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ORIGINAL ARTICLE

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Sward height and bite size affect the functional response of barnacle geese *Branta leucopsis*

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Abstract Intake rate, the rate in which herbivores can process their food, is presumed to be an important factor in habitat selection down to the scale of the foraging patch. Much attention has been given to the selection of swards of high nutritional quality, but much less has been given to the influences of sward structure on patch selection in small herbivores. In this study we tested the effects of sward density and height on the functional foraging response of barnacle geese, *Branta leucopsis*. The functional response curve for herbivores describes how intake rate is affected by food availability. We conducted feeding trials to determine intake rate and bite size of barnacle geese on experimentally manipulated swards. Results indicate that intake rate is mainly dependent on sward height and that there is a strong correlation between bite size and intake rate. Sward density does not influence the rate of food consumption; it is, however, a crucial parameter affecting potential total yield. We conclude that bite size is the crucial parameter influencing intake rate. Bite size is explained both by sward height and individual differences in bill morphology. Furthermore, intake rate seems to be dependent on the physical structure of the grass species consumed.

Keywords Bite size · Feeding trial · Intake rate · Herbivore · Peck rate

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Introduction

Herbivore grazing creates a short, dense canopy of high plant quality. Small herbivores have been shown to prefer these sward properties (McNaughton 1984; Drent and Van der Wal 1999; Van der Graaf et al. 2002; Bos et al. 2005b). As a consequence, they often follow herds of larger herbivores (McNaughton 1984) or prefer fields grazed by livestock (Van der Graaf et al. 2002; Bos et al. 2005b). This process in which one herbivore improves foraging conditions for another is called grazing facilitation. Not only larger herbivores can induce these profitable sward changes, it has recently been shown that small herbivores themselves can create and maintain grazing lawns (Bos et al. 2004; Van der Graaf et al. 2005). Most studies focus on the quality increase of grazed swards, which is measured as nitrogen or protein content. Little is known about the effect of the structural properties of the sward, such as height and density, on forage preferences of small herbivores, though many studies consider this (Van de Koppel et al. 1996; Van der Wal et al. 1998).

The functional response describes the relationship between the individual intake rate and food availability. For herbivores, food availability is expressed as biomass, which is a function of sward density and height. Intake rate (gram biomass per unit time) is the product of bite rate (number of pecks per unit time) and bite size (amount of biomass consumed per bite). Most studies find that the functional response curve initially increases with increasing biomass but decreases or levels off after a certain optimum is reached (Fryxell 1991; Gross et al. 1993; Van de Koppel et al. 1996; Iason et al. 2002; Bos et al. 2004). For small herbivores, intake rate at low sward heights is limited through a decreased bite size (Iason et al. 2002), while at high sward heights intake rate is believed to decrease through handling problems with long leaves (Van der Wal et al. 1998; Hassall et al. 2001), increased costs of locomotion, and increased vigilance due to changes in the perception of predation risk (Van de Koppel et al. 1996).

In addition, sward density might be an important parameter influencing the functional response of small herbivores, but this factor has remained largely unstudied so far. It is hypothesized that an increased sward density will positively affect bite size because it sustains the consumption of multiple leaves per bite, as well as peck rate, as searching time is reduced. We therefore expect a functional response curve in which intake rate will increase with increasing sward density.

Here we experimentally tested the effects of sward density and height on the functional response of barnacle geese, *Branta leucopsis*. We conducted feeding trials with captive barnacle geese to determine intake rate and bite size on swards of different heights and densities. Based on recently published work on the functional response of different waterfowl species, we are now able to discuss the role and significance of the different sward parameters and discuss the implications for our understanding of habitat selection of wild geese.

Methods

Feeding trials

To determine the intake rate of barnacle geese on swards of different height and density, we conducted feeding trials in which three captive barnacle geese were offered turfs with different sward properties. During the feeding trials, geese were taken from their holding pen at 5:00 p.m. daily and put separately in 1×1-m cages consisting of a wooden frame, with netting on the sides and top, and a hardboard floor. During the night the geese had access to water but not to food. Trials were started shortly after sunrise the next morning. Because the geese were starved overnight, they always foraged on the turfs immediately. Each turf was put in the cage for 5 min. We chose this relatively short time period to make sure the geese did not deplete the turf within the feeding trial. In addition, we restricted the number of consecutive turfs a goose was offered each morning to three in order to make sure the geese did not become satiated. In total, 55–57 turfs were presented to each goose during a period of 22 days.

Observations were made by one observer from approximately 10 m distance from the cages, which caused no disturbance because the geese were tame and trained to the routine. In the 5 min of the feeding trial, foraging time (FT) was determined as the time each goose had its head down towards the turf, and the total number of pecks on the turf was counted (P) using a hand counter. Peck rate (PR) was calculated as $\mathrm{PR}=\mathrm{FT}/P$, bite size (BS) as $\mathrm{BS}=I/P$, and intake rate (IR) as $\mathrm{IR}=\mathrm{I}/\mathrm{FT}$. After the feeding trials, the geese were released from the cages and could graze freely in a small group of yearlings until they were caught again in the late afternoon.

Durant et al. (2003) showed that bill size and, in particular, bill width can have a large influence on bite size and therefore on intake rate. In addition, age and sex can be important factors determining intake rate (Lang and Black 2001). From a group of 15 yearlings, we selected three geese that had similar bill size (width and length). All geese selected were males and were accustomed to humans. The experimental routine was started 2 weeks before measurements began in order to habituate the geese to the situation.

Turf preparation

Nine months before the start of the experimental feeding trials, *Festuca rubra* seeds were sown in trays of 40×40 cm; these trays were put inside a greenhouse under optimal growing conditions. Seeds were sown in two densities; however, measurements later revealed a continuous range of tiller densities rather than two density classes. Grass in all trays was regularly cut throughout this period. Prior to the trials, the swards were cut to a height of about 1, 3, or 6 cm, and were allowed to regrow for several days so that fresh leaf tips formed for consumption by the geese. This procedure created a range of sward heights from 2 to 8 cm. Each turf was subdivided into two times four turfs of 10×20 cm. Turfs were put in a plastic container of similar size to prevent soil loss. Of these four turfs, one turf was offered to each individual goose, and one was used as an evaporation control. On each turf all tillers were counted, and sward height was measured to the nearest 0.5 cm using a sward stick on the afternoon prior to the feeding trial. At the start of the feeding trial, each turf and the control turf were weighed (W_1 and WC_1, respectively); weighing was repeated immediately after the feeding trial (W_2 and WC_2). All weighing was conducted on an analytical balance (Mettler Toledo AG204) to the nearest 0.1 mg.

Evaporation (E) was calculated from the weight loss of the control turf:

$$E = 1 - WC_2/WC_1$$

Intake (I) was calculated as

$$I = W_2 - W_1 - (E^* W_1)$$

Two instances when the calculations resulted in a negative intake were discarded. After the feeding trials, a total of 40 randomly selected turfs were clipped, and material was sorted into live *Festuca* tillers and other material. *Festuca* tillers were weighed, dried for 48 h at 60°C, and weighed again afterwards in order to determine the conversion factor of wet weight (WW) to dry weight (DW). The resulting conversion DW = 0.54*WW was used to convert all weights to dry weights. Additionally, biomass (B) of the turfs was characterized by the product of canopy height (H) and density (D), in which W is constant and represents the weight per grass length.

$$B = H^* D^* W$$

Average weight per grass length was calculated from the weighed *Festuca* tillers, divided by the number of tillers and the height, $W = 0.59$ mg/cm.

Results

Table 1 shows test results of a multivariate ANOVA, testing for effects of sward density and height (as covariates) on peck rate, bite size, and intake rate. This test also incorporated the three individual geese (fixed factor). Intake rate and bite size were square-root-transformed to reach normal distribution.

We found no differences between the individual geese or any significant interactions between individual geese and sward parameters, suggesting that all geese responded in a similar way to changes in sward densities and heights. We found no effect of sward density on either peck rate, bite size, or intake rate of the geese (Table 1). There was no significant interaction between sward height and sward density. We found an effect of sward height on both bite size and intake rate (Table 1, Fig. 1); our results thus indicate that intake rate and bite size are only influenced by sward height, not by density. Bite size and intake rate were strongly correlated ($R^2 = 0.92$, $P < 0.001$, $n = 167$, Fig. 2).

Discussion

Effect of sward density and height on bite size and intake rate

Though other studies have tested the effects of sward height or biomass on goose intake rate, no previous study addressed the effects of sward density on goose intake rate. From our results, we conclude that sward density mainly affects the food availability for the geese, i.e., yield to grazers (Van der Graaf et al. 2005), not the rate at which the geese can consume the food. Average sward density in our study was 13.67×10^3 tillers m^{-2} (standard error $= 0.51 \times 10^3$, $n = 167$), which is similar to a long-term ungrazed natural salt marsh in the wintering areas of the Russian barnacle goose population in the Wadden Sea (16.36×10^3 tillers m^{-2}, Van der Graaf et al. 2002) and closely similar to the sward density at the wintering area of the Spitsbergen population of barnacle geese in Caerlaverock, Scotland (12.67×10^3 tillers m^{-2},

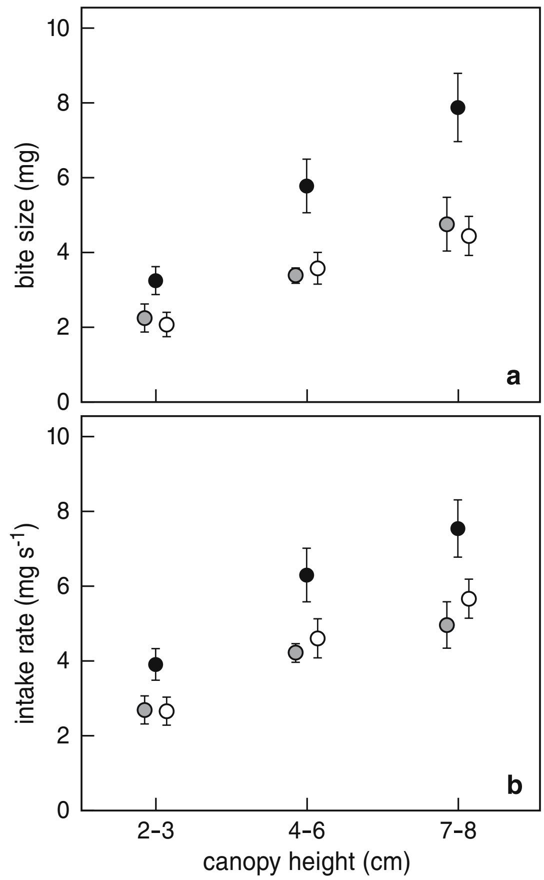

Fig. 1 Relationships between sward height (divided in three classes), (**a**) bite size, and (**b**) intake rate shown as means ± standard error. *Differently shaded symbols* represent the three individual geese. Analyses were performed on the raw data, but mean values are presented for clarity. See Table 1 for test results.

Table 1 Test results of a multivariate ANOVA testing for the effects of sward density and height on (a) peck rate, (b) bite size, and (c) intake rate

Source	*df*	(a) Peck rate		(b) Bite size		(c) Intake rate	
		F	*P*	*F*	*P*	*F*	*P*
Corrected model	11	3.632	0.000	12.017	0.000	7.874	0.000
Intercept	1	120.665	0.000	36.002	0.000	41.812	0.000
Individual goose	2	0.219	0.804	0.624	0.537	0.447	0.640
Sward density	1	1.876	0.173	1.061	0.305	0.431	0.512
Sward height	1	1.168	0.282	10.333[a]	0.002[a]	7.011[a]	0.009[a]
Density × height	1	0.299	0.585	0.663	0.417	0.577	0.449
Goose × density	2	0.255	0.776	0.411	0.664	0.262	0.770
Goose × height	2	0.043	0.958	0.104	0.901	0.058	0.943
Goose × density × height	2	0.192	0.826	0.491	0.613	0.328	0.721
Error	155						
Total	167						

The model is corrected for differences between individual geese. (a) $R^2 = 0.205$, (b) $R^2 = 0.460$, (c) $R^2 = 0.358$
[a]Significant results

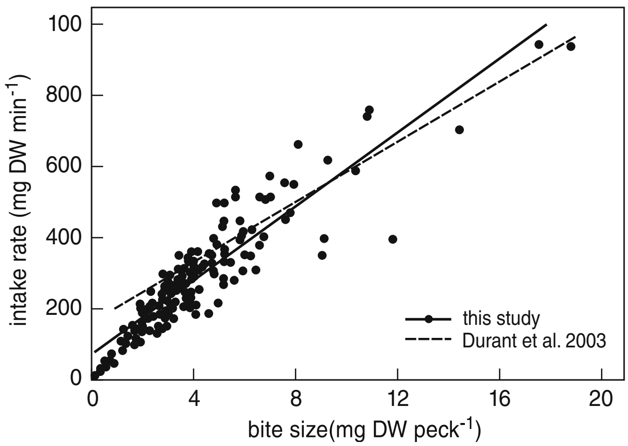

Fig. 2 Relationship between bite size and intake rate found in our study (*dots* and *solid line*, $R^2=0.92$, $P<0.001$, $n=167$) and by Durant et al. (2003; *dotted line*, $R^2=0.76$, $P<0.001$, $n=53$)

Lang and Black 2001). Because biomass is the product of tiller density and height, it is represented in the analysis by the interaction between these two factors. This interaction was not significant, and we therefore conclude that there is no effect of biomass per se on intake rate or bite size in these small avian herbivores.

In contrast, the functional response of mammalian herbivores is most often based on biomass (Gross et al. 1993). However, most of these studies do not include sward height in their analyses. Since sward height and biomass are often closely linked, we expect that even in these studies sward height could turn out to be of prime importance. We detected a strong effect of sward height on bite size and intake rate, plus a strong correlation between those foraging parameters (Fig. 2). A similarly close relationship between intake rate and bite size was found for several species of mammalian herbivores (Gross et al. 1993) as well as for waterfowl (Rowcliffe et al. 1998; Lang and Black 2001; Durant et al. 2003).

Comparing recent studies

Our study corresponds with other recent studies on intake rate in herbivorous wildfowl. Three other studies have looked into the effects of sward height on intake rate in geese. In three out of four studies, bite size increases with increasing sward height (Lang and Black 2001; Durant et al. 2003; this study). Cope et al. (2005) employed the same methods as in our study but failed to detect a significant relationship between sward height and bite size. However, they comment on the large interindividual variation in bite size, which was related to the wide array in bill length of their group of geese. Two studies demonstrate a decreasing peck rate with increasing sward height, a relationship also found for other waterfowl, including wigeon, *Anas penelope* (Jacobsen 1992) and cackling Canada geese, *Branta canadensis minima* (Sedinger and Raveling 1986), whereas we did not encounter this relationship in our own data over the restricted range of sward heights covered (Table 2). Finally, intake rate has been shown either to increase with increasing sward height (this study), to increase to a certain level and decline afterward (Lang and Black 2001), or to remain constant throughout (Durant et al. 2003).

Table 2 provides an overview of the relationships found in the aforementioned studies; also shown are the forage grass species and the sward height range under study. It becomes evident that previous studies used agricultural grasses, mainly *Lolium perenne*, for the feeding trials, whereas we used *F. rubra*, a grass growing on the natural salt marshes that are the traditional feeding ground of barnacle geese. Structural differences between the forage grass species may account for some of the differences indicated above. *Lolium* has broad leaves, whereas *Festuca* leaves are very narrow (Illius et al. 1995). *Lolium* on agricultural meadows will grow taller than *Festuca*. With our experimentally grown turfs, it turned out to be impossible to create a *Festuca* sward with a sward height above 10 cm, since the grasses would start to bend and lay flat.

Similar bite sizes on *Lolium* and *Festuca* swards suggest that the geese take more leaves of the narrower *Festuca* leaves per bite to reach a similar bite size. The lower peck rate on *Festuca* swards, as found in our study, could then be explained by prolonged handling, while, concurrently, the lack of relationship between peck rate and sward height may be attributed to a generally long handling time, even on short swards of *Festuca*. We here refer to a study by Iason et al. (2002), who contrasted the functional response in rabbits, *Oryctolagus cuniculus*, foraging on *Festuca ovina* swards and *Lolium* swards. In distinction to the asymptotic function in *Lolium*, the response to *Festuca* was characterized by peak values at much lower sward height and tended to a negative relationship from that point on. Iason et al. explained this by the complexity of the *Festuca* sward and the increased handling time compared with swards of *Lolium*.

Do feeding trials explain foraging choices?

In close agreement with Lang and Black (2001), our results indicate that intake rate increases with sward height up to a threshold value of about 8 cm. We would thus expect that geese confronted with a choice will select swards of about that height. However, a study by Durant et al. (2003) reveals that barnacle geese prefer foraging on swards of 2–3 cm rather than 5–6 cm or 10–12 cm. Concurrently, field studies indicate a preference of wild geese for swards lower than 8 cm (Summers and Critchley 1990; Hassall et al. 2001; own unpublished data).

A similar discrepancy was found in a study on European rabbits, in which intake rate in feeding trials

Table 2 Between-study comparison of the effect of sward height on intake parameters in barnacle geese

References	Relation between sward height and			Grass properties	
	Peck rate	Bite size	Intake rate	Grass species	Height range (cm)
Lang and Black (2001)	–	+	+	*Lolium perenne*	3.5–12
Durant et al. (2003)	–	+	0	*Lolium perenne*	1–12
Cope et al. (2005)	No data	0 (+)	No data	*Poa* spp./*Lolium perenne*	1.5–23
This study	0	+	+	*Festuca rubra*	2–8

increased with forage biomass, while the rabbits selected swards of low biomass and thus of low potential intake rate when given a free choice (Iason et al. 2002). For rabbits, it was argued that the rate of predator detection is highest in short grasslands and that the animals naturally prefer these open habitats. For geese, we do not expect that swards within the height ranges studied will influence the perception of predation risk. However, there is substantial evidence that shorter swards are of higher nutritional quality, as forage quality of grasses declines with increasing sward height (Summers and Critchley 1990; Hassall et al. 2001; Durant et al. 2004; Bos et al. 2005a). For small avian herbivores, this might be more important than the physical structure of the sward. The digestive system of avian herbivores is characterized by a short retention time and fast passage through the gut. Their digestion is therefore rather inefficient, and they need to consume high-quality food (Prop and Vulink 1992). Future studies should model the combination of intake rate and nutritional quality, i.e., the nutrient intake rate, taking into account different sward structures and forage species.

Conclusions

We conclude that bite size is the most important parameter influencing intake rate. Bite size is explained both by sward height and individual differences in bill size. Moreover, peck rate and the negative relationship between peck rate and sward height are most likely influenced by the choice of forage grass species, both by geese and under the seminatural circumstances of the feeding trials.

Zusammenfassung

Vegetationshöhe und Bissgröße beeinflussen die Nahrungsaufnahmerate von Nonnengänsen (*Branta leucopsis*)

Es wird angenommen, dass bei Pflanzenfressern die Nahrungsaufnahmerate, d.h. die Geschwindigkeit mit der eine bestimmte Menge Pflanzenmaterial gefressen werden kann, in starkem Maße die Wahl von Nahrungsstellen und damit auch die Habitatwahl beeinflusst. Bisher fand vor allem die Rolle der Nahrungsqualität und die Bevorzugung nährstoffreicher Nahrung wissenschaftliche Beachtung, der Einfluss der Vegetationsstruktur auf die Nahrungswahl kleiner Pflanzenfresser wurde weniger untersucht. In dieser Studie testen wir den Effekt von Vegetationsdichte und –höhe auf die funktionelle Reaktion von Nonnengänsen (*Branta leucopsis*). Die funktionelle Reaktionskurve beschreibt den Einfluss der Nahrungsverfügbarkeit auf die Nahrungsaufnahmerate eines Konsumenten. Wir haben Fressexperimente mit in Gefangenschaft gehaltenen Nonnengänsen durchgeführt, um die Nahrungsaufnahmeraten und Bissgrößen auf experimentell manipulierten Grassoden zu messen. Die Ergebnisse zeigen, dass die Nahrungsaufnahmerate vor allem von der Grashöhe bestimmt wird, und weisen auf eine starke Korrelation zwischen Bissgröße und Aufnahmerate. Die Größe eines Bisses wird dabei sowohl von der Vegetationshöhe als auch von der individuellen Schnabelmorphologie bestimmt. Die Vegetationsdichte beeinflußt die Aufnahmerate dagegen nicht, ist allerdings ein bestimmender Faktor des potentiellen Gesamtertrages. Bei einem Vergleich mit publizierten Parallelstudien zeigt sich, dass die äussere Struktur der jeweiligen Nahrungsgrasart die Nahrungsaufnahmerate von kleinen Wasservögeln mitzubestimmen scheint.

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References

Bos D, Van de Koppel J, Weissing FJ (2004) Dark-bellied brent geese aggregate to cope with increased levels of primary production. Oikos 107:485–496

Bos D, Drent RH, Rubinigg M, Stahl J (2005a) The relative importance of food biomass and quality for patch and habitat choice in brent geese. Ardea 93(1):5–16

Bos D, Loonen MJJE, Stock M, Hofeditz F, Van der Graaf AJ, Bakker JP (2005b) Utilisation of Wadden Sea salt marshes by geese in relation to livestock grazing. J Nat Conserv 13:1–15

Cope DR, Loonen MJJE, Rowcliffe JM, Pettifor RA (2005) Larger barnacle geese (*Branta leucopsis*) are more efficient feeders: a possible mechanism for observed body size-fitness relationships. J Zool Lond 265:37–42

Drent RH, Van der Wal R (1999) Cyclic grazing in vertebrates and the manipulation of the food resource. In: Olff H, Brown VK, Drent RH (eds) Herbivores: between plants and predators. Blackwell Science, Oxford, pp 271–299

Durant D, Fritz H, Blais S, Duncan P (2003) The functional response in three species of herbivorous *Anatidae*: effects of sward height, body mass and bill size. J Anim Ecol 72:220–231

Durant D, Fritz H, Duncan P (2004) Feeding patch selection by herbivorous *Anatidae*: the influence of body size, and of plant quantity and quality. J Avian Biol 35:144–152

Fryxell JM (1991) Forage quality and aggregation by large herbivores. Am Nat 138:478–498

Gross JE, Shipley LA, Hobbs NT, Spalinger DE, Wunder BA (1993) Functional response of herbivores in food-concentrated patches: test of a mechanistic model. Ecology 74:778–791

Hassall M, Riddington R, Helden A (2001) Foraging behaviour of brent geese, Branta b. bernicla, on grasslands: effects of sward length and nitrogen content. Oecologia 127:97–104

Iason GR, Manso T, Sim DA, Hartley FG (2002) The functional response does not predict the local distribution of European rabbits (*Oryctolagus cuniculus*) on grass swards: experimental evidence. Funct Ecol 16:394–402

Illius AW, Gordon IJ, Milne JD, Wright W (1995) Costs and benefits of foraging on grasses varying in canopy structure and resistance to defoliation. Funct Ecol 9:894–903

Jacobsen OW (1992) Factors affecting selection of nitrogen-fertilized grassland areas by breeding Wigeon *Anas penelope*. Ornis Scand 23:121–231

Lang A, Black JM (2001) Foraging efficiency in Barnacle Geese *Branta leucopsis*: a functional response to sward height and an analysis of sources of individual variation. Wildfowl 52:7–20

McNaughton SJ (1984) Grazing lawns: animals in herds, plant form and coevolution. Am Nat 124:863–886

Prop J, Vulink T (1992) Digestion by barnacle geese in the annual cycle: the interplay between retention time and food quality. Funct Ecol 6:180–189

Rowcliffe JM, Watkinson AR, Sutherland WJ (1998) Aggregative responses of brent geese on salt marsh and their impact on plant community dynamics. Oecologia 114:417–426

Sedinger JS, Raveling DG (1986) Timing of nesting by Canada Geese in relation to the phenology and availability of their food plants. J Anim Ecol 55:1083–1102

Summers RW, Critchley CNR (1990) Use of grassland and field selection by brent geese *Branta b. bernicla*. J Appl Ecol 27:834–846

Van de Koppel J, Huisman J, Van der Wal R, Olff H (1996) Patterns of herbivory along a productivity gradient: an empirical and theoretical investigation. Ecology 77:736–745

Van der Graaf AJ, Bos D, Loonen MJJE, Engelmoer M, Drent RH (2002) Short- and long-term facilitation of goose grazing by livestock. J Coast Conserv 8:179–188

Van der Graaf AJ, Stahl J, Bakker JP (2005) Compensatory growth of *Festuca rubra* after grazing—can migratory herbivores increase their own harvest during staging? Funct Ecol DOI 10.1111/j.1365-2435.2005.01056.x

Van der Wal R, Van de Koppel J, Sagel M (1998) On the relation between herbivore foraging efficiency and plant standing crop: an experiment with barnacle geese. Oikos 82:123–130