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Scaring waterfowl as a management tool: how much more do geese forage after disturbance?

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Summary

1. With increasing numbers of many herbivorous waterfowl species, often foraging on farmland, the conflict with agriculture has intensified. One popular management tool is to scare birds off the land, often in association with shooting. However, the energy costs of flying are considerably higher than those of resting. Therefore, when birds fly off after a disturbance, they use extra energy that subsequently needs to be compensated.

2. We used the white-fronted goose *Anser albifrons*, the most common (grass-eating) goose wintering in western Europe, as a model species. We measured flight durations by high-frequency accelerometer recordings over 2×24 h in nine focal geese that were only incidentally disturbed. We also made direct observations on these days to determine whether the flight durations were reliably recorded. Using both a simple and a more realistic model of the energy balance, we calculated the extra grass consumption resulting from additional intentional disturbances.

3. On average, the geese flew daily 2×323 s (from and to their roosting sites at 3200 m) and furthermore took to the air 5.3 times during a day (and 1.9 times a night). Multiplied with the average flight durations of 195 s, this gives a total flying time of almost 0.6 h day⁻¹ and a total foraging time of 7.4 h day⁻¹. The extra foraging time needed to compensate for additional intentional disturbances strongly depends on the frequency of such disturbances and the following flight duration. If, for example, flights when intentionally disturbed are twice as long (2×195 s), the extra foraging time will be 3.7% day⁻¹ (2.3–3.2% day⁻¹ in the more realistic model) for each intentional disturbance, and the geese will no longer be able to cover their energy requirements when intentionally disturbed six times per day.

4. *Synthesis and applications.* Recent experiments suggest that geese have to be scared frequently in order to reduce goose visitation to particular fields. With an intentional disturbance rate, for example, of five times a day, the birds' compensation for the increased energy expenditure will lead to a higher overall consumption of grass of 11.5–16% day⁻¹. Accommodation schemes have to take such increases in total grass consumption into account when deciding on the refuge areas to be set aside.

Key-words: accelerometer data, *Anser albifrons*, disturbance, energy budget, flight costs, flight duration, grass damage, white-fronted geese

Introduction

Among waterbirds, herbivorous wildfowl (swans, geese and some ducks) have increased substantially in numbers

over the last 50 years, both in Europa (Fox *et al.* 2010) and in North America (Abraham, Jefferies & Alisauskas 2005; Gauthier *et al.* 2007). These population changes are driven in part by a reduction in hunting (Ebbinge 1991; Menu, Gauthier & Reed 2002) and in part by an increase in food availability (Abraham, Jefferies & Alisauskas

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2005; Van Eerden *et al.* 2005). The increased numbers have sharpened the conflict with agriculture, especially on improved grassland and winter wheat fields, where most damage is occurring (Groot Bruinderink 1989; Percival & Houston 1992; Amano *et al.* 2004; Bjerke *et al.* 2014).

In order to control this conflict and limit the damage by herbivorous birds, particularly to pastures and other grasslands, scaring regimes have been installed at several sites, whether or not in combination with areas where these birds are left undisturbed; examples include parts of Scotland (Percival, Halpin & Houston 1997), Norway (Tombre, Eythorsson & Madsen 2013; Madsen, Bjerrum & Tombre 2014) and the Netherlands (Kwak, Van der Jeugd & Ebbing 2008). Within accommodation areas, farmers may be subsidized in advance to let, for instance, geese forage on their land undisturbed. In practice, this means that the birds are not intentionally disturbed inside the accommodation areas, but incidental disturbance by natural predators or passing humans or vehicles will always occur (Kleijn *et al.* 2008). Outside the accommodation areas, intentional disturbances are usually allowed: birds are scared by approaching them with or without additional shooting in order to chase the birds. The idea is that in this way geese will be concentrated within the accommodation areas, but scaring has to be intense and systematic in order for it to be effective (Tombre *et al.* 2005; Simonsen *et al.* 2016).

For the birds, the escape from disturbance is a waste of both time and energy (Houston, Prosser & Sans 2012). It will cause extra time in flight, by far the most expensive activity (Butler *et al.* 2000), and thus, more food is needed to compensate for the increased energetic cost of flying. Therefore, the net effect of the disturbance will be an increased consumption of grass, perhaps not at the level of a given field, but at least at a regional scale.

Direct measurements of this increased consumption are lacking. In order to get a first estimate about the effects of intentional disturbances in terms of an increase in grass consumption, we measured daily flight times of geese, in a situation with only incidental disturbances. We used white-fronted goose *Anser albifrons* Scopoli as a model species. This is the most numerous goose species wintering in western Europe and moreover forages almost exclusively on grasslands during winter. We used both a simple and more realistic, previously developed energetic model to calculate the increase in foraging time as a result of intentional disturbances on top of incidental disturbances. We varied the frequency of intentional disturbances and the following flight duration; the latter tends to be longer than flight durations after incidental disturbances (Schilperoord & Schilperoord-Huisman 1981; Béchet, Giroux & Gauthier 2004), and we used a factor two as our basic scenario. The more realistic energetic model also provided us with estimates of the frequency of intentional disturbances at which the geese can no longer maintain their energy balance on a daily basis.

Materials and methods

DAILY FLIGHT DURATION

In autumn 2014, a total of 23 white-fronted geese, belonging to four families, were caught in the province of Noord-Brabant (the Netherlands) using a traditional Dutch goose catching technique ('ganzenflappen'). The geese were equipped with plastic neck collars with unique inscriptions and a solar-powered GPS/accelerometer backpack tag (e-obs GmbH, 45 g) attached with a plastic tube/Teflon harness (see Fig. S1, Supporting information). In February–March, enough solar energy was available to collect high-frequency GPS and accelerometer data. Part of the families had fallen apart at that time of the year, and nine geese (one adult male, one adult female, three immature males and four immature females) that were separate from each other, ensuring independence, were chosen as focal birds. At the day of the observation, tags of focal birds were set to collect 20-Hz accelerometer bursts of 5 s every 1 min next to GPS positions every 30 min, and to continuously ping a VHF radio-signal for 24 h. Data were transmitted once per day via GPRS.

On an observation day, an observer (ME) arrived in the morning close to the GPS position of the focal goose of the previous day. The goose was localized by picking up the VHF radio-signal of its tag, or if the goose was too far from its position of the previous day, on the basis of a new GPS position that was recorded and retrieved from Movebank (<http://www.movebank.org>) at 10:00. Subsequently, observations were done using binocular and telescope until 17:00, timing the duration of any flight of the flock that the focal individual was in with a stopwatch and noting the probable cause of a disturbance. Flock size varied between 40 and 4000 (1319 ± 1283 , mean \pm standard deviation). Observations were carried out in 6 February–6 March 2015, spread over six provinces in the SW quarter of the Netherlands (south of $52^{\circ}18'N$ and west of $5^{\circ}20'E$). Each focal goose was observed on two days, 14 ± 4 days (mean \pm standard deviation) apart.

On the tri-axial accelerometer waveforms (made visible with the Movebank Acceleration Viewer), flight was easily distinguishable from non-flight with amplitudes at least three times as large as those of other behaviours (Fig. S2). Flight distance was calculated from the GPS positions before and after the flight. Because accelerometer data were collected more frequently than GPS positions, occasionally ($16\times$) more than one flight occurred in between GPS positions, in which case distances were allocated proportionally to flight durations. Flight speed was then extracted by dividing flight distance by flight duration and is therefore the effective rather than actual speed.

Linear mixed models were run with function lmer (and lmer-Test) in R packages lme4 (Bates *et al.* 2015); to obtain the normality, flight durations were Box-Cox-transformed ($\lambda = -0.7302$). Results are given as mean \pm standard deviation. For summary statistics, non-transformed data were used, with the results of each focal goose being averaged before averaging over all focal geese.

SIMPLE MODEL

In the simple model, we assumed that the geese are energetically in balance throughout the winter. This implies that the daily metabolizable energy intake (MEI , $J \text{ day}^{-1}$) is equal to the daily energy expenditure (DEE , $J \text{ day}^{-1}$). A 24-h period ($T = 86\,400 \text{ s}$

day⁻¹) is divided into time spent resting, flying (T_v , s day⁻¹) and foraging (T_f , s day⁻¹). The daily metabolizable energy intake (MEI) is the product of the metabolic intake rate i (J s⁻¹), which depends on the grass height (see Appendix S2, where $i = qe^{IIR}$), and the daily foraging time T_f :

$$MEI = i \cdot T_f \quad \text{eqn 1}$$

The daily energy expenditure (DEE) is:

$$DEE = (T - T_f - T_v)RMR + T_f \cdot FMR + T_v \cdot VMR, \quad \text{eqn 2}$$

where RMR (J s⁻¹), FMR (J s⁻¹) and VMR (J s⁻¹) are the metabolic costs of resting, foraging and flying, respectively.

When in balance ($MEI = DEE$), the foraging time (T_f^*) is equal to

$$\begin{aligned} T_f^* &= \frac{(T - T_v)RMR + T_v \cdot VMR}{i - (FMR - RMR)} \\ &= \frac{T \cdot RMR}{i - (FMR - RMR)} + \frac{T_v \cdot (VMR - RMR)}{i - (FMR - RMR)}. \end{aligned} \quad \text{eqn 3}$$

Since the first term in the equation is a constant (c), this can be rewritten as:

$$T_f^* = c + \frac{T_v \cdot (VMR - RMR)}{i - (FMR - RMR)}. \quad \text{eqn 4}$$

Disturbance leads to more time spent flying and less time resting, and more time foraging to compensate for the energy lost by this. These energetic costs are equal to the extra flight time due to disturbance multiplied by the difference in metabolic costs of flying and resting. The extra foraging time needed to collect this extra energy is equal to the energetic cost of the disturbance divided by the net energy intake while foraging. This net intake rate is the metabolic intake rate minus the difference in metabolism between foraging and resting. Thus, the extra foraging time per day caused by disturbance is:

$$T_{f,extra} = \frac{n \cdot \tau \cdot (VMR - RMR)}{i - (FMR - RMR)}, \quad \text{eqn 5}$$

where n is the number of disturbances per day and τ is the flight duration following a disturbance. This is a measure for the extra consumption of grass. Parameter values are given in Table S1.

EXTENDED MODEL

We also used an energetic model that was developed to calculate whether the accommodation areas that had been designated in the Netherlands were sufficiently large to harbour all wintering geese and wigeon throughout the winter (Fig. 1, Baveco, Kuipers & Nolet 2011). In this model, we also assume that geese try to maintain their energy balance throughout the winter (October through March), and if any deficits are incurred, they will try to regain any weight losses as soon as possible. The model calculates the foraging time per day that is needed to let the intake of metabolizable energy equal the energy expended (Appendix S2).

When the necessary daily foraging time exceeds day length, the birds either maintain their body weight by foraging at night or lose body weight proportional to the energetic shortage incurred and try to regain weight as soon as circumstances allow (Appendix S2).

Again, energy intake depends on the grass height, which will decrease over the course of winter due to grazing (grass growth only starts again in March (Bos *et al.* 2008) and is neglected in this model). In contrast to the original study (Baveco, Kuipers & Nolet 2011), in our case grass height is not an output, but an input to the model. To describe the observed decrease in sward height (L) (Fig. 8a in Baveco, Kuipers & Nolet 2011), we calculated a second-degree polynomial through the monthly averages: L (m) = 0.00000221 d^2 - 0.000340 d + 0.0501 ($n = 6$, $R^2 = 0.995$), where d is the corrected day number, that is day number - 366 for days in autumn.

As in the simple model, we use three types of behaviour that differ in energetic costs: resting, foraging and flying. In a bioenergetic part of the model, we calculate how much energy a goose has to spend to maintain its body temperature depending on air temperature, wind velocity and solar radiation ('heating metabolic rate', Appendix S2). When this is more than the standard costs for resting or foraging, these additional costs are taken into account (Fig. S6).

The calculations were made for the northern part of the Netherlands (53°N, latitude determining day length and solar radiation; Appendix S2), where traditionally most white-fronted geese stay in winter (Bijlsma, Hustings & Camphuysen 2001) and by far most goose damage compensation is paid (Schekkerman 2015). Weather data (daily minimum and maximum temperatures, minimum and maximum wind speeds and sunshine) were taken from the weather station in Leeuwarden (53°13'N, 05°45'E). We made the calculations with the data from three winters that are representative for a mild (2006–07), normal (2005–06) and cold (2009–10) winter.

As in the simple model, disturbance leads to more time spent flying and less time resting, and more time foraging to compensate for the energy lost by this.

Results

FIELD DATA

The accelerometer recordings of the 18 days of data collection revealed 164 flights in total; 23 of those were also successfully timed by stopwatch. The flight duration according to the accelerometer (170 ± 143 s flight⁻¹) did not differ significantly from that recorded by stopwatch (200 ± 133 s flight⁻¹) (paired t -test: difference 30 ± 73 s, $t_{22} = 1.99$, $P = 0.06$) and certainly did not overestimate the flight duration. The 5-s accelerometer measurements were therefore taken to be representative for the given minute, and we used the flight durations as recorded by the accelerometers.

Roost flights were undertaken twice a day, typically initiated c. 1 h before sunrise and c. 0.5 h before (!) sunset (but in days just before and around full moon the return flights were up to a few hours after sunset) (Fig. S3). Roost flights were more direct and as a result could be discriminated from other flights by their higher effective flight speed (9.44 ± 4.44 vs. 5.34 ± 5.76 m s⁻¹; linear mixed model with random variables goose-id and day: d.f. = 151.0, $t = 3.90$, $P < 0.0002$) (Fig. S4). The average distance covered to or from the roost was

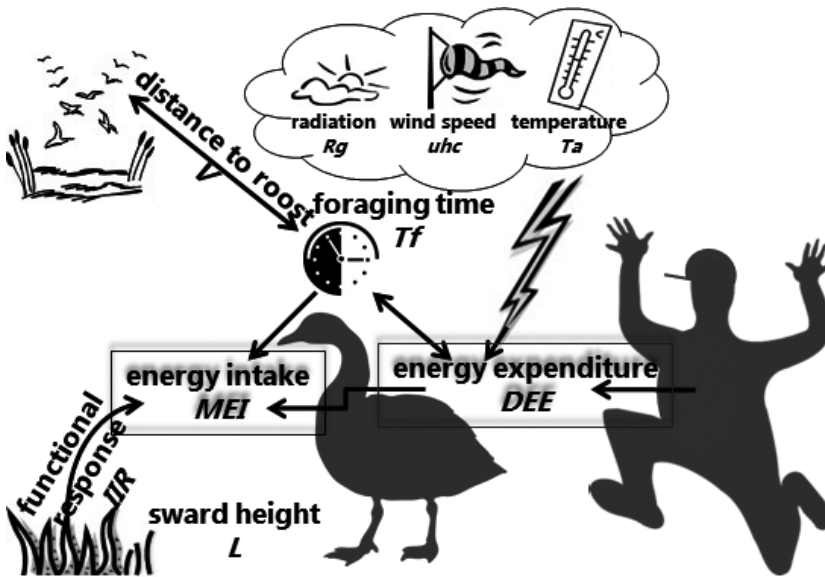


Fig. 1. A scheme of the components in the extended energetic model. Disturbance increases daily metabolizable energy intake (MEI) through an increase in daily energy expenditure (DEE) and foraging time to restore the energy balance.

3189 ± 1434 m, taking the geese on average 323 ± 124 s, to be flown twice a day.

Considering flights other than roost flights, 7.2 ± 1.6 flights of 195 ± 117 s each were undertaken per day (Fig. S5). Of those, 5.3 ± 1.4 were during the day and remarkably, 1.9 ± 0.9 flights during the night. The flights recorded by stopwatch did not differ in duration from non-observed flights (linear mixed model with random variables goose-id and day: d.f. = 126.7, $t = 0.64$, $P = 0.52$). Similarly, flights during the day did not differ in duration from those during the night (linear mixed model with random variables goose-id and day: d.f. = 124.6, $t = -0.32$, $P = 0.75$). Including the two roost flights, total flight time was on average 2103 ± 999 s day⁻¹.

Intentional disturbances were not observed. Instead, directly observed flights were a reaction to passing airplanes ($n = 11$), helicopters ($n = 7$), land vehicles or machinery ($n = 9$), persons ($n = 2$), large birds ($n = 4$), horse ($n = 1$), fireworks ($n = 1$) or to unknown causes ($n = 8$).

SIMPLE MODEL

The geese fly daily from and to their roosting sites, and furthermore, in case no intentional disturbances occur, take to the air 5.3 times during a day (and 1.9 times a night). Multiplied with the average flight durations of 323 and 195 s for roost and other flights, respectively, this gives a total flying time of almost 0.6 h day⁻¹, requiring according to eqn 3 a total foraging time of 7.4 h day⁻¹.

In our basic scenario, when intentionally disturbed, geese fly up and then stay in the air for twice the duration of a flight after an incidental disturbance (= 2 × 195 s). This has two effects. The primary effect is that this extra flight time diminishes the resting time, so that the energetic cost per disturbance is equal to the difference

in metabolism between flying and resting = 2 × 195 × (114 – 10) = 40 560 J. The secondary effect is that extra foraging time is needed to eat these extra joules. The net intake rate is the metabolic intake rate (for a grass height of 5 cm, this is 45 J s⁻¹) minus the difference in metabolism between foraging and resting (14 – 10 = 4 J s⁻¹; Fig. S6), or 41 J s⁻¹. One disturbance thus costs 40 560/41 = 989 s to compensate the extra energetic costs of flying. In order to compensate for this loss, an extra foraging time of 3.7% is needed for each intentional disturbance.

This calculation gives us the net extra foraging time per intentional disturbance. This increase in foraging time also gives us an estimate of how much extra grass is consumed. When considering the question of whether the winter days are long enough for the geese, one has to add the length of the disturbance (2 × 195 s) to the extra foraging time (at least 989 s) to come to the conclusion that every disturbance costs 1379 s extra. At six intentional disturbances per day, the geese will no longer be able obtain enough energy during daytime to cover their energy requirements on an average winter day (Fig. 2).

EXTENDED MODEL

The extended model predicts that the foraging time will increase in the course of winter due to shorter grass and cooler weather. The shorter grass leads to a decrease in the metabolic intake rate from 52 to 41 J s⁻¹. From February onwards, the predicted foraging time levels off because normally the weather conditions do not deteriorate any further. The most critical period is around New Year, when days are at their shortest. Even in the absence of intentional disturbances ($d_i = 0$ day⁻¹), only in mild winters days appear long enough for sufficient foraging (Figs 3a and 4a). In a normal or severe winter, the geese will either have to use their reserves or forage at night in

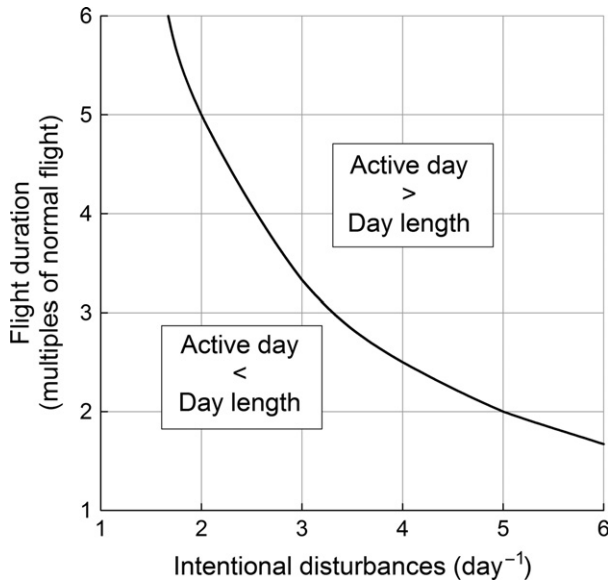


Fig. 2. The break-even line when, according to the simple model, daytime foraging and flying of white-fronted geese fills the entire day length in winter (9.65 h on average), as a function of the number of intentional disturbances per day as well as the duration of flights after an intentional disturbance (as multiple of normal flights). Above the line, the geese cannot cover their energy requirements with daytime foraging alone.

order to cover the deficits of daytime foraging (Figs 3a and 4a).

When the frequency of intentional disturbance goes up, the geese cannot forage long enough during daylight to cover their energy requirements in any of the winter months (December through February (Fig. 3b,c) and, if they do not forage at night, they will need the entire day length till the end of March for foraging in order to regain body weight (Fig. 4b,c).

Assuming that the geese forage sufficiently to meet their energy requirements on a daily basis (and therefore forage at night when necessary), the total foraging time will increase linearly with the number of disturbances (Fig. 5a). If flight duration after an intentional disturbance is twice as long as after an incidental disturbance, the increase in foraging time will be 3.2, 3.0 and 2.9% per intentional disturbance for mild, normal and cold winters, respectively (Fig. 5a). If the geese do not compensate by foraging at night, this is a bit less, namely 2.8, 2.3 and 2.4% per intentional disturbance for mild, normal and cold winters, respectively (Fig. 5b).

Intentional disturbances quickly lead to energetic deficits in case only daytime foraging is allowed. In theory, at $d_i = 3 \text{ day}^{-1}$ the geese are just capable of fully compensating for these losses at the end of winter by increasing the foraging time to the entire daytime period until sometime in March (Fig. 4b). At higher disturbance frequencies, weight loss over the course of winter can be substantial (17%, 21% and 24% of the starting weight at $d_i = 6 \text{ day}^{-1}$ in a mild, normal or cold winter, respectively; see eqns 4 and 5 in Appendix S2).

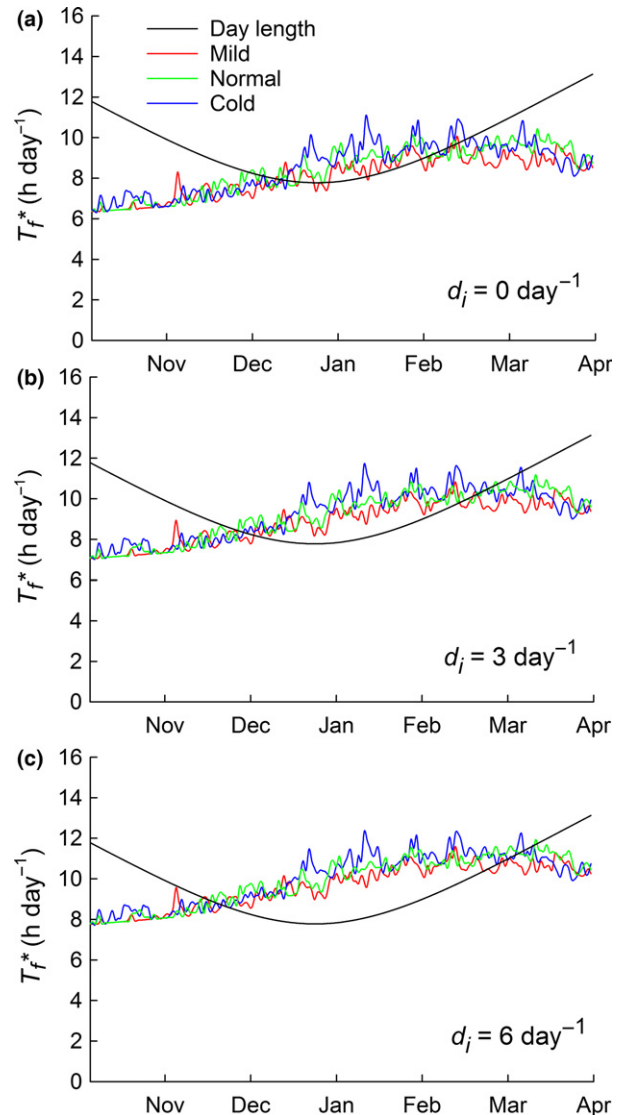


Fig. 3. The calculated foraging time necessary to cover the daily energy expenditure in three types of winter for three frequencies of intentional disturbance (a) $d_i = 0$, (b) $d_i = 3$ and (c) $d_i = 6 \text{ day}^{-1}$, respectively, when compensation by night-time foraging is possible. Flights after an intentional disturbance are assumed to be twice as long as flights after an incidental disturbance.

Discussion

Several studies have quantified the energetic consequences of disturbance for geese (White-Robinson 1982; Bélanger & Bédard 1990; Riddington *et al.* 1996; Stock & Hofeditz 1997; Clausen *et al.* 2013). To our knowledge, however, our calculations are a first attempt to translate these into potential damage (to grasslands). The general result is that we indeed expect an increase in the daily consumption by geese when they are intentionally disturbed. Of course, this depends to a large extent on the frequency and duration of flights after intentional disturbances. When the geese fly twice as long after such a disturbance than they do after incidental ones, the simple model

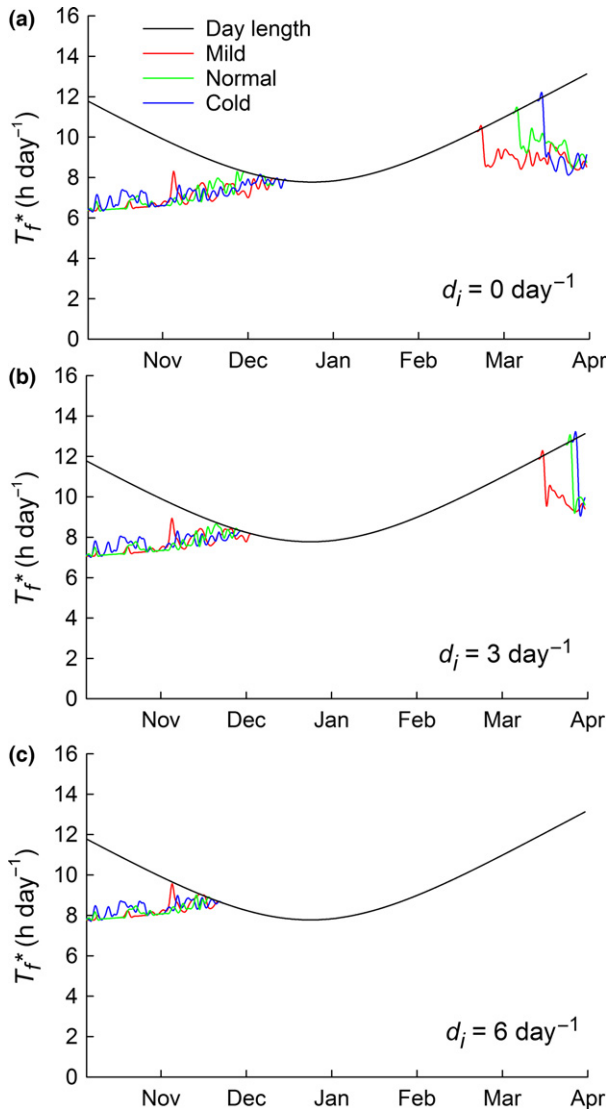


Fig. 4. The same as in Fig. 3, but when only daytime foraging is possible. When the time necessary is more than the day length (above the black line), the foraging time is set equal to it. Flights after an intentional disturbance are assumed to be twice as long as flights after an incidental disturbance.

estimated an increase in foraging time of 3.7% (= 976 s) per intentional disturbance. That model did not take costs of thermoregulation into account which leads to an underestimate of the total daily foraging time in the absence of intentional disturbances, and hence, the same increase in consumption constitutes a higher percentage. Therefore, the extended model predicted a slightly lower increase of 2.3–3.2% per intentional disturbance (at $d_i = 1 \text{ day}^{-1}$), depending on the severity of the winter and whether the geese can forage at night to make up for the extra energy expended during the day.

In a model similar to our simple model, Houston, Prosser & Sans (2012) found that the foraging time was an accelerating function of the disturbance level. This is, however, dependent on the energetic cost of foraging relative to the energetic cost of other activities. In the

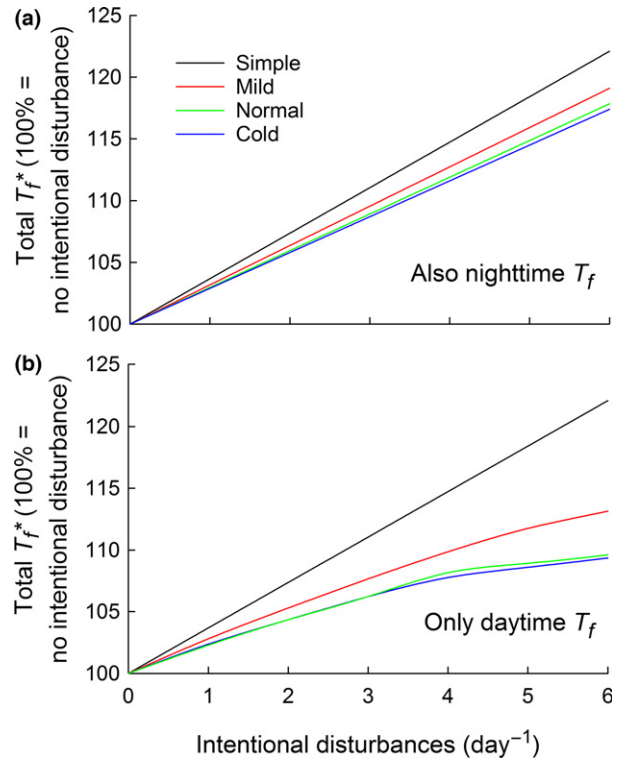


Fig. 5. The calculated foraging time of an average goose summed over the entire winter in relation to the frequency of intentional disturbances (a) under the assumption that any shortages are compensated for by foraging at night and (b) when foraging is limited to daytime. The increase in foraging time as predicted by the simple model is given for comparison. Flights after an intentional disturbance are assumed to be twice as long as flights after an incidental disturbance.

example concerning African wild dogs *Lycaon pictus*, the foraging costs were very high (Gorman *et al.* 1998), but in our case the energetic costs of foraging are moderate and those of fleeing much higher. This results in an (almost) linear relationship between frequency of disturbances and the increase in foraging time. Nevertheless, the foraging time can increase substantially at higher disturbance frequencies.

The tags could only record accelerometer data continuously at a high rate when enough solar power was available to prevent battery failure. This meant that our recordings were restricted to the period when days were getting longer again at the end of the winter. This might have affected our flight estimates, because in the light of the starvation–predation risk trade-off birds may be expected to respond differently to disturbance at the end of the winter than at the beginning, probably being less inclined to fly off later in winter when they have lost weight (McNamara, Houston & Lima 1994). On the other hand, under very cold conditions, flight activity is reduced to save energy (Mooij 1992). In addition, flock size has been found to affect the disturbance rate (Bélanger & Bédard 1989), and also varies with season (Amano *et al.* 2006). Our number of observations was too low to account for the differences in flock size.

In our calculations, the time that geese stay in the air after a disturbance is a critical parameter. An observational study on greater snow geese *Chen caerulescens atlantica* staging in Québec recorded shorter flight durations (56 s in autumn and 77 s in spring) than our study, probably because of the relatively small area of movement of these geese (Bélanger & Bédard 1989). In autumn, when hunting took place, flights caused by hunting activity were no longer (50 s) than the average flight duration. A follow-up study on radio-tagged geese during spring hunt in Québec found 3.9 and 7.1 times longer flight distances after scaring and hunting, respectively, than after incidental ('fortuitous') disturbance in one region, but no significant differences in two other regions (Béchet, Giroux & Gauthier 2004). Another observational study on pink-footed geese *Anser brachyrhynchus* in the Netherlands in autumn found that flights were 3.5 times as long when scared or hunted (399 s) than when incidentally disturbed (Schilperoord & Schilperoord-Huisman 1981). There is clearly some variation among (and within) studies, but flights after intentional disturbances are consistently as long as or longer than flights after incidental disturbances. For our basic scenario, we assumed a factor of two, but in order to make more definitive quantitative assessments, experimental or at least observational work to measure the flight duration after intentional disturbances in our study system is needed. This follow-up study should preferably (again) be based on geese carrying GPS/accelerometer loggers or similar tracking devices, in order to measure the reaction of geese at the level of the individual.

Another critical parameter is the energetic cost of flight. We used flight costs derived from an allometric relationship based on empirical flight costs of various bird species (McWilliams *et al.* 2004). Short flights may, however, be more costly than long flights, because the proportion of the relatively expensive take-off is larger in the former (Powell & Engelhardt 2000; Bairlein *et al.* 2015). Higher flight costs lead to more compensatory foraging. On the other hand, frequently disturbed geese may lower their body mass in response to the starvation–predation risk trade-off, lowering their wing loading and hence their flight costs (Zimmer *et al.* 2010).

We made our calculations for two extreme scenarios, namely one in which geese forage exclusively during the day and a scenario in which they fully compensate any energetic deficits during the day by foraging at night. Our data indicated that geese returned to their roost later in the days around full moon, when evenings are lighter. Also, while many geese roost on water, white-fronted geese sleeping on land have been observed to forage on their roost at night (Mooij 1992) and regularly disturbed brent geese *Branta b. bernicla* were compensating by feeding for almost 20% of the night (Riddington *et al.* 1996). On the other hand, we know from catches that white-fronted geese lose weight in the course of winter (G. Müskens, unpublished data), so

reality is likely to be somewhere in between these two scenarios.

In the long run, disturbance during the non-breeding season might potentially lower damage. This would be the case if the resulting reduction in body condition of the birds carries over into the breeding season, leading to a lower reproduction and, consequently, lower population growth rate. Evidence for such long-term effects was found in greater snow geese that were repeatedly disturbed on a spring staging site. The geese had a reduced energy intake (Béchet, Giroux & Gauthier 2004) and lost weight (Féret *et al.* 2003), which in turn led to smaller and later clutches (Mainguy *et al.* 2002) and a lower reproductive success (Juillet *et al.* 2012). We think these carry-over effects exist in greater snow geese, because disturbance takes place at the spring staging ground, implying limited opportunities to replenish any shortfalls in energy intake before reaching the breeding grounds. However, our study considers disturbance at the wintering grounds. In pink-footed geese *Anser brachyrhynchus*, no effect was found of varying body condition after winter on the subsequent body condition in spring (Clausen, Madsen & Tombre 2015). And in barnacle geese *Branta leucopsis* repeatedly disturbed at a wintering site, no effects on the subsequent breeding success were found (Percival, Halpin & Houston 1997). Because white-fronted geese use several stopover sites on their way to the Arctic breeding site (van Wijk *et al.* 2012), these birds probably have enough leeway during their spring migration to make up for any losses in body weight on the wintering grounds (Bauer, Eikelenboom-Kil & Nolet 2015). In fact, in our calculation, the white-fronted geese are able to compensate their weight loss even before the onset of spring migration, except at the highest disturbance frequencies modelled.

IMPLICATIONS FOR MANAGEMENT

The increase in many goose populations has resulted in more and more conflicts with agriculture, particularly on growing grass and winter wheat. Different approaches have been set up to control the damage. Scaring geese to alleviate damage, in particular to vulnerable crops, is widely used. In some regions, farmers are financially compensated for damage incurred by the geese. In other regions, accommodation areas are created where farmers are being paid beforehand to allow geese to feed undisturbed. Outside these areas, damage is reduced by intentionally disturbing geese, trying to scare them away and into the accommodation areas (Kwak, Van der Jeugd & Ebbing 2008).

Experiments have shown that scaring has to be done frequently in order to reduce goose visitation; two times a day had no effect, while 5, 7 or 10 times a day had (Simonsen *et al.* 2016). Our best estimate is that disturbing geese, say, five times a day will lead to 11.5–16% increase in grass consumption. More grass consumption by geese

not necessarily means proportionally more damage, as the damage may depend on the moment of grazing. In that light, it is noteworthy that the model predicted a compensatory behaviour of long grazing days at the end of winter (when geese were assumed not to forage at night), because goose grazing later in winter causes greater grass yield loss (Groot Bruinderink 1989). Hence, disturbing geese earlier in winter may lead to more grazing with heavier damage later in winter. With regard to the increase in goose consumption as a result of scaring, this has to be taken into account in the design of accommodation schemes, and specifically in the decision how much refuge area should be set aside, as long as disturbance is needed to avoid the geese to forage outside these areas.

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Data accessibility

Tracking data are at <http://dx.doi.org/10.5441/001/1.7tp81b7b>, and compiled flight data are at Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.n4m05> (Nolet et al. 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1 Additional figures.

Appendix S2 Method to calculate energy intake rate and expenditure.

Fig. S1 Picture of tagged white-fronted geese.

Fig. S2 Example recording of accelerometer.

Fig. S3 Timing of roost flights relative to sunset and sunrise.

Fig. S4 Flight distance against flight duration.

Fig. S5 Distribution of durations of roost and non-roost flights.

Fig. S6 Calculated metabolic rates in three types of winter.

Table S1 Parameter values for white-fronted geese.