metabolisable Energy

(ME, kJ gAFDW^{-1}) for 10 species of seeds was calculated according to the formulae derived for *Branta leucopsis* in Prop and Vulink (1992) and ADF was used as a marker. Digestibility of fat was estimated at 30%, based on the digestibility of fat by geese (unpubl. data W. Van Marken Lichtenbelt, Buchsbaum *et al.* 1986). We used the following energetic return for the different food components according to Schmidt-Nielsen (1975): fat 39.3 kJ g^{-1}, protein 17.8 kJ g^{-1}, structural and soluble carbohydrates 17.6 kJ g^{-1}. All analyses are presented on the basis of ash-free organic matter (AFDW).

Results

Seed preference and seed morphology

Teal foraged on seeds ranging from 0.3 mm in natural seeds such as *Juncus bufonius* and *J. effusus* to more than 7 mm in cultivars such as sunflower, peas and rice varieties. Depletion trials of single species, lasting up to 24 h showed that Teal discriminated strongly among seeds. Out of 35 varieties, 10 were not taken at all and others were only partially ingested. Definitively refused were *Bidens tripartita*, *B. bipartita*, *Rumex maritimus* and *R. palustris*, all having heteromorphic achenes with long spikes. The calcareous oogonia of *Chara globularia* were also not taken. Somewhat surprisingly, from the commercial seeds Red Milo, Linseed and Rapeseed were completely avoided, notwithstanding a relatively large size (3 - 5 mm) and strong differences in shape. Other species were eaten to various levels, ranging from 20 - 100% patch depletion.

When equal volumina of seeds were offered per patch, the percentage harvested in the first 5 seconds of foraging varied with individual seed mass (Fig. 1: 1-12). Intake rate was lower in those species
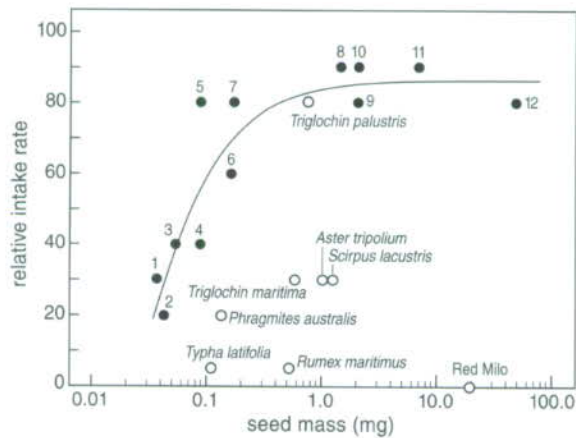

Figure 1. Individual seed mass of 20 species in relation to relative handling capacity by Teal. Plotted are harvesting levels (average and maximum) within the very first feeding bout in a patch. Data are calculated back to a fixed 5 seconds base, assuming linear harvest rate. All species had equal volumina at the start of the experiment. Two groups are visible, a preferred (1-12) and a (morphologically determined) non-preferred group of seeds (A-I).

(1) *Juncus gerardii*, (2) *Veronica beccabunga*, (3) *Spergularia salina*, (4) *Spergularia maritima*, (5) *Rorippa palustris*, (6) *Salicornia dolichostachya*, (7) *Ranunculus sceleratus*, (8) *Suaeda maritima*, (9) *Atriplex hastata*, (10) Millet, (11) Birdseed, (12) Barley, (A) *Typha latifolia* [1], (B) *Phragmites australis* [1], (C) *Rumex obtusifolius* [2], (D) *Triglochin maritima* [3], (E) *Triglochin palustris* [2], (F) *Aster tripolium* [1], (G) *Scirpus lacustris* [3], (H) *Scirpus maritimus* [3], (I) Red Milo [3].

In the non-preferred group seeds were characterised by: [1] long hairs, [2] spines, [3] hard seed coat.

with either (1) tough seed coats (*Scirpus maritimus, S. lacustris,*), (2) a high ratio between seed coat and seed content (*Triglochin maritima, T. palustris*), (3) feathery structures for wind dispersion (*Typha latifolia, Phragmites australis, Aster tripolium*) or with membranous or spiny structures (*Spergularia media, Rumex obtusifolius*) enhancing transport by water or animals (Fig. 1: A-H). All the latter species were also accidentally found transported in small numbers (1 - 5, max. 18 in Rumex) to patches with preferred seeds. None of the preferred species was found outside their original patches, which underlines the differences in handling ability of seed species.

Digestibility of seeds

In digestibility trials testing 10 species of seeds, large differences were found in ME ranging from 2.98 kJ gDW^{-1} in *Rumex maritimus*, 7 - 9 kJ gDW^{-1} in *Scirpus lacustris, Salicornia dolichostachya, Spergularia salina* and *Juncus effusus* to 11 - 14 kJ gDW^{-1} in *Suaeda maritima, Spergularia maritima* and the cultivars Barley, Sorghum and Millet (Table 1). A significant negative linear relationship exists between ME and NDF content ($R^2 = 0.82$, $P < 0.001$, Fig. 2A). The 100 - NDF content will therefore be used as an estimator of seed quality for Teal. Large seeds have a higher apparent digestibility than small seeds, and below 1 - 2 mgDW, seed quality drops sharply (Fig. 2B). The ratio of volume to surface is also related to apparent digestibility (Fig. 2C). *Scirpus maritimus, S. lacustris* and *Rumex obtusifolius*, all non-preferred species, have a relatively low digestibility. However, other non-preferred species, such as Rapeseed and Linseed, are only slightly lower than expected, whereas Red Milo has the highest apparent digestibility. As Teal may use information about specific gravity of seeds as estimator of quality, this parameter was calculated using optical measurements to calculate volume. When plotted against specific gravity (Fig. 2D), no relationship with apparent digestibility exists, both large and very small seeds may have high specific gravities, irrespective of fibre content.

To conclude, seed digestion is positively related to size, which might be used by Teal as the most direct quality estimator upon touch. Additionally, seed volume and, in particular, the protuberances which hamper intake rate, may provide information about digestibility as well.

Table 1. Chemical analysis of food quality and digestibility for different seeds using ADF as marker. Metabolisable energy (ME) was calculated from digestion of components and substitution of energetic values according to Schmidt-Nielsen (1975): fat 39.3 kJ g^{-1}, protein 17.8 kJ g^{-1}, structural and soluble carbohydrates 17.6 kJ g^{-1}. All values on the basis of AFDW. Seed origin given in brackets.

Species	Ash (%)	N (%)	NDF (%)	ADF (%)	ME (kJ g^{-1})	Seed mass (mg + SD)
Juncus effusus (f)	2.5	3.10	87.59	36.21	7.53	0.011 + 0.001
Spergularia salina (b)	5.1	4.18	74.18	27.82	8.81	0.053 + 0.004
Spergularia maritima (s)	3.9	2.85	52.24	19.46	11.11	0.087 + 0.002
Salicornia dolichostachya (s)	14.9	4.35	60.63	33.49	7.69	0.161 + 0.008
Rumex maritimus (b)	4.6	2.19	85.22	71.49	2.98	0.517 + 0.049
Scirpus lacustris (b)	1.7	1.04	55.95	34.59	9.17	1.191 + 0.051
Suaeda maritima (s)	13.6	3.68	29.40	14.24	11.25	1.415 + 0.078
Sorghum (c)	5.9	3.53	25.61	16.90	12.20	2.023 + 0.077
Millet (c)	3.5	1.72	22.18	9.74	13.73	2.516 + 0.186
Barley (c)	2.5	1.74	19.90	4.51	14.15	46.012 + 0.984

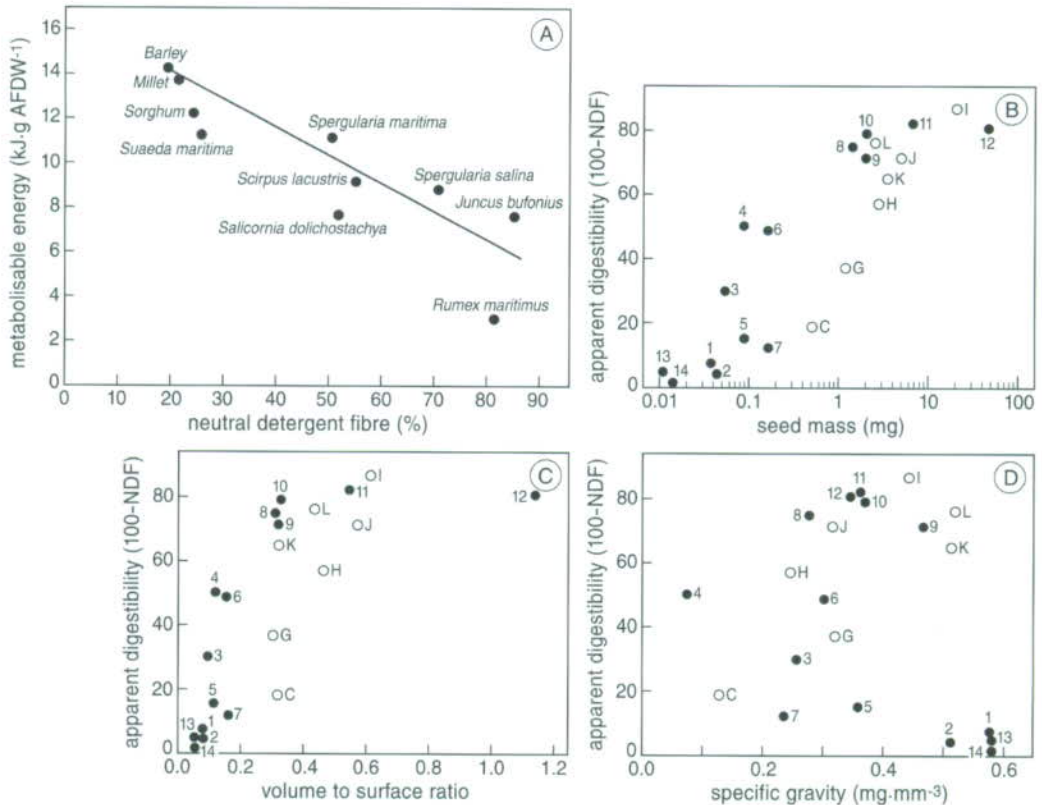(f) freshwater, (b) brackish water, (s) saline, (c) cultivar.

Figure 2. (A) Neutral Detergent Fibre content in relation with metabolisable energy for 10 different species of seeds in digestibility trials. NDF was used as a quality estimator in other seeds in relation to (B) seed mass, (C) volume to surface ratio and (D) specific gravity. Non-preferred species are indicated suggesting that Teal have little information available as to discriminate seeds by volume or mass.

Intake rate and patch quality

As shown by feeding trials with Millet, a highly preferred species, intake rate is strongly related to seed density (Fig. 3A). To avoid effects of depletion and to standardise the results, only data with a foraging duration between 15 - 30 s per patch was used. No threshold density existed within this time frame: intake rate was directly proportional to seed density, the fitted regression line passing through the ordinate. Within the range of densities used, no effect of levelling off in intake rate was apparent.

Seed size also affected intake rate (Fig. 3B). When offered equal volumina of 20 species of seeds increasing by a factor 1000 in mass, the overall intake rate increased by a factor 2500. Smaller seeds are thus handled at a relatively lower rate than larger seeds. Especially for seeds smaller than 0.2 mgDW, this depression of handling time is even stronger than when judged by the deviation of the data points from the linear regression. The non-preferred seeds had a lower rate of ingestion, being on average 40% of that of the preferred species. The slope of the regression was not different, however (ANCOVA).

Deterring matter was added to manipulate intake rate. As debris, seeds of *Rumex maritimus* and Rapeseed were used, added in different quantities (0, 1, 2, 4 and 8 volume units) to 5 different densities of Millet. Figure 4A shows the suppressing effect of one debris species, *Rumex,* being more consistent
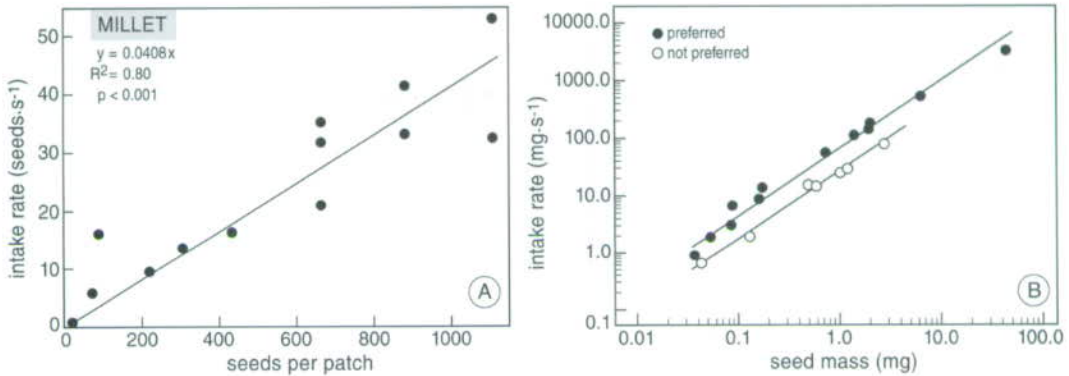
Figure 3. (A) Intake rate for Millet in relation to seed density per patch. Plotted are data from three trials on different days. Only observations between the first 15 and 30 s of cumulative foraging time per patch were used. (B) Relationship between individual seed mass and intake rate for preferred and non-preferred seeds when offered equal volumina per patch. The slope of the regression lines does not differ between the two categories (ANCOVA), the intercept of the non-preferred species was 40% lower.

in its effect. The response curve of intake rate on seed density clearly deviates from linearity at higher seed densities, in contrast to the undisturbed situation. Apparently, the total seed density sets an upper limit to the ingestion rate of the preferred seeds. Figure 4B shows the decelerating effect of suppression of the intake rate at increasing levels of deterring matter. The fitted sigmoid functions show an asymptote of suppression of initial intake rate between 46% (*Rumex*) and 54% (Rapeseed) compared to the situation without deterring particles.

Both debris species in the trials used were comparable in size to the preferred seed, and in a further experiment it was tested how seed uptake was affected by the relative size of the debris particle compared to the preferred seed. Using Rapeseed as debris, patches with smaller seeds (*Ranunculus* and *Juncus*) were depleted in 24 h to a greater extent than the larger seeds (Birdseed and Wheat) (Fig. 4C). With respect to size, Teal can discriminate between particles better when the difference is greater. Especially particles smaller than the deterring objects can be filtered effectively, larger seeds on the contrary causing greater problems.

As in nature seeds may also be filtered from a water-logged soil, a series of tests was carried out with a variety of preferred seed sizes being mixed with five types of soil. Again, patch depletion in 6 h was used instead of the actual intake rate, due to the difficulty of quick interval sampling within one test period. Figure 5 shows that in both clayey soil types Teal extracted 80% of the small seeds (< 0.7 mm), 85 - 95% of the medium sized seeds (0.7 - 2.0 mm) and almost 100% of the large seeds (> 2.0 mm). As particle size in the different soil types increased, the proportion of seeds that was harvested decreased. A strong depressing effect existed when already 5 - 10% of the average size of soil particles was larger than the seed size. In contrast to feeding in water, Teal were hampered by debris *larger* than the average size of the food particles. Both soil type and seed mass contributed significantly to the harvest level observed (Friedman two way ANOVA for soil type $\chi_r^2 = 30.32$, $P < 0.0001$, df = 4, for seed mass $\chi_r^2 = 24.77$, $P < 0.005$, df = 9). A stepwise multiple regression entering both variables resulted in (adjusted) $R^2 = 0.38$; $F = 16.06$, $P < 0.0001$.

Patch use and feeding behaviour

Teal which foraged on the experimental tray often engaged in agonistic interactions. The five birds dif-
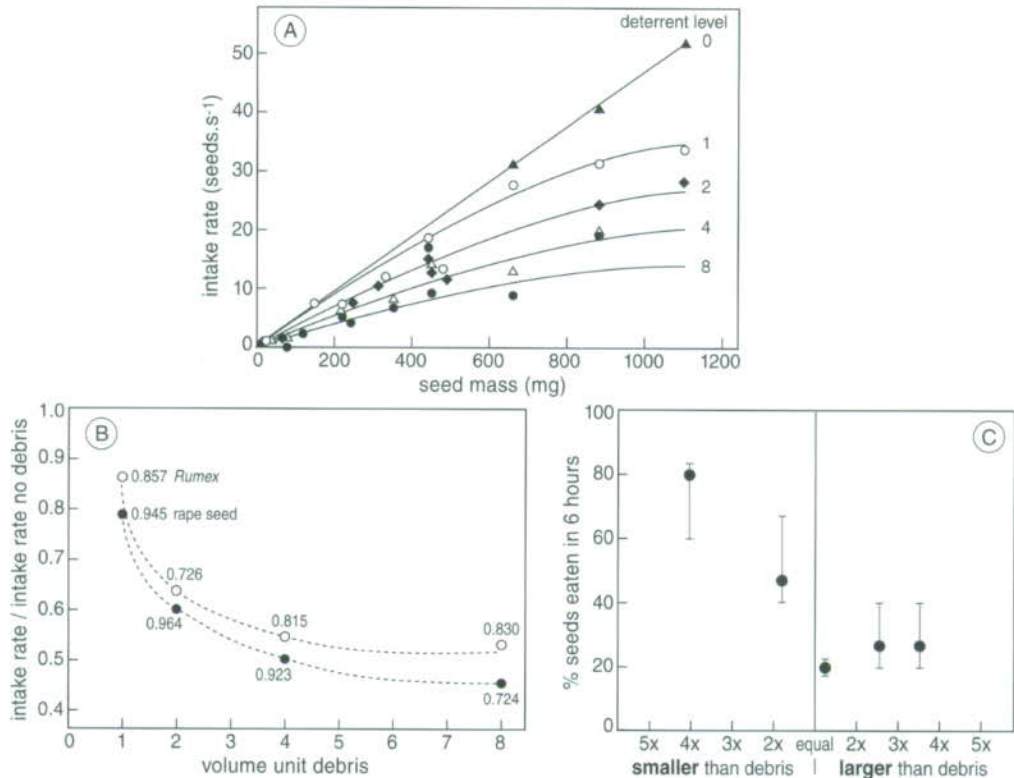
Figure 4. (A) Effect of different quantities of debris (here seeds of *Rumex maritimus*) on intake rate of Millet. (B) Suppression levels expressed in relation to the situation without debris present. At greater quantity, the effect diminishes as indicated by asymptotes of the fitted curves, being 46% and 54% suppression for *Rumex* and Rapeseed respectively. Data labels refer to coefficients of determination (R^2) of different trials as in (A). (C) Effect of size of debris particle in relation to seed size on ability to harvest a patch of seeds in 6 h. Only preferred seeds were used which were taken between 98-100% in situations without debris present. Seeds smaller than the average debris particle size are being taken up easier than the larger seeds.

Table 2. Parameters determining structural size in relation to dominance and patch allocation for five individual Teal used during the experiments. Bill height is vertical distance from the ventral side of the mandible at the base to the dorsal end of the maxillary at the feathers' base, perpendicularly to the mandible. Interactions were observed over the entire experimental period of 20 days. The time foraging in 3 × 8 patches of different profitability is given relative to the most dominant individual (=100). (1) = Rich; 100% Millet, (2) = Intermediate; 50/50% mix of Millet and Rapeseed, (3) = Poor; 90/10% mix of Rapeseed and Millet. Total seed volume was equal in all classes.

Individual	mass	wing	tarsus	bill length	bill height	interactions total	interactions won	time foraging	patch quality and time allocation		
	(g)	(mm)	(mm)	(mm)	(mm)	N	(%)	(% dom.)	(1)	(2)	(3)
male yellow	315	200	30.8	37.1	13.4	60	85	100	100	0	0
male blue	275	192	32.0	38.0	12.4	96	64	100	100	0	0
male white	271	198	31.7	37.2	12.7	75	28	105	50	34	16
male green	267	191	31.2	35.8	12.2	45	42	115	54	8	38
female red	271	188	31.5	35.6	12.9	38	13	204	30	10	60