Moulting Greylag Geese *Anser anser* on Saltholm, Denmark do not cease feeding midday in response to diurnal oscillation in food quality

ANTHONY D. FOX & JOHNNY KAHLERT[1]

Department of Bioscience, Aarhus University, Kalø, Grenåvej 12, DK-8410 Rønde, Denmark.

[1]Present address: Teglbrændervej 16, DK-8800 Viborg, Denmark.

E-mail: tfo@bios.au.dk

Abstract

To seek support for the hypothesis that diurnal rhythms in protein and sugar levels in food plants were responsible for the largely nocturnal foraging of moulting flightless Greylag Geese *Anser anser* (which ceased feeding to rest during the middle part of the day), we sampled the laminae of Common Saltmarsh Grass *Puccinellia maritima* at two hour intervals over 24 h on 14 June 1998. There was no diurnal pattern in the proportion of selected amino acids (including sulphur-containing amino acids) in the laminae of this, the most important dietary item. Despite a cycle in lamina sugar content that peaked at *c.* 18:00 h and was lowest at *c.* 06:00 h, this failed to explain why moulting geese ceased foraging in the middle of the day, when sugar levels were highest. Rather we contend that geese trade-off diurnal variation in food energy content against the probability of lost time feeding to disturbance from predator-like stimuli, which were more common during the midday period. Elevated disturbance levels were the likely cause of geese roosting on offshore islands during daylight hours, despite increasing sugar levels in their food plants at this time. A simple model demonstrated that geese potentially derived the same energy intake from soluble carbohydrates by feeding during the undisturbed period from 01:00–08:00 h (when food quality was lowest) as by foraging in the evening (18:00–01:00 h) when soluble carbohydrate content was highest and frequent daytime disturbance from helicopters had begun to decline.

Key words: Amino acids, grazing, leaf protein content, leaf sugar content, predation risk, *Puccinellia maritima*.

Prior to becoming flightless during the moult, Greylag Geese *Anser anser* foraging on the island of Saltholm, Denmark, fed throughout the 24 hour period (Fox & Kahlert 1999). However, moulting, flightless birds ceased foraging and swam to roost on

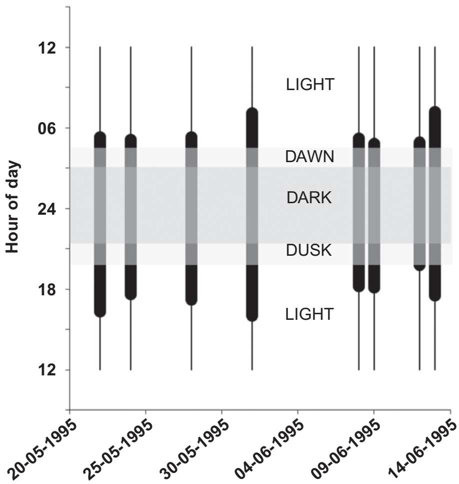

Figure 1. Duration of stay on the Saltholm mainland feeding areas of moulting Greylag Geese (thick bars) and when the majority of the geese roosted on offshore skerries (thinner lines) recorded throughout continuous 24 h periods in May and June 1995. Light conditions during the study period are indicated in different background shadings, where dusk and dawn are defined as the period between sunset/sunrise and the time when the sun is 6° below the horizon (reproduced from Kahlert *et al.* 1996).

offshore unvegetated islets by day (08:00–18:00 h), coming ashore to feed in the evening and returning offshore in the morning (see Fig. 1 from Kahlert *et al.* 1996). In an earlier analysis, we speculated that this was a behavioural mechanism to compensate for the lowered tolerance threshold of geese towards predator-like stimuli that were least frequent at night (Kahlert *et al.* 1996). This was based on evidence that as moult progressed, so geese responded more strongly to predator-like stimuli, such as gull alarm calls, over-flying Grey Herons *Ardea cinerea*, Marsh Harriers *Circus aeruginosus* and helicopters, even though "genuine" predators were absent (Kahlert 2006a). However, there was no evidence available at that time to reject the alternative hypothesis that the cessation of feeding during the middle part of the day related to some diurnal nutritional cycle in dietary items (see discussion in Kahlert *et al.* 1996). In the study presented here, we investigate whether diurnal patterns in amino acid and soluble sugar content of dietary food items could support this hypothesis.

Geese are predominantly herbivorous, have poorly developed digestive systems and hence spend much of their time feeding to meet nutritional demands (Owen 1980). Indeed, behaviours which optimise or maximise nutrient intake rates are widely described (*e.g.* Drent *et al.* 1978; Prop *et al.* 1978; Loonen *et al.* 1991). It has been suggested that, in waterfowl, the period of wing moult represents a period of nutritional stress because flight feathers need to be replaced as quickly as possible (*e.g.* Hanson 1962), although this has been disputed by other authors (see discussion in Hohman *et al.* 1992 and Fox *et al.* 2014). Laboratory evidence suggests that the replacement of flight feathers is relatively energetically costly in Greylag Geese (van der Wal 1992). Correspondingly, on Saltholm, moulting Greylag Geese lost an average of 12–26% of their body mass (mostly depletion of fat stores) during the flightless period (Fox *et al.* 1998a; Fox & Kahlert 2005), due to a failure to balance energy intake over expenditure (Kahlert 2006b). Indeed, van Eerden *et al.* (1997) also found that, under some circumstances, Greylag Geese moulting in the Netherlands obtained < 50% of their daily energy requirements from their diet. Since feathers are composed almost exclusively of protein, including a high proportion of sulphur-containing amino acids (Murphy 1996), limits to protein availability may also play a role. Geese moulting at Saltholm select the most proteinaceous food (Common Saltmarsh Grass *Puccinellia maritima*) in excess of its availability (Fox *et al.* 1998b), maximise protein uptake in the gut and reduce protein excretion products (Fox & Kahlert 1999). In addition, they harvest their food supply sequentially in a manner that maximises the protein content of the food (Fox & Kahlert 2003). Feather protein is rich in sulphur-containing amino acids, especially cysteine which comprises 8–13% and methionine (< 1%) of all amino acids in feathers (King & Murphy 1987; Murphy 1996). For herbivorous birds, both cysteine and methionine are relatively rare in plant protein, generally constituting 0.25–1.25% of the nitrogen in total protein levels recorded for grass species (Pollard & Chibnall 1934; Lugg 1938; Murphy 1996), which in *Puccinellia maritima* represents 12–26% of dry weight matter (Fox *et al.* 1998b). All this suggests that food selection (*i.e.* for the most protein- and/or energy-rich food) should play a fundamental role in the spatial distribution of the geese during moult.

So why should moulting Greylag Geese stop feeding by day? It is known that storage polysaccharides (especially fructan) can be accumulated in stems and laminae of graminaceous plants during daylight hours through the normal photosynthetic process (Salisbury & Ross 1985), an accumulation which is further stimulated by falling temperatures (Hendry 1987). It has also been shown that diurnal oscillations in quantity occur amongst amino acids in some plant leaf tissue (*e.g.* Espinoza *et al.* 2010). We therefore propose four hypotheses to account for night-time feeding by Greylag Geese on Saltholm. First, that the geese may respond to a diurnal cycle in food energy content (especially soluble sugars which constitute some of the most easily absorbed energy sources in the cell contents of grass laminae) because of the energetic demands of moult. Secondly, the geese may respond to a diurnal cycle in protein content of their food because they need to regrow flight feathers as fast as possible (assuming that sulphur-containing amino acids are not limiting). Thirdly, that the geese may respond to a diurnal cycle in cysteine and/or methionine, the major sulphur-containing amino acid content of their food (assuming that it is the availability of these amino acids which are limiting regrowth of flight feathers). Finally, it may be that geese are responding to the predictable pattern in disturbance frequency at different times of the daily cycle.

This paper describes a study of the diurnal variation in nutritional quality and energy content of *Puccinellia maritima* laminae on Saltholm to test for support for the hypotheses that changes in food quality (particularly the proportion of amino acids, including sulphur-containing amino acids, and/or energy content in the vegetation) explains diurnal foraging patterns amongst moulting Greylag Geese.

Study area

Between 7,000–14,000 Greylag Geese moulted annually on the Danish island of

Saltholm (55.633°N 12.767°E), in Øresund between Danish Zealand and Swedish Scania, during a 6-year study undertaken from 1993–1998 inclusive (Fox *et al.* 1995; A.D. Fox, unpubl. data). The geese (predominantly young and non-breeding birds) arrive on the island in late May, moult throughout June and most have dispersed from the island by early July (Fox *et al.* 1995). Saltholm is a flat island of 16 km^2 (~7 km by 3 km; highest point is 2 m), inundated periodically by salt water, and dominated by halophytic and saltmarsh grassland. The majority of the moulting geese concentrated along the southern and eastern coasts of the island and moved to largely unvegetated shoals and skerries up to 3 km offshore southeast of their foraging area during the middle part of the day, where they were not subject to the same high level of disturbance by the birds of prey, gulls and herons that were typical of the main island feeding areas (Fox *et al.* 1998b).

Materials & Methods

Puccinellia maritima laminae were clipped from plants from the lower saltmarsh vegetation of the island at 2 h intervals throughout the 24 h period on 14 June 1998, *i.e.* at the peak of the moult period (Fox *et al.* 1995). We attempted to sample normal "representative" laminae from plants that were neither drought stressed nor water logged and reflected the general forage available to geese on a day when the weather was considered typical for the season. Approximately 30 g of material were collected at each interval within an area of 30 m^2 where the geese had been actively foraging 2–4 days earlier (to allow for regrowth of suitable laminae length). Clipped laminae were placed in plastic phials and immediately plunged into liquid nitrogen for preservation before subsequent analysis. Financial and logistical constraints in transporting a flask of liquid nitrogen to a remote field site, for rapid analysis of plant material, unfortunately limited the collection of vegetation samples to a single day. At the laboratory, the material was washed in distilled water and dried in a drying cupboard at 50°C for 72 h before being analysed for nutritional content. The material was then analysed for the content of specific soluble sugars and of specific amino acids of laminae for each sample taken. The ash-free dry weight content of protein amino acids was determined from a standard amino acid analyser after oxidation and acid hydrolysis, using standard protocols at the Danish Centre for Food and Agriculture (DCFA), Aarhus University, Foulum. Ash-free dry weight measures were made for four essential amino acids: cysteine, methionine, lysine and threonine. The ash-free dry weight content of fructose, sucrose and glucose were determined by standard enzyme assay by DCFA and collectively summed as the soluble sugar fraction. The metabolizable energetic content of this soluble sugar fraction was then calculated on the basis of 17.6 kJ g^{-1} of soluble carbohydrate (Schmidt-Nielsen 1975).

To model the potential relative energy gain of Greylag Geese feeding at different times of the day, we also assessed the costs and benefits of foraging during three periods: 01:00–08:00 h, 18:00–01:00 h (when geese come ashore to feed) and 08:00–18:00 h (when feeding is generally abandoned and geese resort to offshore loafing areas, Kahlert *et al.* 1996). For each period, we established the theoretical net energy gain from plant soluble sugar per hour, based on: 1) a peck rate of 75.3 pecks per minute (Fox & Kahlert 1999), 2) mean bite size of 5.214 mg (calculated based on the mean lamina length removed by grazing geese and length/weight ratio, as described in Fox & Kahlert 2003), 3) mean soluble sugar content determined for the material analysed above, and 4) 17.6 kJ g^{-1} energy conversion factor for soluble carbohydrates (see above). To measure the costs associated with each time period, we had previously recorded (based on studies of the behaviour of geese moulting on Saltholm in 1996) the time lost from feeding either through loafing or from "spooks", *i.e.* events where > 20% of feeding geese abandoned feeding and ran to open water (Kahlert *et al.* 1996). These spooks were often in response to predator-like stimuli, such as overflying herons and helicopters, but also occurred with no obvious cause. The general mean time taken for focal birds to resume feeding after such a spook was *c.* 19.5 min (n = 35, based on data from 191.75 h of observations gathered daily throughout the entire 1996 moult period, Kahlert 2006a). As the frequency of spooks increased as a function of disturbance, so the amount of feeding time lost also increased. We therefore balanced the mean loss of energy intake per hour for each of the two feeding periods of the day incurred by differing frequencies of spooks (each lasting 19.5 min), when birds were unable to forage, and deducted this from the energy gain described above. Spook frequency data were not available for the period 08:00–18:00 h, when all flightless birds ceased feeding and roosted on unvegetated offshore islands, because distance to the skerries made it difficult to record accurate time budget data during this period.

Finally, we calculated the mean number of helicopter flights per hour overflying the study area throughout the moulting period in 1993–1995 as an index of typical diurnal anthropogenic disturbance to moulting Greylag Geese (as reported in Kahlert *et al.* 1996).

Results

There were no clear trends in amino acid content of *Puccinellia* laminae despite an anomalous minor peak at 09:00 h (Fig. 2), and no difference between feeding and loafing periods (Table 1). Fructose was present in significantly greater amounts during the loafing period than the feeding period (Table 1). Only sucrose, of the three analysed sugars, showed any strong diurnal pattern (Fig. 3). Its relative abundance resulted in the overall diurnal rhythm of soluble sugar abundance (Fig. 3). Soluble sugars increased during the period of daylight to peak levels at 19:30 h (based on the fitted regression shown in Fig. 3). However, its rapid decline in lamina tissue during the course of the night meant that there were no significant differences in any measure of sugar content of *Puccinellia* laminae between the feeding and loafing periods of the day (Table 1).

Spook rates were higher during the 18:00–01:00 h feeding period (0.803 spooks h^{-1}, based upon 118.25 h of observations in 1996) than during the 01:00–08:00 h feeding period (0.490 spooks h^{-1}, n = 73.5 h).

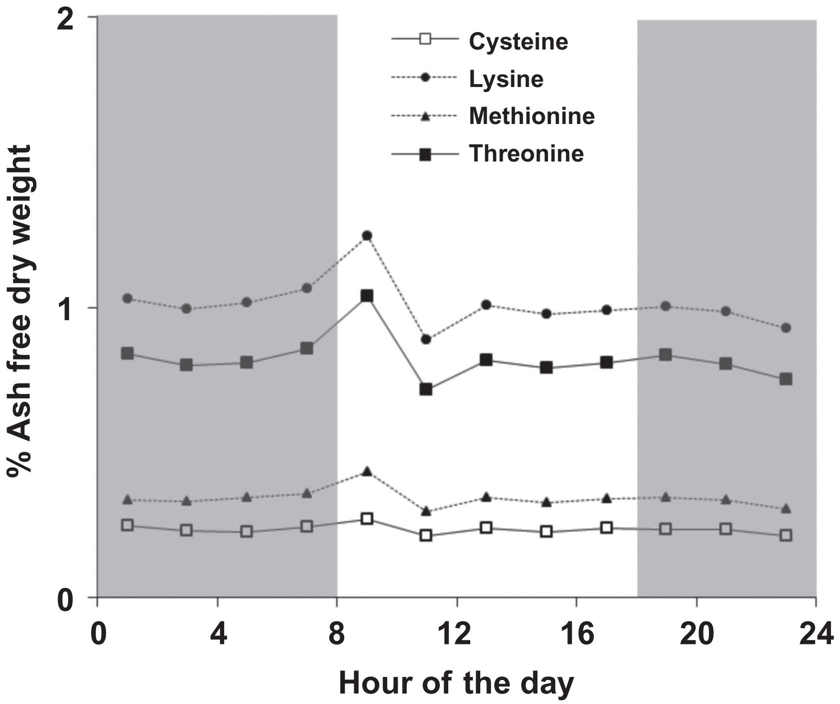

Figure 2. Diurnal changes in amino acid (cysteine, lysine, methionine and threonine) ash-free dry weight percentage content of *Puccinellia maritima* laminae harvested every 2 h throughout the 24 h period on the Danish island of Saltholm on 14 June 1998. Shaded areas represent the period of most active feeding (18:00–08:00 h, Kahlert *et al.* 1996).

Although spook frequency data were not recorded during 08.00–18:00 h when geese roosted offshore, we got the impression that the birds were much less likely to exhibit spook behaviours when resting on the islands. Predicted energy intake (based on soluble sugar content of *Puccinellia* laminae and observed dry matter intake rates) declined linearly with increasing frequency of spook events (Fig. 4). However, because of the accumulation of soluble sugars towards the end of the daylight period, net intake rates (43.0 kJ soluble carbohydrate h^{-1}) were only 1.3% lower during the 18:00–01:00 h period when birds came ashore to feed than during the 01:00–08:00 h period (43.6 kJ soluble carbohydrate h^{-1}). The greater soluble sugar energy content during this period appeared to be sufficient to compensate for the lost feeding opportunity caused by observed levels of spook events, in comparison with intake rates during 01:00–08:00 h when soluble sugar energy content of the food was lower, but helicopter activity had largely yet to commence (Fig. 3). Helicopter flights (which we equated with spook rates) were most frequent during the period 08:00–18:00 h (3.6 h^{-1}), but were also high during 18:00–01:00 h (2.6 h^{-1} mostly because of

Table 1. Analyses of specific amino acid and sugar content of *Puccinellia maritima* laminae harvested every two hours on Saltholm throughout a 24 h cycle on 14 June 1998. Data are pooled by "loafing period" (the period when Greylag Geese slept and loafed on offshore islets: 08:00–18:00 h inclusive) and "feeding period" (the periods when geese came ashore to feed upon *Puccinellia* laminae: 18:00–08:00 h inclusive) and compared for statistical differences using *t*-tests. Only the test for fructose attained statistical significance (* = $P < 0.05$; n.s. = not significant); mean values (± s.e.) are given for percentage nutrient content expressed as ash-free dry weight.

% Nutrient content of:	**Loafing period** ($n = 5$)	**Feeding period** ($n = 7$)	***t*-test results**
Fructose	6.851 ± 0.065	6.346 ± 0.043	$t_{10} = 2.12^{*}$
Sucrose	9.765 ± 1.101	9.711 ± 0.583	$t_{10} = 0.57^{\text{n.s.}}$
Glucose	2.432 ± 0.046	2.438 ± 0.029	$t_{10} = -0.06^{\text{n.s.}}$
Cysteine	0.235 ± 0.001	0.233 ± 0.001	$t_{10} = 0.21^{\text{n.s.}}$
Lysine	1.021 ± 0.008	1.002 ± 0.001	$t_{10} = 0.35^{\text{n.s.}}$
Methionine	0.347 ± 0.001	0.336 ± 0.001	$t_{10} = 0.51^{\text{n.s.}}$
Threonine	0.834 ± 0.007	0.814 ± 0.001	$t_{10} = 0.42^{\text{n.s.}}$

commuter traffic around 19:00 h) compared to 01:00–08:00 h (0.13 h^{-1}). With an estimated mean of 19.5 min of feeding time lost to spooks (Kahlert 2006a), as spook rate exceeded 3 h^{-1} geese would have been completely denied the opportunity to feed on Saltholm, even if food quality was more profitable to the birds at the time.

Discussion

We found no support for the hypothesis that the diurnal pattern in Greylag Goose feeding activity was related to cycles in protein content of their food. There was no diurnal pattern in abundance of specific amino acids (including the sulphur-bearing amino acids) for which the geese might be positively selecting during moult. Although moulting Greylag Geese select food with high protein content, it is known that they at least partially mobilise protein from body reserves for investment in feather tissue production (Fox *et al.* 2009; Rohwer *et al.* 2015). Hence, it is likely that other external factors could affect their foraging behaviour in both time and space. Soluble carbohydrates represent phyto-metabolic products that offer foraging geese relatively high energetic return, which are likely to accumulate by day in association with photosynthetic processes (*e.g.* Kjær *et al.* 2012). Many studies show a consistent increase in non-structural carbohydrate content of monocotyledonous laminae

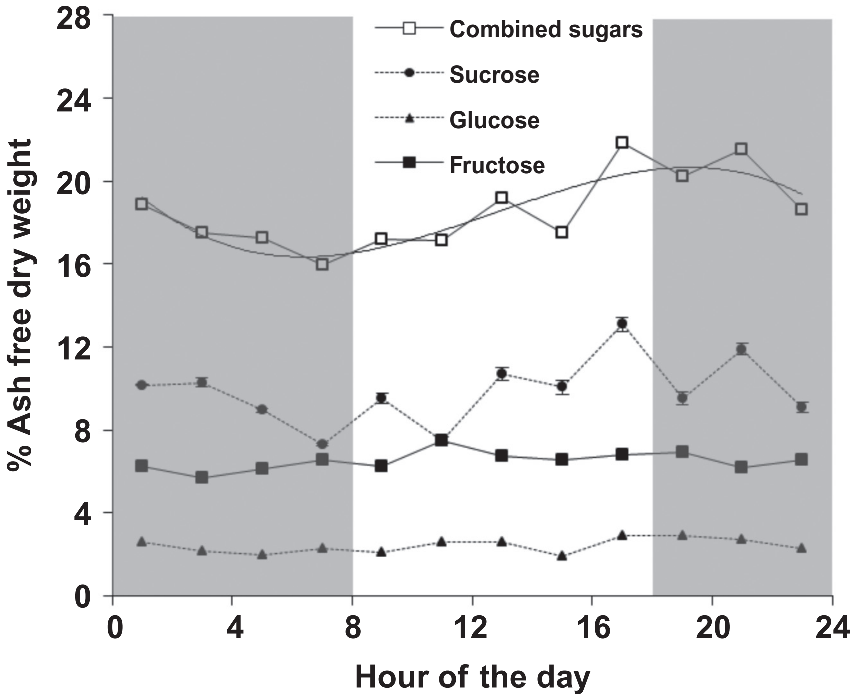

Figure 3. Diurnal changes in soluble sugar (fructose, glucose and sucrose) ash-free dry weight percentage content of *Puccinellia maritima* laminae harvested every 2 h throughout the 24 h period on the Danish island of Saltholm on 14 June 1998. Values represent means of two determinations for each sample, but s.e. bars are shown only for sucrose to aid clarity (all s.e. values were < 0.1 for fructose and glucose). Best fitted polynomial least squares regression expression for combined sugar content (S) has the formula $S = 20.552 - 1.487\ h + 0.155\ h^2 - 0.004\ h^3$, where h = hour of the day ($r = 0.74$, $F_{3,11} = 7.20$, $P = 0.01$). Shaded areas represent the period of most active feeding (18:00–08:00 h).

through the course of a day as a result of photosynthesis, diluting fibre and crude protein content (*e.g.* Delagarde *et al.* 2000; Griggs 2005; Gregorini *et al.* 2009). Although our analyses showed the same pattern of accumulated soluble sugars during the period of daylight, this does not explain why Greylag Geese should modify feeding patterns to cease foraging in the middle part of the day. There were no apparent differences between foraging and daytime loafing periods for any of the protein (amino acid) measures, nor did the timing of diurnal variation in energetic content explain the birds' behaviour.

Despite the build-up of sugars (primarily sucrose), as a result of the accumulation of daytime photosynthetic products up until the point at which moulting Greylag Geese on Saltholm started to come ashore to feed, the rapid depletion during the hours of darkness meant that lowest tissue sugar levels also occurred during the period when most feeding occurred. Hence, although daytime

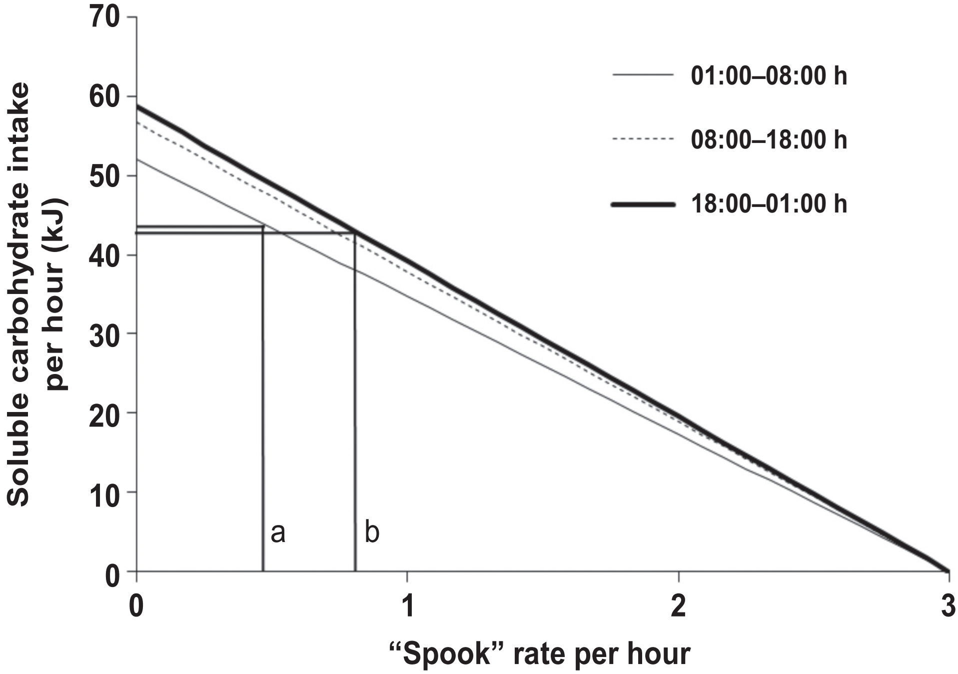

Figure 4. Model showing potential energy intake rate (kJ h^{-1}) from soluble carbohydrates obtained by Greylag Geese feeding on *Puccinellia maritima* laminae on Saltholm at different disturbance intensities. Intake rates were calculated on the basis of observed peck rates, bite size and soluble carbohydrate content of food material (based on laboratory analysis) for three periods of the diurnal cycle: 01:00–08:00 h (thin solid line), 08:00–18:00 h (pecked line) and 18:00–01:00 h (heavy solid line). Interruption to intake rate was calculated on the observed basis of each spook resulting in the abandonment of feeding by an individual for 19.5 mins. The lines a and b represent observed levels of spook intensity for two of the periods based upon field observations. These suggest that higher spook rates during 18:00–01:00 h can be balanced by higher energy content of food at that time, resulting in energy intake rates only slightly (1.3%) lower than that obtained from undisturbed foraging activity during 01:00–08:00 h when the energy content of food is lowest.

accumulation of sugar may contribute to the timing of arrival of moulting geese onshore in the evening, the diurnal cycle in sugar content of laminae does not alone account for the observed night-time feeding during the flightless period.

Rather, we contend that the geese may make a trade-off between diurnal variation in the energy content of their food and the probability of lost feeding time caused by disturbance. Our simple model showed that the geese could potentially derive the same energy intake from soluble carbohydrates by foraging during the undisturbed period from 01:00–08:00 h (*i.e.* up to the time when helicopter traffic commenced) as by foraging during the evening period (when soluble carbohydrate content peaked in the food and disturbance from helicopters began to decline). Although the passage of helicopters directly over the moulting geese did not result in spooks on every occasion, their distribution throughout the day reflects general anthropogenic activity around Saltholm (in terms of aircraft traffic operating in and out of the neighbouring Copenhagen International Airport and shipping in the busy waters of Øresund). In addition, the avian species which cause most disturbances to the geese (principally Grey Herons, Marsh Harriers and Herring Gulls *Larus argentatus*) are all day-active, adding to the sources of potential onshore spooks particularly during the 08:00–18:00 h period. In contrast, these avian species were far less common on the offshore islands to which the geese sought refuge during midday and we were not aware of highly frequent spooks amongst the large dense aggregations of geese roosting and preening there. Hence, we contend that the high level of disturbance during the day was the reason why the geese moved to sleep and loaf on offshore islands at this time. We argue that geese may be able to tolerate the observed disturbance levels from 18:00 h onwards because of the diurnal rhythm in accumulated soluble sugars which peaked in the favoured food at this time. Moreover, the largely undisturbed remainder of the night enabled geese to accumulate sufficient biomass during uninterrupted foraging to offset the subsequent decline in soluble carbohydrate content of the food.

Overall, although our results were based on data gathered on a single day and their application is limited until confirmed by replication, nonetheless they confirmed expectations that soluble sugars would peak in *Puccinellia* leaf tissue from 18:00 h onwards when falling disturbance levels favoured feeding. At the same time, we found no evidence to suggest that diurnal patterns in food quality could explain cessation of feeding by moulting geese on Saltholm during 08:00–18:00 h, which coincided with increased human and quasi-predator activity in the area.

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