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Greylag geese (*Anser anser*)–*Scirpus maritimus* relationships in a newly colonised wintering area in the Camargue (France)

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In order to evaluate the proportion of *Scirpus maritimus* tubers consumed by a growing population of wintering Greylag goose (*Anser anser*) in Camargue, Southern France, we (1) measured the biomass of *Scirpus maritimus* tubers on the main resting and feeding marsh for geese in the area; and (2) evaluated, on the basis of their feeding behaviour, the consumption of *Scirpus maritimus* tubers by geese and changes in this consumption in relation to environmental factors. Mean tuber density and biomass were estimated at 7078 tubers per m² and 0.61 g per tuber, respectively. The mean number of tubers taken per goose per day was estimated at 633 tubers. The foraging efficiency of geese was greatest when birds used head-dip (vs. up-ending) feeding in water depths of approx. 30 cm. Consumption by geese during the winter was estimated at 20.71 tons. Annual consumption by geese (> 50,000 goose-days) represented 1.2% of all tubers present in the whole area. On the basis of these results, we suspect that the marsh could potentially support a number of geese considerably larger than currently present in winter. Nevertheless, the preferential use of some parts of the marsh seems to indicate that parameters other than food availability could also determine geese feeding behaviour.

1. Introduction

The quantitative assessment of feeding habitat for wildlife has emerged as an important component of management planning in protected areas (Guillemain *et al*. 2002). This evaluation is often difficult to undertake as it depends on numerous parameters (Bakker 1989, Sutherland & Allport 1994, MC Leod 1997, Van Andel 1999, Stahl *et al*. 2002, Rowcliffe *et al*. 2004). The global food intake of a population can be extrapolated from feeding behaviour measurements of the individuals in the field (Sutherland 1996). It can then be compared with food production of the habitat. This comparison is an important step but it only represents a rough evaluation of the feeding sustainability of this habitat. Nevertheless it can be used as a predictive indicator for adaptive management.

During the last 50 years, a major increase in Greylag goose (*Anser anser*) numbers and range has been recorded in Europe (Dick *et al*. 1999, Nilsson *et al*. 1999, Kampe-Persson 2002). This increase is thought to be due to the reduction of persecution, creation of refuges, year-round improvement of feeding conditions and the opportunistic exploitation of agricultural lands on staging and wintering areas (van Eerden *et al*. 1996, Kampe-Persson 2002). This expansion not only results in damage for cultivated areas (Paterson 1991, Patterson 1991), but also leads to conservation conflicts (Owen 1990) as these herbivores can strongly influence plant community dynamics in natural habitats (Esselink *et al.* 1997, Bakker *et al*. 1999).

In the Camargue, delta of the Rhone (South of France), the wintering of Greylag geese is a recent phenomenon (Walmsley 1988, Kayser *et al.* 1992). Since the early 1980s the numbers of geese have increased exponentially (Desnouhes *et al.* 2003). Geese generally gather in large protected Camargue areas for resting and feeding (Kayser et al. 2003). In these shallow brackish marshes, *Scirpus maritimus* is the dominant plant species (Charpentier *et al.* 1998), and represents the principal food resource for geese, especially tubers and roots (Desnouhes & Lepley 2004).

The objective of our study was to estimate the proportion of food consumed by geese on the main wintering area used for feeding and roosting in the Camargue, the St Seren marsh. For this purpose, we (1) measured the biomass of *Scirpus maritimus* tubers present on the St Seren marsh, and (2) evaluated the consumption of *Scirpus* tubers by geese on the basis of their feeding behaviour. We also studied the changes of this consumption in relation to variations of water levels.

2. Material and methods

2.1. Study area

The Camargue (Rhône delta, Southern France, Fig. 1) is a mosaic of fresh, brackish and salted wetlands and agricultural fields of 1,450 km^2 (Tamisier & Grillas 1994). In the Camargue, Greylag geese are mainly observed at three important protected areas (Kayser *et al.* 2003), but have also been sporadically observed on sown winter wheat (Desnouhes *et al.* 2003).

The St Seren marsh (70 ha) lies in the centre of the Tour du Valat nature reserve (Fig. 1). This marsh fills up naturally with autumn rain and generally dries up in June (Duncan *et al.* 1982). However, since 1978 the water regime has been artificially managed in order to ensure a short summer draining period before re-flooding in early August. The vegetation is dominated by *Scirpus maritimus,* which covers more than 50% of the marsh; less abundant plants are *S. lacustris*, *S. littoralis* and *Aeluropus littoralis*. The marsh is grazed by cattle from April to September (0.5 animals per hectare) to control the re-growth of emergent vegetation. St Seren is an important wintering area for dabbling and diving ducks, with peak numbers of up to 20,000 Anatidae using it as a diurnal roost (Duncan *et al.* 1982, Tamisier & Dehorter 1999). It supports the majority of wintering geese in the Camargue (i.e. approximately 60% of the Camargue population) and the grazing pressure was estimated at 53,627 goose-days ± 6,575 (SE) between 1997–2002, with a peak at nearly 75,000 goose-days during winter 2001–2002 (Desnouhes *et al.* 2003).

The activity budgets of geese on St Seren were recorded in 2001 and 2002 by Desnouhes *et al.* (2003), 45% of the daily activity of geese was allocated to feeding, corresponding to a mean of 4.5 hours per daylight period throughout the season.

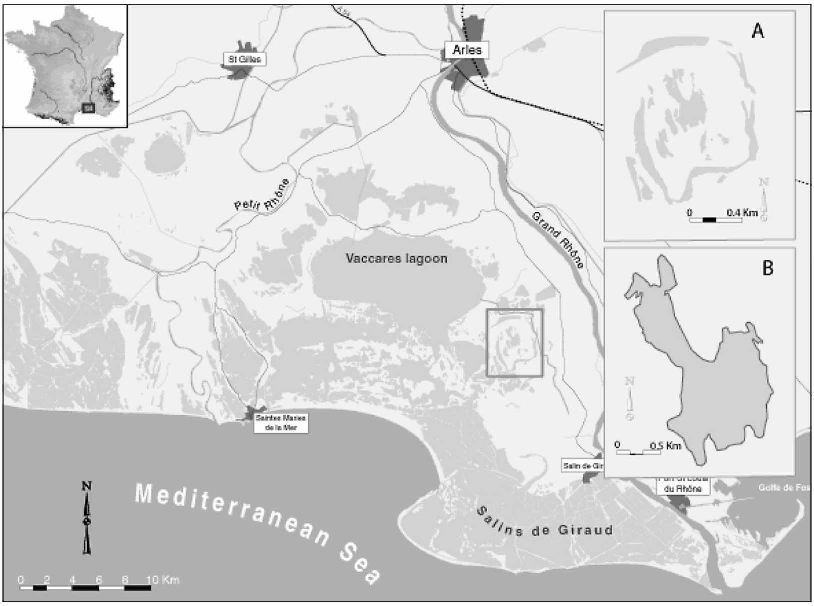

Fig. 1. Location of the study site in the Camargue, southern France, (A) within the Voluntary Nature Reserve of Tour du Valat and (B) in the central part of it, the marsh of St Seren.

2.2. *Scirpus martimus* underground biomass

We sampled underground biomass of *Scirpus maritimus* during July 2002 and 2003 when the marsh dried up and before the autumn arrival of geese. Random sampling plots were chosen and localized along an altitudinal transect through the *Scirpus maritimus* area. The geographical position of each sampling point was recorded and a digital elevation model was developed to describe the topography of the St Seren (Chauvelon & Sandoz 1999), enabling a flooding period to be computed for each plot. Tuber density was calculated from samples of 15x15 cm in area, 15 cm in depth. Vertical distribution of tubers within this 15 cm core was not determined. A maximum depth of 15 cm was used because it was assumed that digging in the sediment with their bill, geese could search for tubers down to this depth. After washing, the tubers were separated from roots and stems, oven-dried at 70°C for 48 h and weighed to the nearest 0.01 g. Throughout the paper, all biomass data are presented as dry biomass.

2.3. Behavioural observations of geese

From November 2002 to February 2003, behavioural observations on focal individuals were performed one day per week (Altmann 1974). Each focal bird was observed continuously for 10 minutes using a telescope (20–60 ×) and a camcorder (× 100) between 0800 and 1800 hours. From a hide, the position of the sampled bird was plotted on the vegetation map of the marsh. To check observer accuracy in positioning geese on the map, 20 previously geo-referenced points were randomly distributed more than 200 m from the hide. The observer determined the position of these test points using a 20x60 telescope based on vegetation features (*Tamaris*, *Juncus*), islands, water and marsh edges and other landscape elements. We determined the coordinates of these reported points using a GIS and compared to the actual GPS coordinates. Errors were less than 20 m for all test points. This accuracy was considered acceptable in view of the distances involved (between 0 and 700 m).

Only complete 10 minute focal samples were analysed, and we rejected those where birds mainly engaged in non-feeding activities. We distinguished 4 behaviours: (1) feeding (head-dipping, i.e. foraging head and neck underwater and up-ending, i.e. foraging with the anterior part of the body submerged), (2) movement and vigilance, (3) mastication and ingestion, and (4) preening.

Duration of different behaviours was timed to the nearest 0.5 s for each 10-minute sequence (Guillemain *et al.* 1999).

As a baseline we measured water levels at a permanent station. This served to calculate water depth at any observation location using the digital elevation map. We used either feeding depth or water depth in the text because geese reach the bottom of waterbodies when they feed.

2.4. Estimation of the consumption of *Scirpus maritimus*

Food consumption by geese was derived from previous field studies conducted on Greylags in our study area. We considered an extraction attempt to be equal to only one tuber extracted (cf. Amat 1986).

Individual daily food intake (expressed as numbers of tubers or as grams) and the total amount of food consumed per wintering season (TFC, in tons) were estimated as follows:

$$DNI = nTC \bullet DfT \quad (1)$$

where DNI is the number of tubers taken per individual per day, nTC is the number of tubers taken per individual per minute; DfT is the time spent feeding by individuals during a daily period. For the time spent feeding, we used the daily activity budget previously estimated during the wintering season 2001–02 on the St Seren (Desnouhes et al. 2003).

$$DFI = DNI \bullet M \quad (2)$$

where DFI = mass (g) of food taken per individual per day, and M = median tuber mass

and $TFC = DFI \bullet N$ (3)

where N is the number of goose-days.

The geese consumption per m² (GCS) was estimated by dividing the TFC by the total area (m²) of the *Scirpus maritimus* stand. The proportion of food consumed (PFC) was calculated by dividing the recorded density of tubers per m² by the GCS. The result is expressed in grams and was transformed into tons when appropriate.

2.5. Data analysis

We used regression analyses to test for the dependence of vegetation parameters, goose behaviour and grazing pressure on water depth. Mann-Whitney U tests were employed on the *Scirpus* underground biomass data because the distributions of residuals were non-normal. The tests were used to detect differences between annual densities, in order to subsequently consider the average of these samplings for calculations, in case of the absence of significant difference. Student's t tests were used to compare foraging efficiencies between upending and head-dipping geese. The rate of successful extraction is presented as percentages, but was arcsine-transformed for the analyses (Sokal & Rohlf 1995). Throughout this paper, averages are presented together with standard errors (Mean ± S.E.).

3. Results

3.1. *Scirpus maritimus* underground biomass

Tuber density on the St Seren marsh did not significantly differ between the two sampling seasons (n = 34, Z = –0.70, P = 0.48), with an average of 7078 ± 284 tubers per m² (n = 34, 95%CI: 6501–7656). Individual tuber mass was 0.61 ± 0.08 g on average (n = 3222). The number of tubers per sample explained 57% of the variance in underground biomass between samples ($F_{1,34} = 42.7$, $P<0.001$). The number of tubers was independent of the number of flooding days ($F_{1,14} = 0.69$, P = 0.421). Individual tuber biomass increased significantly with the number of flooding days ($r^2 = 0.53$, $F_{1,13} = 12.7$, P = 0.004).

3.2. Foraging behaviour

During the winter 2002–03, more than 75% of the time spent in feeding behaviour was devoted to two main activities: the extraction of *Scirpus* tubers and the handling and ingestion of these tubers, while movement and preening were minor activities (Table 1). The recorded movie sequences showed the Greylag geese loosening the sediment by trampling with their feet and dipping their head

Table 1. Behaviour of feeding geese in the St Seren *Scirpus* stand, Camargue, South of France, based on 10-minute focal individual samplings (n = 46). Results are expressed as percentage of time spent per activity ± SE.

Extraction	Movement	Mastication and ingestion	Preening
44.85 ± 11.08	22.66 ± 10.90	32.50 ± 10.46	0.42 ± 0.91

and neck under water, or up-ending in order to extract roots.

The time spent in tuber extraction (time spent in apnea) varied with foraging behaviour (t = 3.16, P = 0.010), being significantly longer when the geese foraged by up-ending (5.2 ± 1.4 s., n = 29) than when they relied on head-dipping (4.1 ± 0.8 s., n = 14).

The number of extraction attempts was greater when the geese grubbed by head-dipping (7.4 ± 0.53 attempts per minute, n = 14) than by up-ending (5.02 ± 0.29 attempts per minute, n = 29; t = 3.91, P < 0.001).

The number of tubers extracted (i.e. successful extraction attempts) per unit of time also was higher when the birds used head-dipping than up-ending (3.22 ± 0.22 min^{-1}, n = 14 and 2.13 ± 0.12 min^{-1}, n = 29, respectively; t = 4.52, P < 0.001). The proportion of tuber extractions that were successful did not differ between foraging modes (t = 0.04, P = 0.97), the rate of successful extraction being 44.69 ± 2.17% (n = 14) and 43.8 ± 3.94% (n = 29) when geese foraged by up-ending and head-dipping, respectively. On the St Seren, the average number of *Scirpus* tubers extracted by Greylag geese was estimated at 2.38 ± 0.81 per minute (CI 95%: 2.13–2.63).

The number of tubers extracted did not differ between wintering seasons for any of the two feeding methods (t = 0.043, P = 0.97).

Geese appeared to be slightly selective in the choice of their feeding area. The feeding goose density was inversely correlated with the underground biomass of tubers on St Seren (r^2 = 0.33, $F_{1,13}$ = 5.31, P = 0.042).

The water depth differed significantly (t = –2.42, P = 0.021) between feeding methods: to extract tubers, geese went down to 30.7 ± 0.67 cm (n = 14, CI 95%: 28.8–32.5) by head-dipping and 46.9 ± 2.7 cm (n = 29, CI 95%: 41.4–52.4) by up-ending.

The area potentially usable by geese for feeding (irrespective of *Scirpus maritimus* distribution) on the whole marsh, calculated after the depth they reach when feeding with different methods, showed strong variations according to water levels (Fig. 2). This potential area appeared to never exceed 23 ha (1/3 of the total marsh area).

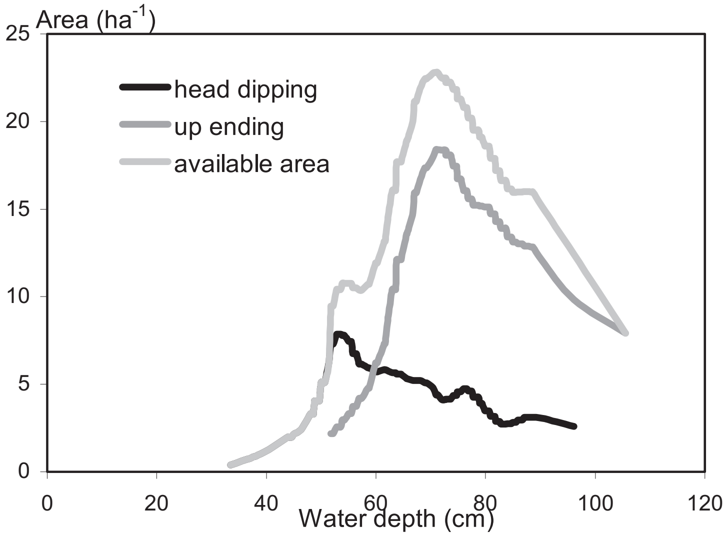

Fig. 2. Estimated area available to feeding geese depending on water levels and feeding method on the marsh of St Seren (based on an elevation map of the area).

3.3. Estimation of the proportion of tubers consumed by geese

The number of tubers taken per individual goose per day was estimated at 633 (95% CI: 567–700) (equation 1). During the two sampling seasons, average tuber mass was 0.61 g. Consequently, using equation (2), a goose consumed approximately 386 g of tubers per day [DFI] (95% CI: 346–427). During a wintering season, the consumption by the whole goose population therefore corresponds to 20.71 tons [TFC, formula 3] (95% CI: 12.23–30.69), or a total number of almost 34×10^6 tubers. On this marsh the *Scirpus maritimus* stand covers an area of 40 hectares; the geese consequently consume an average of 84.9 tubers per m² [GCS] (95% CI: 50.1–125.8), or only 1.2% of the total amount of tubers present [PFC] (95% CI: 0.65–1.94).

On the 10% of the marsh area where high grazing pressures were observed, the consumption by geese can be estimated at approximately 770 tubers per m² during a wintering season, which corresponds to 10.9% (95% CI: 10.1–11.8) of the quantity of tubers present by m² in the area.

4. Discussion

4.1. Feeding behaviour in the French wintering area

The feeding behaviour of geese observed at the St Seren was similar to that described for Bewick swans (*Cygnus columbianus bewickii*) by Nolet *et al.* (2001). Individuals used trampling to remove the sediment covering the tubers. According to the water depth and to tuber accessibility, geese too practice either head dipping or up-ending to extract food (Nolet *et al.* 2001). The relationship between water depth and the preponderance of one of the two feeding methods has already been described for the Greylag goose (Amat *et al.* 1991). These authors found the number of tubers extracted by head dipping geese to be higher than for up-ending individuals. Exactly the same result was observed in the present study. The respective numbers of tubers extracted per unit of time with the two feeding behaviours were similar to those measured by Amat (1986). Nevertheless, we found foraging success (in terms of tubers extracted per extraction attempt) to be lower, particularly when geese fed by head dipping.

The quantity of food consumed by geese in Dutch *S. maritimus* stands was estimated to be 185 root-pieces for 5.5 hours spent in feeding activity per day, which corresponded to a biomass of 800 g (Loosjes, 1974). Our estimation of daily consumption by Greylag geese on the St Seren was equivalent to ca. 1300 g fresh weight per bird (field measurements providing the following relationship between *Scirpus* tubers fresh and dry weights: Fresh Weight = (Dry Weight – 0.775)/0.304, $r^2 = 0.885$, $P < 0.0001$; Gouraud 2004). Estimates from Loosjes and our study therefore seem to be of the same order of magnitude, despite the potential differences in habitats and field procedures used.

Because our study is only based on short-term measurements, it is difficult to evaluate the grazing pressure sustainable for the *S. maritimus* stands in the long term. Yearly consumption by more than 50,000 goose-days corresponds to 1% of the food available on the whole area. On this basis, the marsh could potentially support a considerably higher number of geese. Experimental work on a *Scirpus* population in microcosm has shown an impact of geese only above 20% of tuber depletion (Desnouhes, unpublished data). Based on this result, the increase of the goose population recorded during the last decade at this site (Desnouhes *et al.* 2003) should have little or no effect on the *Scirpus* stands in the coming years. The great capacity of resilience of *S. maritimus* following disturbance supports this idea (Charpentier 1998). Nevertheless, earlier measurements (Pichaud *et al.* in prep.) showed that the area actively used by geese to feed only represented a small part of the marsh. Furthermore, we found that the preferential goose feeding area did not correspond to the one where ground biomass was the highest. The relative impact of the geese at their actual preferred foraging area may therefore be far higher than the 1% above. The quantity of food consumed not only depends on the amount of food present in the habitat and the animals' food requirements – other factors like water levels, the energy necessary to extract food or the size of food items also may largely influence feeding behaviour (Guillemain *et al.* 2000, Fritz *et al.* 2001, Durant *et al.* 2003), which is very likely to be the case for geese on St Seren.

The mean dry weight of tubers sampled in this study was close to the one recorded in Camargue marshes where *Scirpus maritimus* stands were strongly disturbed (i.e. cattle grazing, drought), with numerous disconnections between tubers (Charpentier 1998). The presence of numerous independent small groups of unconnected tubers suggests that the *S. maritimus* stand on the marsh of St Seren too had already been strongly disturbed. Charpentier *et al.* (1998) have suggested that *Scirpus maritimus* dormant buds may provide a capacity to rapidly recover from damage to the rhizomes and tubers (Amat 1986, Kantrud 1996). Nevertheless, Charpentier *et al.* (1998) have also shown that the capacity of resilience after disturbance has a cost, especially in terms of the size of the new tubers produced. The fact that geese prefer small tubers (Amat 1995, Desnouhes 2004) suggests, until a certain level of predation, that their consumption of *Scirpus maritimus* could lead to auto-facilitation (i.e. consumption by the forager may help its own future foraging). This mechanism could partially explain why we did not record geese feeding preferentially where underground biomass was the highest.

Following the Marginal Value Theorem (Charnov 1976), the determination of the exact geese number that the marsh can sustain does not only depend on the accessibility of food, but also on the energy which the birds consent to spend before they choose to feed elsewhere. This determination requires a better understanding of the relationships between individual mechanisms of food acquisition and plant dynamics (Hobbs & Hanley 1990). Also, the role of density, size and connection between tubers (e.g. difficulty of extraction) on the feeding behaviour of geese, and in return the impact of goose predation on these three parameters, will have to be further studied.

4.2. Management implications

Our results suggested that the St Seren could potentially be used by numerous flocks of geese without short-term conspicuous deleterious effect on the *Scirpus* beds. In this case, we think that the following management options may help keep goose foraging sustainable. We determined that the largest feeding area for geese corresponded to a water depth of about 75 cm at the geo-referenced point (Fig. 2) where measurement of the marsh water level is performed weekly. Nevertheless, we also found that the feeding efficiency of geese (number of tubers extracted per minute) was higher when the birds relied on head dipping, which corresponded to a water level lower than 75 cm at the geo-referenced point. Therefore, the best management option to optimise the feeding value of the marsh appears to be a compromise between the maximum area where geese can feed, represented here by a high water level at the geo-referenced point, and the possibility for them to practice head dipping (i.e. shallower water). This compromise seemed to be reached at the end of November 2002, and the maintenance of the water level as it was during this month (e.g. 73 cm at the geo-referenced point) should be looked for during the presence of geese on the marsh. Most years the water level of the marsh appears to be too high to fulfil the conditions suitable for geese during several months: the typical Mediterranean early autumn precipitations (Chauvelon *et al.* 1999) lead to increases in earlier water levels. In this sense the artificial filling of the marsh by summer pumping, which offers favourable conditions for waterbird day-roosts at this period of the year, does not seem to be a judicious management for the feeding of geese later on, i.e. from October to February.

Our results suggest that only a small fraction of tubers were consumed by geese. Nevertheless, the cumulative consequences of tuber predation on *Scirpus* stands by this growing population of birds, in addition to summer grazing by domestic cattle, remains unknown. The predation of tubers (i.e. reserves for the plant) by geese added to the consumption of green parts by cattle could lead to the replacement of *Scirpus* by other plant species non-palatable for geese. An adequate monitoring of the vegetation and an evaluation of the exact impact of cattle on the production and size of *Scirpus* tubers need to be performed. To pursue simultaneously two objectives as distinct as to feed a growing goose wintering population and to feed a domestic herd in summer may rapidly become unrealistic. On the other hand, summer grazing by cattle, combined with adequate water management, may be the easiest way to favour the goose population at this site in the future.

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Merihanhet *Scirpus maritimus* -kaislan kuluttajina talvehtimisalueillaan Camarguessa Ranskassa

Arvioidaksemme merihanhien kasvavan talvehtimispopulaation kulutuksen vaikutuksen kaislan mukuloiden määrään mittasimme (1) kaislojen mukuloiden biomassan merihanhien talvehtimiseen pääasiallisesti käyttämällä suolla sekä (2) arvioimme hanhien ruokailukäyttäytymisen perusteella niiden syömien mukuloiden määrän. Lisäksi selvitimme ympäristötekijöiden vaikutuksia hanhien ruokailutehokkuuteen. Arvioimme talvehtimissuon mukulatiheydeksi 7 087 mukulaa/m² ja mukuloiden biomassaksi 0,6 g/mukula. Yhden hanhen arvioitiin syövän 633 mukulaa päivässä. Ruokailutehokkuus oli suurin, kun hanhet söivät noin 30 cm:n syvyisessä vedessä, eikä niiden tarvinnut poimia ruokaansa syvemmältä. Talven aikana hanhien arvioitiin syöneen 20,71 tonnia kaislan mukuloita. Vuosittainen kulutus oli 1,2 % mukuloiden kokonaismassasta talvehtimisalueella. Talvehtimisalue kestääkin todennäköisesti paljon suuremman määrän hanhia. Hanhet suosivat tiettyjä osia suosta. Tämä johtunee ravintotiheyden lisäksi myös muista ympäristötekijöistä.

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