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Constraints of feeding on *Salicornia ramosissima* by wigeon *Anas penelope*: an experimental approach

Abstract The coastal marshes of the Charente-Maritime (western France) are a major wintering area for wigeon *Anas penelope*. In these marshes, wigeon feed mainly on grasses, while foraging on *Salicornia* (a fleshy, succulent halophyte) is uncommon. In order to understand the reason for this under-exploitation, an experimental study was carried out with captive wigeon in autumn 1998 on a *Salicornia ramosissima* marsh in the Charente-Maritime. Birds were unable to maintain their body weight when feeding on *Salicornia*. Measurements of food chemical composition and metabolisability, as well as instantaneous intake rate of the birds (g/min) could not explain these weight losses. However, the time budget of wigeon revealed that they spent a maximum of 10–11 h per 24 h consuming *Salicornia*, whereas 18–19 h would have been needed to meet their daily energy requirements. The daily foraging time on *Salicornia* may have been limited by physiological constraints due to: (1) a high ash content (mainly salt, about 34% of dry matter), and/or (2) a digestive bottleneck, because of the waxy cuticle covering the leaves, which is likely to have

constrained processing rate of *Salicornia* ears in the gut of birds. In the discussion, we address the question of the potential geographical differences in the use of *Salicornia* by birds.

Introduction

Herbivorous Anatidae (ducks, geese and swans) are known to be selective grazers, consuming some plants and avoiding others (Lieff et al. 1970; Owen 1978/79; Gauthier and Bédard 1991). During the past 20–30 years, ecologists have shown that these birds discriminate between preferred and non-preferred plant species according to the relative nutritional benefits obtained from each of them (Coleman and Boag 1987). Several factors are involved in this food selection. First, herbivorous Anatidae prefer plants of higher quality/metabolisability, higher nutrient (in particular nitrogen) and lower fibre content (Boudewijn 1984; Buchsbaum et al. 1986; Gauthier and Bédard 1991), and avoid plants with high levels of secondary metabolites (Buchsbaum et al. 1984). Second, the components of feeding behaviour (i.e. intake rate, pecking rate, handling time...) vary with plant species, which has an effect on the observed patterns of plant selectivity by birds (Owen 1978/79; Black et al. 1991; Prop and Deerenberg 1991; Therkildsen and Madsen 1999). It is also accepted that digestive constraints, such as the throughput rate of food in the gut, are important factors governing intake rate, potentially leading to a digestive bottleneck: e.g., in woodpigeon *Columbia palumbus* (Kenward and Sibly 1977), Canada goose *Branta canadensis minima* (Sedinger and Raveling 1988), oystercatcher *Haematopus ostralegus* (Kersten and Visser 1996) and, presumably, food selection in birds.

The coastal marshes of the Charente-Maritime (western France) are a major wintering area for dabbling

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ducks, the populations and ecology of which we have been monitoring for the last 8 years (Guillemain 2000; Durant 2001). Wigeon *Anas penelope* wintering in these marshes have access to a variety of food types. Among them, *Salicornia* spp. are fleshy, succulent halophytes which grow in salt marshes. *Salicornia europaea* is present on the coasts of the north of France, but disappears south of the Morbihan, where it is replaced by *S. ramosissima*, which is one of the most abundant *Salicornia* species in the Charente-Maritime. Despite the fact that wigeon are known to consume *Salicornia* spp. (Campbell 1946; Campredon 1982, 1984; Van Eerden 1984), they forage on this plant only rarely (personal observation), although *Salicornia* communities are abundant (C. Lahondère, personal communication). Wigeon seem to prefer foraging on grasslands where they graze graminaceous plants such as *Lolium prenne*, *Dactylis glomerata* and *Poa pratensis* (Durant 2001). These observations are consistent with those in the Camargue (Rhône delta, France), where *Salicornia* is sometimes used by wigeon, but does not constitute their major food (Campredon 1982, 1984).

Little information is available on wigeon feeding on *Salicornia* in France (e.g. daily food intake and time activity budgets; see, however, Van Eerden 1984, in the Netherlands), and only one study reports the chemical composition of *Salicornia* spp. (Geslin 1983; see, however, Summers et al. 1993, in England). We investigated why *Salicornia* consumption by wigeon is not higher in the Charente-Maritime. Our main hypothesis is that wigeon avoid *Salicornia* because they cannot meet their daily requirements when feeding on this plant. The foraging behaviour of wigeon was studied at an individual level, with captive ducks feeding on a natural *S. ramosissima* marsh. The daily metabolizable energy intake of an animal is the product of the instantaneous metabolizable energy intake and the mean daily foraging time. The instantaneous metabolisable energy intake is calculated as the product of the instantaneous rate of food intake and the energy content of food corrected for the apparent metabolisability of the dry matter (Ebbinge et al. 1975).

In this study, we first assessed the quality of *S. ramosissima* as a food resource for wigeon by examining body weight changes of captive wigeon (mean body weight 650 to c.700 g for wild birds in winter; Marchant and Higgins 1990) foraging on *Salicornia* for 3 weeks. We then measured the three main parameters, which influence daily metabolizable energy intake.

1. Metabolisable energy content of *Salicornia*: this may be so low that the birds cannot compensate by eating enough to cover their energy requirements.
2. Instantaneous intake rates: these may be so low that wigeon are not able to feed during enough hours per day to ingest sufficient food to meet their requirements.
3. Throughput rate of *Salicornia*: the time needed for *Salicornia* to pass through the gut may be too long

for wigeon to achieve a sufficient daily intake rate to meet their requirements.

The results of this study have implications for reserve managers whose aim is to improve foraging conditions for Anatidae in order to increase the carrying capacity of reserves. The presence of vast areas of *Salicornia* in the Lauwersmeer (The Netherlands) is of great importance to species such as wigeon in autumn (Van Eerden 1984). Since the lack of large areas of *Salicornia* could be a factor explaining the under-exploitation of *Salicornia* marshes, it is relevant for nature conservation in France to know whether management or promotion of *Salicornia* fields could improve wintering conditions for wigeon in this region, particularly in a situation where surface drainage lines are often created to control salt water residence time, hence encroachment by *Salicornia*.

Methods

Study area

The study site was 'La Vieille Perrotine' (45°57′N, 1°14′W) on the Ile d'Oléron, an island located along the western coast of France. It comprised 0.3 ha of *Salicornia* marsh, mainly *S. ramosissima* Woods (Lahondère 1993; Stace 1995 for classification). The ears began to ripen, and changed colour from green to red during the study period (from 23 September 1998 to 12 October 1998). The *Salicornia* marsh was connected to the sea by a system of channels: water levels were maintained at 1–2 cm by using a sluicegate.

Materials and birds

We used seven captive European wigeon (three males and four females), which came from the Centre d'Etudes Biologiques de Chizé (France), where they were raised in enclosures with poultry pellets ad libitum (composition of the pellets: foliage and seeds of leguminous plants; proteins 15%, cellulose 8%, ash 7%). The birds also had access to grass and animal prey from the ground during the day. They had been at the laboratory for at least 6 months before the start of the experiments. Each bird had a colour ring for individual identification.

In addition to their common food, the birds were provided with *Salicornia* plants for a few days before departure from Chizé. On arrival at the study site they were acclimatised to the new environment and food for a period of 5 days (pellets were still provided but in small quantities). We performed two trials of the same experiment, on 28–29 September 1998 and on 2–3 October 1998, where the wigeon were allowed to graze for 24 h (from 1530 hours to 1530 hours the following day). The birds were able to move freely together in a 13-m^2 mobile aviary (3.6×3.6 m^2; hereafter named the enclosure) constructed on the *Salicornia* marsh. Fresh water was provided ad

libitum, as was grit (sand) to aid the breakdown of *Salicornia* leaves in the gizzard. Plants of other species (e.g. *Aster tripolium*) were removed from the experimental enclosure before the beginning of the trials. Between the trials, the birds were kept in the enclosure (which was moved each day in order to provide them with ungrazed *Salicornia* plants), and they were provided poultry pellets, as their weight had declined sharply.

Body weight

The net benefit offered by a food type can be measured in terms of changes in the consumer's body weight over time (Coleman and Boag 1987). Throughout the 20-day study period, the ducks were weighed to the nearest gram: on our arrival on the site, then every 2–3 days, and again after their return to Chizé when they were on a diet of poultry pellets.

The chemical composition of Salicornia

Samples of *Salicornia* were collected at random just outside the enclosure every 2–3 days throughout the study from 24 September 1998 to 10 October 1998 (a total of 36 samples). Additional *Salicornia* samples were collected in September 1999. All plants within a 25×25-cm^2 quadrat were counted, and their aboveground parts harvested. We picked the green matter (ears) off the stem for each plant separately. The green matter was then weighed, dried at 60°C to constant weight (for c. 3 days), and reweighed.

The energy content of *Salicornia* ears was determined using a bomb calorimeter. The ears were also analysed for crude protein (total nitrogen content × 6.25; Kjeldahl method), fibre (acid detergent fibre, ADF, and neutral detergent fibre, NDF; Van Soest 1982) and the ash content by incineration at 550°C for 3 h. *Salicornia* is known to be poor in lipids (Geslin 1983; Summers et al. 1993), so these were not measured. Water-soluble carbohydrate contents (WSC) in per cent dry weight (DW) were calculated from the formula: WSC = 100% − % Ash − % NDF − % Crude Protein (Coleman and Boag 1987). Two replicates of most samples were analysed in two laboratories of the Institut National de la Recherche Agronomique (Magneraud and Lusignan).

Daily food intake

We used two methods to calculate daily food intake.

1. The difference method: we placed the wigeon in the enclosure for 24-h feeding trials, and measured the aboveground biomass of *Salicornia* before and after.
2. As the product of instantaneous intake rate (pecking rate × bite size), and average daily foraging time (Therkildsen and Madsen 2000).

The difference method

Plant biomass was highly variable between quadrats, so it was not feasible to use this method to estimate the biomass of ears accurately. However, wigeon do not consume stems of *Salicornia*, i.e. the woody part of a plant remains the same after grazing by wigeon, and the biomass of ears of a plant can be predicted accurately from the weight of its woody parts (see below).

The weight of wood per plant (fresh weight) measured from samples of *Salicornia* collected outside the enclosure for chemical composition (see above) was closely related to the weight of ears per plant (DW, Fig. 1) The following equation was fitted to the data:

$$\text{biomass of ears/plant} = 1.14(\text{wood biomass/plant}^{0.91})$$

and explained 98% of the variance (assessed by the regression of the observed on the fitted ear weights: $r^2 = 0.98$, $n = 36$, $p \leq 0.001$). We used this equation to estimate the biomass of ears available to wigeon before feeding, from weights of individual stems collected after the ears had been consumed by birds, assuming that disappearance of ears was due to grazing by wigeon only.

After grazing the following observations and calculations were made:

1. The proportion of the area used by the birds (A, m^2) (i.e. area with grazing marks on plants).
2. The number of plants in each of six randomly placed quadrats (25×25 cm), and the weight of the ears and the woody part of each plant.
3. The weight of ears per plant before feeding, estimated using the equation above.
4. The total weight of ears consumed/quadrat, i.e. the difference between the calculated weight of ears before and the measured weight after feeding.
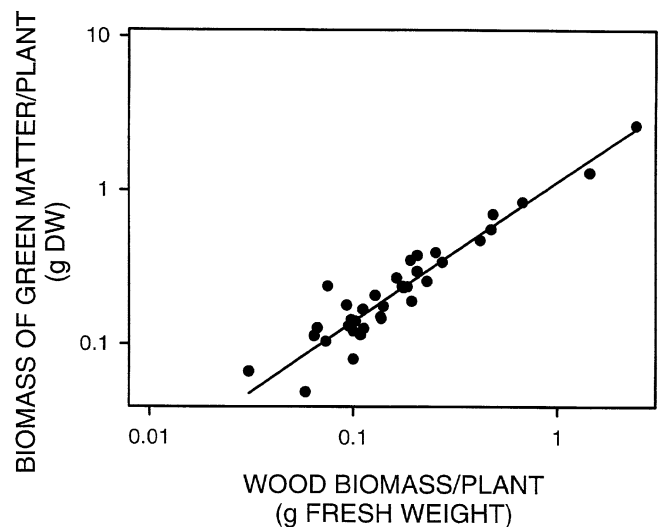

Fig. 1 Regression of the biomass of ears per plant (gram DW) on wood per plant (gram fresh weight). Both scales are logarithmic. $y = 1.14 \times x^{0.91}$, $r^2 = 0.98$, $F = 1512.68$, $n = 36$, $P < 0.001$

5. The total weight of food consumed (i.e. ears g DW) from the mean weight consumed/quadrat (DW)×16×*A*. Daily food intake per individual (g DW) was calculated by dividing the total weight of food consumed by the number of birds in the enclosure.

Time spent feeding per day, pecking rate and bite size

With the second method we estimated daily food intake from the instantaneous intake rate (pecking rate × bite size) and the time spent feeding per day. The time–activity budgets were calculated from scan samples (Altmann 1974) at 30-min intervals throughout the 24-h cycle from a distance of about 20 m, using binoculars by day and a light intensifying vision scope (Thompson Optronique UGO) by night. We distinguished 'grazing' (pecking *Salicornia* ears from plants), 'drinking', 'resting' and 'preening' as well as 'other activities' (head up, loafing, walking and aggressive behaviours). The time spent in these different activities was calculated by averaging the percentage of birds involved in each activity over the 24 h.

The pecking rate was measured during trials 1 and 2 as the time for an individual to perform ten pecks and expressed as pecks per minute. If a bird did not perform ten pecks continuously (i.e. interruption by head-up posture), the measure was discarded. The observations covered all the daylight hours. Since the individuals could not always be identified (the rings were not always visible), we noted the sex of each individual.

Direct observations of our tame birds showed that wigeon removed a single ear per peck, and that virtually every peck was successful. We estimated mean bite size from the mean weight of the ears. The first step was to determine whether wigeon showed a preference for ears from a particular position on the stem, i.e. whether wigeon showed a preference for larger ears. Plants collected after trials 1 and 2 were cut into three equal segments corresponding to three categories: top, middle and bottom of the stem. Each segment of each category was assigned an index depending on its degree of consumption by wigeon. The index values were: 0, no consumption (100% of ears remaining); 1, 1–25% of ears consumed; 2, 26–50%; 3, 51–75%; 4, 76–100%.

In order to estimate mean ear size in each of the three categories above, we collected seven plants in mid-September 1999 in the study area, the height of which was similar to that consumed by wigeon, i.e. 9–10 cm high. Each plant was divided into three equal segments as described above; the ears of each segment were collected, dried and weighed to the nearest 0.1 mg. Bite size was calculated by multiplying the median weight of ears of each segment with the corresponding proportion of ears removed in each segment.

The metabolisability of Salicornia

Acid detergent fibre, ADF, has been shown to be a reliable marker for the estimation of metabolisability in several studies of the nutrition of Anatidae (Marriott and Forbes 1970; Summers and Grieve 1982; Sedinger et al. 1989; Prop and Deerenberg 1991; Manseau and Gauthier 1993; see also Durant (2003) for a discussion on the use of ADF as a marker in herbivorous Anatidae). We used the method of Ebbinge et al. (1975):

$$\text{apparent metabolizability} = \left[1 - \left(\frac{M_f}{M_d} \right) \right] \times 100,$$

where M_f and M_d are, respectively, ADF contents of food and droppings (% DW). The values of these variables were estimated from samples of food and droppings collected after the period of habituation, and during the two trials. The results are expressed as a mean of these three measures as all droppings collected were mixed, giving one ADF value for the period of habituation, and one ADF value for each trial.

Defaecation rate

The defaecation rate was measured as the time between two successive droppings (Owen 1971). The abdomen of an individual was observed for as long as possible (at least 30 min) and the interval between successive droppings was noted. We measured defecation intervals throughout the daylight cycle, and only on birds that had been grazing for at least 30 min prior to observations. The mean value for each individual was used in the analyses.

Statistical analysis

We tested for differences in pecking rates between trials 1 and 2 using residual maximum likelihood (REML), a procedure for non-orthogonal data (Robinson 1987). 'Trial' was considered as fixed effects and sex as a random effect (since the identity of the bird for each pecking rate value was not always known, individual effect could not be assessed). We tested differences in mean proportion of time spent in the different activities between trials 1 and 2 using a Mann–Whitney *U*-test (arcsin-transformed data). The significance of differences in proportions of ears consumed in each category was tested with *G*-tests.

Results

Changes in body weight

The wigeon lost weight when feeding on *Salicornia*: the average weight loss over 20 days represented 27.6% (±8.3 SD; *n*=7 individuals, range: 18.2–36.7; Fig. 2). After the trials they recovered their initial weight.
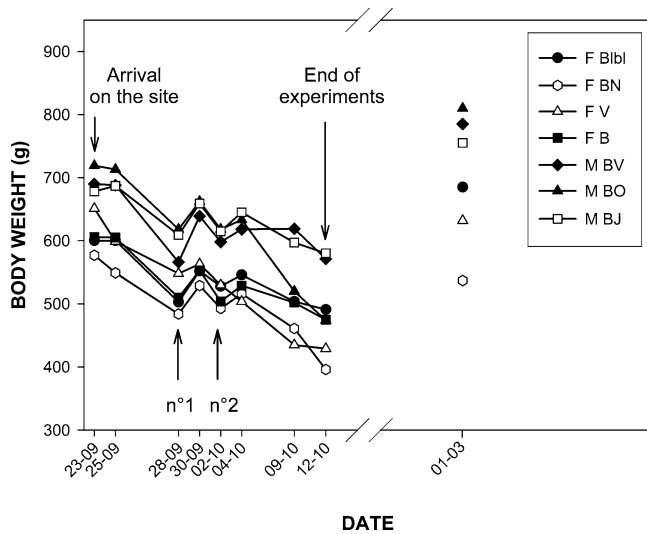
Fig. 2 Changes in body weight of captive individual wigeon *Anas penelope* foraging on *Salicornia* during the study period. *Arrows n°1* and *n°2* show first and second trials. Birds were reweighed a few weeks after the study (weights are indicated)

Plant standing crop, chemical composition and metabolisability of *Salicornia*

The mean density of plants was 473 plants/m² (± 353 SD; $n = 36$) and the biomass of *Salicornia* was 93.6 g DW/m² (± 51.2 SD; $n = 36$). In the 13-m² enclosure, the estimated amount of *Salicornia* available to captive wigeon was thus 1.2 kg (DW). The chemical composition of *Salicornia* is presented in Table 1. The mean metabolisability of *Salicornia* was 27.4% (± 7.1 SD; $n = 3$) (after the period of habituation: 35.5%; after the first trial: 24.1% and after the second trial: 22.5%).

Defaecation rate

The mean interval between defaecations during foraging was 422.8 s (± 87.8 SD; $n = 5$ individuals, i.e. about 7 min).

Instantaneous food intake rate

Pecking rates averaged 27.02 (± 1.75 SD; $n = 101$) and 28.38 pecks/min (± 1.78 SD; $n = 89$) for trials 1 and 2, respectively. The difference between the two trials was not significant (residual maximum likelihood method, REML: $F_{1,187} = 1.46$, NS) so we pooled the data from both trials, which give an average rate of 27.72 pecks/min (± 7.92 SD).

The degree of consumption of ears by wigeon for the three segments of *Salicornia* plants in trials 1 and 2 is shown in Fig. 3. The proportions of ears consumed from each index category (from 0 to 4) were significantly different for the three segments in both trials (trial 1: $G = 117.48$, $df = 4$, $P \leq 0.0001$; trial 2: $G = 178.55$, $df = 4$, $P \leq 0.0001$). The majority of ears (74%) were concentrated in the middle of the plant. The wigeon preferred grazing ears from the top of the plant, so a larger proportion of ears was taken from the top, and to a lesser extent, from the middle of a *Salicornia* plant. Table 2 shows the calculation for the mean bite size for both trials in 1998 (see Fig. 4 for the frequency distribution of weights of individual ears removed from the three segments of the seven plants collected in 1999). We estimated that wigeon removed 6.1 and 5.7 mg of ears (DW) per bite in trials 1 and 2, respectively. Thus, instantaneous intake rates were 165 mg DW/min (27.02 peck/min ×6.1 mg/bite) and 162 mg/min (28.38 ×5.7 mg/bite).

Daily food intake

The difference method

The daily food consumption calculated from the values of the biomass of ears available before and after the trials was 53.1 g DW/individual (± 21.3 SD; $n =$) in the first trial and 110.7 g DW/individual (± 70.3 SD; $n =$) in the second trial.

Time spent feeding per day, pecking rate and bite size

The time–activity budgets are shown in Table 3. Grazing and resting were the main activities of the ducks. They

Table 1 Chemical composition of *S. ramosissima*, means $\pm$ SD

	Season	Energy[a] (kJ/g DW)	Crude protein (% DW)	NDF[b] (% DW)	ADF[b] (% DW)	WSC (% DW)	Ash[b] (% DW)	Percentage dry mass
S. ramosissima	October	12.12±0.59 (n=23)	15.36±1.36 (n=20)	30.27±2.37 (n=21)	13.16±1.46 (n=21)	19.90±2.30 (n=20)	34.39±2.72 (n=21)	12.35±0.79 (n=23)
S. europaea[c]	September–October	–	10.9±0.6	–	–	10.3±1.0	43.2±2.7	–
S. europaea[d]	October	–	13.1	18.3	6.5	35.0	33.5	–

Number of samples analysed in parentheses
WSC water-soluble carbohydrates
[a] INRA de Magneraud
[b] INRA de Lusignan
[c] Summers et al. (1993) (n=5)
[d] Samples collected on the island of Schiermonnikoog (n=1)

Fig. 3 The degree of consumption of the three segments of *Salicornia* plants in **a** trial 1 and **b** trial 2. Five levels of consumption were used (from 0 'no consumption' to 4). The numbers of plants measured are indicated; these are different for the three segments since some of these had no ear to consume
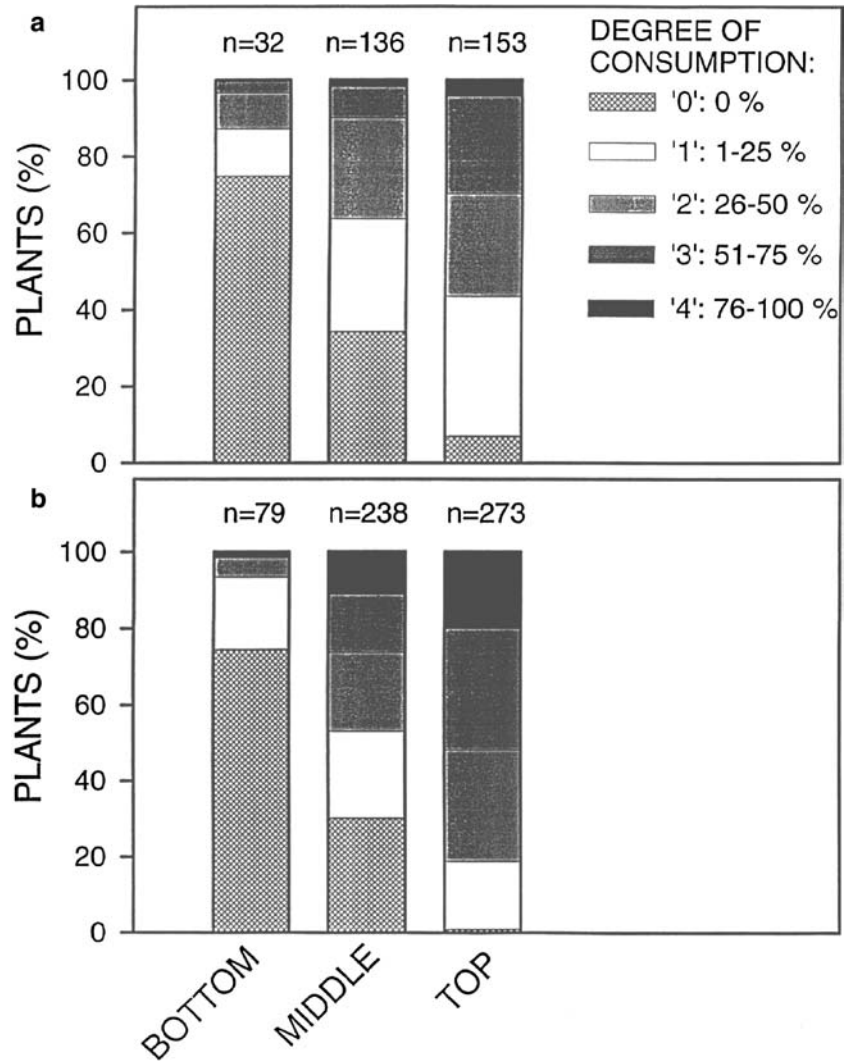

Table 2 Details of the calculations of the mean bite size of *Salicornia* for trials 1 and 2

|	Trial 1			Trial 2		
	Top	Middle	Bottom	Top	Middle	Bottom
Ears removed (%)	34.0	11.0	7.0	50.5	29.6	5.4
Ears/segment[a]	146	615	72	146	615	72
Ears consumed	50	68	5	74	182	4
Median ear[b] size (mg/ear)	8.55	4.55	3.55	8.55	4.55	3.55
Bite size (mg/bite)	6.1			5.7		

[a] From data collected in 1999
[b] From data collected in 1999; see Fig. 4

spent 24.5% (5 h 53 min) and 43.1% (10 h 20 min) of the 24-h grazing in trials 1 and 2, respectively. In the second trial, the wigeon thus fed almost twice as long as in the first one. Apart from the fact that wigeon fed slightly more during the day in trial 2 compared to trial 1 (proportion of daylight feeding: $35.0 \pm 27.3\%$ in trial 2 vs $23.7 \pm 22.8\%$ in trial 1), this difference could be due to the fact that the night was brighter in the second trial (almost full moon) compared to the first one (around first quarter). This may have facilitated nocturnal feeding by wigeon (proportion of night time feeding: $50.5 \pm 29.1\%$ in trial 2 vs $24.1 \pm 22.4\%$ in trial 1).

Birds alternated feeding and non-feeding bouts (resting and preening) throughout the 24-h cycle

(Fig. 5). About a third of the 24-h cycle was spent resting in both trials. The instantaneous intake rates calculated above were 165 and 162 mg DW/min in trials 1 and 2, respectively. Since wigeon foraged during 5 h 53 min and 10 h 20 min, the estimates of *Salicornia* ears ingested by wigeon per day were 58.2 and 100.4 g DW in trials 1 and 2, respectively. These results are close to those calculated using the difference method, 53.1 and 110.7 g DW/individual/day in trials 1 and 2, respectively. The daily energy expenditure (DEE) of wigeon has been calculated as 630 kJ/bird/day on grass (Mayhew 1988) and 592 kJ/bird/day on *Zostera noltii* in winter (Madsen 1988). Assuming the DEE of a wigeon to be 592 kJ (we chose the lower value because our

Fig. 4 The frequency distribution of weights of individual ears for *top*, *middle* and *bottom* segments. Weights from seven plants collected in September 1999
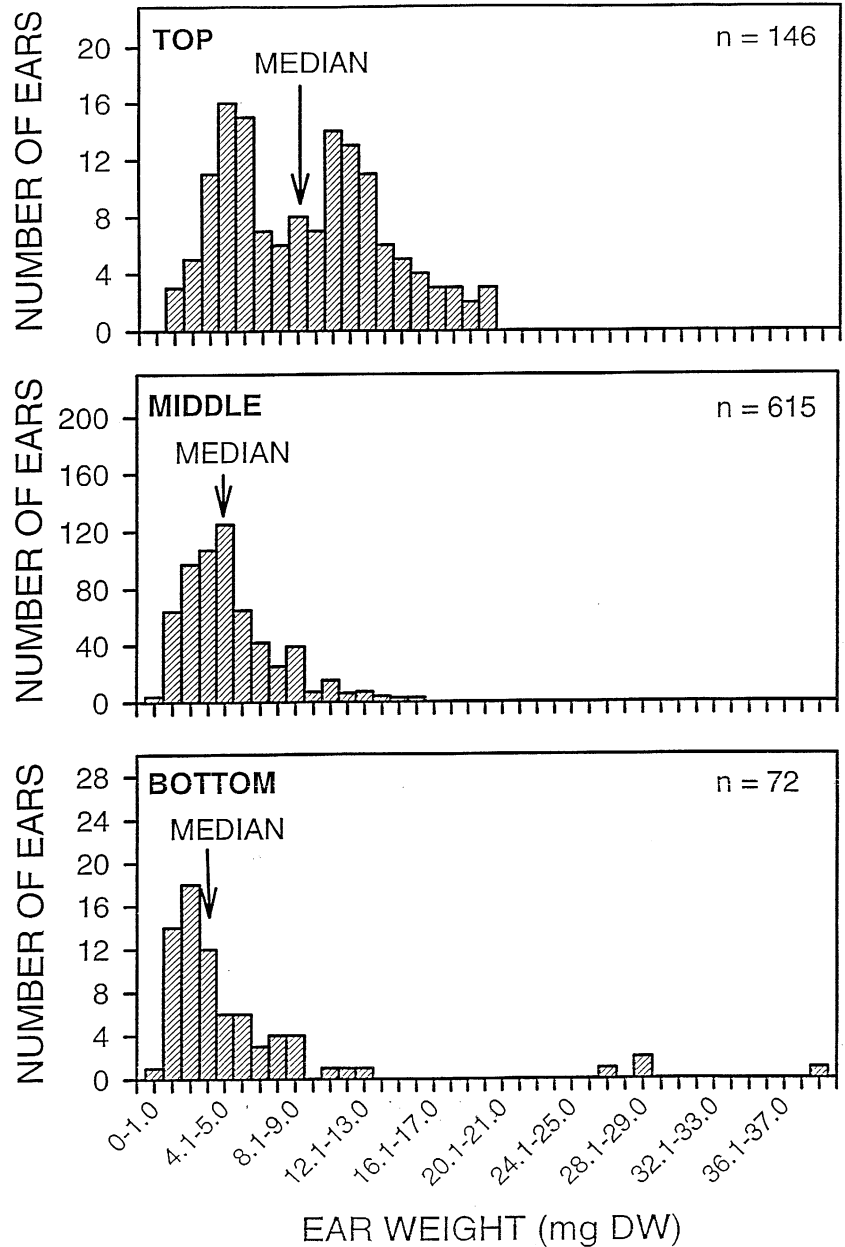
ducks did not fly) and knowing the mean energy content and metabolisability of *Salicornia* and their instantaneous intake rate, 18–19 h (i.e. the total daily foraging time required) would have been needed to meet their DEE. Moreover, knowing quantities of plants ingested by wigeon, we can calculate the daily energy intake (kJ/bird/day) and the daily energy balance of birds (Table 4). This indicates that, in both trials, captive wigeon had a negative energy balance as their estimated energy intake was about half their requirements.

Table 3 Proportions of time spent in major activities by seven wigeon foraging on *Salicornia* over 24 h

	Trial 1	Trial 2	Mann-Whitney U-test	
Number of scans	52	48	U	P
Grazing	24.5	43.1	788.0	0.001
Drinking	5.6	9.8	924.0	0.078
Resting	31.5	26.8	1272.5	0.260
Preening	7.6	6.0	1247.0	0.238
Other activities	30.8	14.3	1533.5	0.007

Discussion

Changes in body weight, plant chemistry and instantaneous intake rate

Captive wigeon were unable to maintain their body weight by foraging only on *Salicornia* and survived on

Fig. 5 The percentage of wigeon foraging during **a** the first and **b** the second 24-h trial
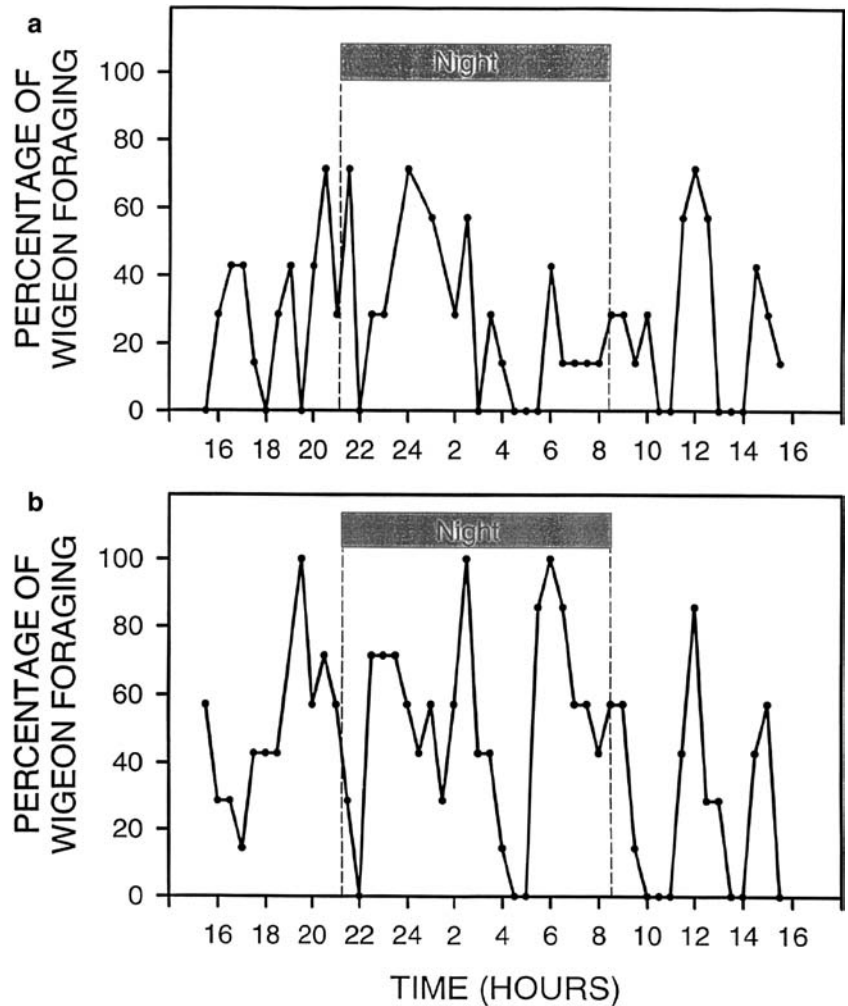
their energy reserves. Although some decrease in body weight can be attributed to stress (transport, handling and a new environment), seasonal loss of body mass in waterfowl throughout autumn, and a lower profitability of the food during the trials as compared to the maintenance diet at Chizé (poultry pellets and grass), such large changes in body weight were surprising. A control, i.e. seven wigeon kept in the same conditions as the experiments, but fed with poultry pellets, would have been useful to determine if the loss of weight was due to the food change, to stress or both. Unfortunately, we did not have such a control. However, we feel quite confident that our tame individuals were able to acclimate readily to the trial conditions. It is also unlikely that

these weight losses came from the fact that captive wigeon digest *Salicornia* less efficiently than wild birds. It is well known that the gut of herbivorous birds can change with the nature of the diet (and in particular fibre content; Miller 1975; Kehoe et al. 1988). However, birds grazed swards at Chizé and were thus used to digest plant tissues (with a content of fibre of about 20% ADF; unpublished data). Moreover, it could be argued that bird density within the enclosure was too high, which leads to social stress for birds. The space available was however about 2 m^2/bird, which is not less than that observed in the wild (in winter quarters) where birds forage in very dense flocks. The period of acclimatisation of 5 days feeding on this plant was short, but wild birds arriving at staging sites in the Dutch Lauwersmeer from their breeding grounds (where they mainly consume invertebrates) do not have more time to acclimatise to feeding on *S. europaea*.

There are three possible explanations for these weight losses:

1. The wigeon could have undergone food restriction during the trials. The available plant biomass (94 g DW/m^2) was close to that found in the wild (e.g. 100–

Table 4 Comparison of the energy intake (kJ/bird/day) of wigeon measured here and their theoretical daily energy expenditure. DEE, from Madsen (1988)

Trial	Energy intake (kJ/bird/day)	DEE (kJ/bird/day)	Energy balance
1	182	592	−410
2	345	592	−247

130 g DW/m^2 of *S. europaea* on the North Norfolk coast, England; Summers et al. 1993). However, the estimated total food available in the enclosure was 1.2 kg DW, or c. 170 g/individual/day, while the birds consumed only 80–90 g/day. Wigeon thus consumed more than 50% of their available food and would have significantly depleted their preferred food, the upper leaves. However, the remaining material was of similar quality and allowed a high intake rate, so food limitation seems unlikely.

2. The quality of *Salicornia* could have been too low. The comparison of the chemical composition of *Salicornia* with other plants consumed by wigeon in winter shows that the fibre content was quite low (ADF: 13.16%) since most temperate grass species have an ADF content between 10 and 30% DW (Van Soest 1982). The energy content of *Salicornia* (12.12 kJ/g DW) was higher than *Enteromorpha* spp. or *Ulva lactuca* (8 and 10 kJ/g DW, respectively), and nearly as high as *Zostera* sp. with 13 kJ/g DW (Mathers and Montgomery 1997), but poorer than grasses such as *Agrostis stolonifera*, *Puccinellia maritima* or *Lolium perenne* (15–18 kJ/g DW; Mayhew 1988; Mathers and Montgomery 1997). Moreover, the metabolisability of *Salicornia* by wigeon (about 27% of DW) was quite similar to the metabolisability of grass by these birds, i.e. 29% DW (Mayhew 1988). Consequently *Salicornia* ears were at least as profitable nutritionally as many of the other foods of Anatidae.

3. The instantaneous intake rate of *Salicornia* could have been too low. Pecking rates of 70 pecks/min are commonly observed on grass (Jacobsen 1992). With a mean bite size of 1 mg DW/bite (D. Durant, unpublished data, calculated from a mean leaf length of 2 cm/bite according to Rijnsdorp 1986 and Jacobsen 1992), the instantaneous intake rate of a bird on grass would be 70 mg DW/min, which is about half that on *Salicornia* (165 and 162 mg DW/min in trials 1 and 2, respectively).

None of these three factors can therefore explain the weight losses. To check the accuracy of the observed value of food consumption, we calculated whether the energy equivalent of the weight loss of birds over the study period was sufficient to make up for the deficit in the energy balance. Over the short-term (3 weeks), weight losses of animals usually consist of equal proportions of fat and protein (Davidson 1984). With an energy content of 40 kJ/g for fat and 5.1 kJ/g for protein (Schmidt-Nielsen 1975), the energy equivalent of this weight loss is 22.6 kJ/g [(0.5×40)+(0.5×5.1)]. Since the birds lost an average of 8.3 ± 3.1 g/day over the study period, which amounts to 187 kJ/day. This value is lower than the estimated 410 and 247 kJ/day in trials 1 and 2. The difference is likely to be due to the fact that some wigeon were fed with poultry pellets between trials, and thus their weight losses (and their energy deficit) would

have been higher on *Salicornia* alone. It is thus likely that the estimated intake is not too far from the true value.

We therefore suggest two possible processing constraints, which may prevent the birds from eating enough to cover their food requirements.

Processing constraints

Two constraints which may operate are: (1) the throughput rate may be very low, as the plants may be refractory to digestion due to the cuticle covering the ears, and (2) the high salt content of the plants may limit daily food intake.

The limitation of food intake by the throughput rate of food in the gut, a digestive bottleneck, has been shown to be an important factor governing daily intake rate in the woodpigeon *C. palumbus* (Kenward and Sibly 1977), the Canada goose *B. canadensis minima* (Sedinger and Raveling 1988), and the oystercatcher *H. ostralegus* (Kersten and Visser 1996). Campredon (1982) analysed guts of wild wigeon shot in the Camargue and suggested that *Salicornia* leaves occurred more frequently in the gizzard than in the crop, which could be due to a slower throughput rate of *Salicornia* than of the other more metabolisable plants. We hypothesise that a slow throughput rate is the reason why wigeon could not ingest sufficient energy to maintain their body weight. The ears were ingested as a whole by wigeon (personal observation) and it is possible that the presence of the thick waxy cuticle covering the ears slows down transit. Such a process has been reported for reptiles (Bjorndal and Bolten 1992). The cuticle may slow the breakdown of the ears into small particle sizes in the gizzard, and thus reduce the digestive processes (Bjorndal et al. 1990; Bjorndal 1991).

The second factor influencing the intake of this plant could be the high ash content of *Salicornia* (about 34%), which is essentially salt (Geslin 1983). Ducks are known to avoid salty foods (Nyström and Pehrsson 1988) since salt elimination has a physiological cost. Wigeon do not have fully developed nasal glands to reduce levels of salt in the blood as in brent geese *Branta bernicla* (Summers and Smith 1990). They therefore control their salt levels by regular drinks of fresh water as do barnacle geese *Branta leucopsis* when feeding on *Salicornia* (4.1% of daylight hours drinking as opposed to 0% on other marsh plant species; Ebbinge et al. 1975). Secondly, the excretion of salt is likely to have a high energy cost because of the active transport of Na$^+$ and K$^+$ ions (Milligan and McBride 1985). Nevertheless, Nehls (1996) reported that the time a bird takes to evacuate salt imposes an even greater constraint than the energy needed for the physiological processes involved in salt regulation. As a high salt concentration in tissues prevents an animal from maintaining homeostasis and may even be lethal, excessive salt must be quickly evacuated after intake. A high level of salt intake is likely to con-

strain food intake, and thus daily energy acquisition in these birds.

Two observations substantiate these two non-exclusive explanations. First, a slow throughput rate could limit the intake rate by constraining ducks to frequently interrupt their foraging periods until their guts are empty and/or to excrete excess salt. Such interruptions were frequently observed (Fig. 5). Second, the mean defaecation interval of wigeon on *Salicornia* was about 7 min. This value is about twice the defaecation interval for wigeon foraging on grass (3.8 min, D. Durant, unpublished data; 3.12 min, Mayhew 1988) suggesting a low throughput rate for *S. ramosissima* in the gut.

Geographical differences in the use of *Salicornia* by herbivorous Anatidae

The little scientific information available on wigeon feeding on *Salicornia* suggests the existence of major regional differences in the bird strategies of *Salicornia* use. Indeed, in the Netherlands (the Lauwersmeer), wigeon have been observed to feed preferentially on *Salicornia* (mainly *S. europaea*) in early autumn, during the ripening of the seeds (October). They shifted to other food types, mainly grasses, as the availability of *Salicornia* decreased (Van Eerden 1984; Drent and Prins 1987). In south Wales, Campbell (1946) also reported a particular interest of wigeon for *Salicornia*. A similar preference for *Salicornia* was also observed in barnacle geese in the Netherlands (Ebbinge et al. 1975) and in brent geese in autumn on the North Norfolk coast, England (Summers et al. 1993; Rowcliffe et al. 1998). In order to try to understand these differences, the chemical composition of *S. ramosissima* in our study area can be compared with that of *S. europaea* plants we collected on the island of Schiermonnikoog (The Netherlands) in October 1997 (Table 1). The structure and the ecology of this latter species are very similar to *S. europaea* and they are so closely related that they were long considered to be the same species (Lahondère 1985). The ears of five plants were sorted from the stem, pooled, dried and analysed exactly as described above. Protein content and ash content were similar. However, fibre content was much lower in *S. europaea* (NDF: 18.3% against 30.27% and ADF: 6.5% against 13.16%); WSC was higher in *S. europaea* (35.0% against 19.90%). Since organic matter metabolisability of herbivorous Anatidae is inversely related to fibre content of food (Prop and Vulink 1992), the lower fibre content of *S. europaea* may result in a higher metabolisability of this plant species. Besides, the smaller ears of *S. europaea*, i.e. 2–3 mg DW/ear (Van Eerden 1984), than those found in our study site (see Fig. 4) could make them easier to digest, resulting in a higher throughput rate. This is supported by the higher defaecation rate of wigeon feeding on *S. europaea* of about 3 min (Van Eerden 1984), which is less than half that reported in our study. This could explain why wigeon fed entirely on *S. europaea* in the Netherlands and only need 5 h of foraging per 24 h to cover their daily energy requirements (Van Eerden 1984). We also compared *S. ramosissima* with *S. europaea*, which formed much of the brent geese diet in autumn on the North Norfolk coast, England (Summers et al. 1993). The former had more crude protein (15.36% against 10.9%), more WSC (19.90% against 10.3%), and less ash (34.39% against 43.2%) (Table 1).

These results suggest that there may be large geographical variations in chemical composition, metabolisability and ear size of *Salicornia* plants, which could explain differences in their use by birds. However, it is possible that phenological changes in the plants account for part of the differences between regions. To separate these effects it will be necessary to analyse more samples of *Salicornia* from a range of regions and dates.

Management implications

In France, large numbers of wigeon winter in protected areas such as nature reserves (Guillemain 2000). The results of this study suggest that *S. ramosissima* is not a profitable food for wigeon, and that they benefit from grazing on graminaceous plants in pastures, which is what they do. These measurements need to be repeated, nonetheless, but this study provides no evidence that management in favour of *S. ramosissima* will improve wintering conditions for wigeon in coastal wetlands.

Zusammenfassung

Beschränkungen in der Ernährung mit *Salicornia ramosissima* durch Peifenten *Anas penelope*: ein experimenteller Ansatz

Die Feuchtgebiete an der Küste der Charente-Maritime (West-Frankreich) sind ein wichtiges Überwinterungsgebiet für Pfeifenten *Anas penelope*. Hier ernähren sich Pfeifenten hauptsächlich von Gräsern, während das Fressen von Queller *Salicornia ramosissima*, eine fleischige, sukkulente Halophyte, selten ist. Um die Ursache für diese mangelnde Nutzung der Ressourcen zu verstehen, wurde im Herbst 1998 eine experimentelle Studie mit in Gefangenschaft gehaltenen Pfeifenten auf einem *Salicornia*-Standort in der Charente-Maritime durchgeführt. Die Vögel waren nicht in der Lage, ihre Körpermasse zu halten, wenn sie sich nur von *Salicornia* ernährten. Sowohl Messungen der nahrungschemischen Zusammensetzung und Metabolisierbarkeit als auch der Nahrungsaufnahmerate der Vögel (g/min) konnten diese Gewichtsverluste nicht erklären. Allerdings zeigte ein Zeitbudget der Pfeifenten, dass sie ein Maximum von 10-11 Stunden pro Tag mit der Aufnahme von *Salicornia* zubrachten, wogegen 18-19 Stunden nötig gewesen wären, um ihren täglichen Energiebedarf zu decken. Die Zeit, die täglich für die Aufnahme von *Salicornia* aufgewandt wurde, könnte

durch physiologische Beschränkungen eingeschränkt worden sein: (1) durch einen hohen Ascheanteil (hauptsächlich Salz, etwa 34% Trockenmasse), und/oder (2) einen Engpass in der Verdauung aufgrund der wachsartigen Cuticula, die wahrscheinlich die Verdauung von *Salicornia* limitiert hat. Geographisch Unterschiede in der Nutzung von *Salicornia* durch Vögel werden diskutiert.

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