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

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## Appendix S2. Method to calculate energy intake rate and expenditure

### Energetics

We assume that the birds aim to be in weight balance, meaning that on a daily basis metabolizable energy intake ( $MEI$ ,  $J d^{-1}$ ) is equal to energy expenditure ( $DEE$ ,  $J d^{-1}$ ), or in case an energetic deficit is incurred, it will be counterbalanced by an energetic surplus as soon as the circumstances allow. A 24h day ( $T = 86,400 s d^{-1}$ ) is split into time spent resting, foraging  $T_f$ ,  $s d^{-1}$ , and flying ( $T_v$ ,  $s d^{-1}$ , from and to a roost).

The daily intake of metabolizable energy ( $MEI$ ,  $J d^{-1}$ ) is the product of the instantaneous intake rate  $IIR$  ( $g s^{-1}$ ), a function of the sward height (see section *Intake rate* below), after conversion to metabolizable energy (*q.e.IIR*,  $J s^{-1}$ ), and the daily foraging time  $T_f$ :

$$MEI = q \cdot e \cdot IIR \cdot T_f \quad (\text{eqn 1})$$

where  $q$  is the assimilation and  $e$  ( $J g^{-1}$ ) the energy content of the food.  $T_f$  is a function of the energy balance (see below).

The daily energy expenditure ( $DEE$ ,  $J d^{-1}$ ) is:

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

where  $RMR$  ( $J s^{-1}$ ) is resting metabolic rate,  $FMR$  ( $J s^{-1}$ ) is field metabolic rate, and  $VMR$  ( $J s^{-1}$ ) is flying metabolic rate.

Flying is an energy-demanding activity. Flight time  $T_v$  ( $s d^{-1}$ ) is  $2V/v$  where  $V$  is the average distance (m) from the roost to the foraging site and  $v$  is the average flight speed ( $m s^{-1}$ ) [11]. The flight costs  $VMR$  ( $J s^{-1}$ ) are allometrically scaled to body mass according to empirical data from other bird species [10]. For parameter values see Table S1.

The bird is in balance when the time spent foraging yields a *net* intake of foraging exactly covering the costs of resting and flying. Equalling  $MEI$  to  $DEE$ , the required time spent foraging amounts to

$$T_f^* = \frac{(T - T_v)RMR + T_v \cdot VMR}{q \cdot e \cdot IIR - (FMR - RMR)} \quad (\text{eqn 3})$$

However, because the geese only forage during the day, the foraging time is limited by  $T_l$ , the available time (day length including civil twilight; day length was calculated from geographical location, [http://herbert.gandraxa.com/length\\_of\\_day.xml](http://herbert.gandraxa.com/length_of_day.xml), adding 0.5 h to account for the timing of roost flights). Hence, if  $T_l < T_f^*$ , the bird cannot cover its energy requirements on this day, and it loses weight [12]:

$$\Delta M = k_m (MEI - DEE) / e \quad (\text{eqn 4})$$

where  $k_m$  is the efficiency for utilization of metabolizable energy during maintenance (0.95, [3]) and  $e$  is the energy density of the tissue (27.5 kJ/g, [9]). As soon as the circumstances allow, and as long as the current weight is below the starting weight, body weight is gained again:

$$\Delta M = k_g (MEI - DEE) / e \quad (\text{eqn 5})$$

where  $k_m$  is the efficiency for utilization of metabolizable energy during fat synthesis (0.8, [3]).

Within the thermoneutral zone,  $RMR$  is  $1.4 \times BMR$  (basal metabolic rate) and  $FMR$  is  $1.9 \times BMR$  [17]. During cold weather with wind and little radiation from the sun, the costs of maintaining body temperature can be higher than these standards ( $RMR_s$  and  $FMR_s$ ). Therefore, using the theory on heat exchange, we calculate the metabolic rate  $HMR$  needed to keep a bird body at  $40^\circ\text{C}$ , both during the day ( $HMR_d$ ) and during the night ( $HMR_n$ ) [4, 14, 18]. Thus, realized resting metabolic rate  $RMR = \max(RMR_s, HMR_n)$  and, likewise, realized field metabolic rate  $FMR = \max(FMR_s, HMR_d)$ .  $HMR$  is a function of ambient air temperature  $T_a$  ( $^\circ\text{C}$ ), wind speed  $u_{hc}$  ( $\text{m s}^{-1}$ ) at  $h_c = 10$  m, and the global radiation  $R_g$  ( $\text{W m}^{-2}$ ). The effect of cooling by wind is a function of the sward height. We neglect the heat loss through evaporation [4]. For further details see *Thermoregulation costs*.

### Intake rate

On grassland, bite size  $S$  (g; all biomass in dry weight) is a function of sward height  $L$  (m) [6, 19]:

$$S_{(L)} = \frac{b_1 L}{1 + b_2 L} \quad (\text{eqn 6})$$

where  $b_1$  and  $b_2$  are regression-coefficients. As these herbivores are foraging on spatially concentrated plants [process 3, 15], total handling time  $T_h$  (s) is:

$$T_{h(S)} = T_c + \frac{1}{R_{\max}} S \quad (\text{eqn 7})$$

where  $T_c$  is cropping time (s) and  $R_{\max}$  the maximum rate of chewing (in the absence of cropping,  $\text{g s}^{-1}$ ). The cropping time  $T_c$  is in turn a function of sward height  $L$ , presumably because the birds are becoming more selective with increasing sward height [6]:

$$T_{c(L)} = T_{c0} + cL \quad (\text{eqn 8; [Box 1, 8]})$$

One should also consider that geese regularly look up during foraging in order to check their surroundings. The ratio alert : feeding varies between 0.22 to 0.03, being lower the larger the group size [16] and the shorter the day length [7]. During alert the heart beat is elevated above resting levels [1, 13], and therefore we modelled alert as part of foraging. The intake rate is calculated over the time span feeding + alert, assuming a minimum proportion alert of 0.05. These processes together result in a type 4 functional response, with an instantaneous intake rate  $IIR$  ( $\text{g s}^{-1}$ ) as function of sward height  $L$ :

$$IIR_{(L)} = \frac{S_{(L)}}{\alpha T_{h(S)}} = \frac{1}{\alpha} \left\{ \frac{1 + b_2 L}{b_1 L} (T_{c0} + cL) + \frac{1}{R_{\max}} \right\}^{-1} \quad (\text{eqn 9})$$

where  $\alpha$  is the factor with which the feeding time is multiplied to account for the alert time ( $\alpha = 1.05$ ). See Table S1 for parameter values.

**Table S1.** Parameter values for white-fronted geese

| Variable   | Value      | Footnote, [Ref] |
|--|------------|-----------------|
| body mass $M$ (g)  | 2094       | 1,[5]           |
| functional response $b_1$ (g m <sup>-1</sup> )                     | 0.246      | 2               |
| functional response $b_2$ (g m <sup>-1</sup> )                     | 29         | 3               |
| functional response $c$ (s m <sup>-1</sup> )                       | 0.5        | 4               |
| minimal cropping time $T_{c0}$ (s)                                 | 0.59       | 5               |
| maximal chewing rate $R_{max}$ (g s <sup>-1</sup> )                | 0.032      | 6               |
| metabolic energy content of grass $q \cdot e$ (J g <sup>-1</sup> ) | 7300       | [2]             |
| basal metabolic rate $BMR$ (J s <sup>-1</sup> )                    | 7.35       | 7               |
| resting metabolic rate $RMR$ (J s <sup>-1</sup> )                  | 1.4× $BMR$ | [17]            |
| foraging metabolic rate $FMR$ (J s <sup>-1</sup> )                 | 1.9× $BMR$ | [17]            |
| flight speed $v$ (m s <sup>-1</sup> )                              | 9.44       | 8               |
| flight metabolism $VMR$ (J s <sup>-1</sup> )                       | 114.4      | 9,[10]          |
| distance from roost $V_{max}$ (m)                                  | 3200       | 8               |

<sup>1</sup> average of adults in winter  
<sup>2</sup> based on allometric relationship:  $\log b_1 = -0.332 \log M + 0.493$  ( $R^2 = 0.66$ ,  $N = 4$ )  
<sup>3</sup> based on allometric relationship:  $\log b_2 = -1.49 \log M + 6.40$  ( $R^2 = 0.85$ ,  $N = 3$ )  
<sup>4</sup> interpolation  
<sup>5</sup> average of other waterfowl species  
<sup>6</sup> based on allometric relationship:  $\log R_{max} = 0.871 \log M - 4.38$  ( $R^2 = 0.84$ ,  $N = 4$ )  
<sup>7</sup> based on allometric relationship:  $\log BMR = 0.755 \log M - 1.642$  ( $R^2 = 0.97$ ,  $N = 9$ );  
in [2] erroneously listed under pink-footed goose  
<sup>8</sup>this study  
<sup>9</sup>based on allometric relationship in [10]

## Thermoregulation costs

Input variables are the ambient air temperature  $T_a$  ( $^{\circ}\text{C}$ ), windspeed  $u_{hc}$  ( $\text{m s}^{-1}$ ) at 10 m height and daily sunshine duration  $SSD$  ( $\text{h day}^{-1}$ ). For daytime we used maximum temperature and windspeed and daily sunshine, and for nighttime minimum temperature and windspeed and no sunshine. Output is  $HMR$ , the metabolic rate needed to heat the body and keep it at  $40^{\circ}\text{C}$ .

$$HMR = H \cdot 4\pi \cdot r^2 \quad (\text{Note: [18] uses } \pi \cdot r^2)$$

where

$r$  (m) is the *radius* of the bird, calculated from body mass  $M$  (g) using an empirical relationship (Birkebak 1966 in [18]):

$$r = \sqrt{((485.6 \times M / 1000 + 592.83) / (4\pi))} / 100$$

and

$H$  ( $\text{W m}^{-2}$ ) is the *heat flux per surface area*, which in turn is calculated as:

$$H = (\rho \cdot cp) \cdot (T_b - T_{es}) / (r_p + r_e)$$

where

$\rho$  ( $\text{g m}^{-3}$ ) is the *density of dry air* as a function of  $T_a$ :

$$\rho = 1292 - (5 \cdot T_a) + (0.01567 \cdot T_a^2) \quad (\text{Monteith 1973 in [14]})$$

$cp$  is *specific heat of air* ( $1.010 \text{ J g}^{-1} \text{ }^{\circ}\text{C}^{-1}$ )

$T_b$  is *body temperature* ( $40^{\circ}\text{C}$ )

$T_{es}$  is *standard operative temperature* ( $^{\circ}\text{C}$ ) (see below)

$r_p$  is *plumage resistance* ( $867 \text{ s m}^{-1}$ ) [18]

$r_e$  ( $\text{s m}^{-1}$ ) is *equivalent outer resistance*:

$$r_e = (r_r \cdot r_a) / (r_r + r_a) \quad [14]$$

with:

$r_r$  ( $\text{s m}^{-1}$ ) is *radiation resistance*:

$$r_r = (\rho \cdot cp) / [4 \cdot \varepsilon \cdot \sigma \cdot (T_a + 273)^3]$$

where

$\varepsilon$  is *emissivity of the surface* of the bird (0.98) [4]

$\sigma$  is the *Stefan-Boltzmann constant* ( $5.67 \cdot 10^{-8} \text{ W m}^{-2} \text{ }^{\circ}\text{C}^{-4}$ )

$r_a$  ( $\text{s m}^{-1}$ ) is *convection resistance*:

$$r_a = (r_{fr} \cdot r_{fo}) / (r_{fr} + r_{fo})$$

with:

$r_{fr}$  ( $\text{s m}^{-1}$ ) is *free convection resistance*:

$$r_{fr} = 820 [2 \cdot r / (T_s - T_a)]^{1/4}$$

and

$r_{fo}$  ( $\text{s m}^{-1}$ ) is *forced convection resistance*:

$$r_{fo} = 307 \sqrt{(2 r / u)}$$

where:

$u$  ( $\text{m s}^{-1}$ ) is the wind speed experienced by the bird (see below).

Furthermore:

$$T_{es} = T_b - (1 + 0.26 \cdot \sqrt{u}) \cdot (T_b - T_e) \quad (\text{Bakken, 1990 in [4]})$$

where:

$T_e$  ( $^{\circ}\text{C}$ ) is *equivalent temperature*:

$$T_e = T_a + (R_{abs} - R_{emi}) \cdot r_e / (\rho \cdot cp) \quad (\text{Campbell, 1977 in [4]})$$

in which:

$R_{abs}$  ( $\text{W m}^{-2}$ )<sup>\$</sup> is the *radiation absorbed* by the bird:

$$R_{abs} = \alpha \cdot A_{ratio} \cdot R_g + \epsilon_s \cdot \sigma \cdot (T_a + 273)^4 \quad (\text{Campbell, 1977 in [4]})$$

where:

$\alpha$  is *absorptivity to radiation* (0.75) (Calder & King 1974 in [14])

$A_{ratio}$  is *relative surface receiving direct radiation* (0.29) [4]

$\epsilon_s$  is *emissivity of the surroundings* (0.94) [4]

$$R_g (\text{W m}^{-2}) = R_a \cdot (A_a + B_a \cdot (SSD / DL))$$

where:

$R_a$  ( $\text{W m}^{-2}$ ) is the *extra-terrestrial radiation* calculated according to

<http://www.supit.net>

$A_a$  and  $B_a$  are *Ångström-Prescott constants* (calculated with tool on

<http://www.supit.net>)

$SSD$  ( $\text{h day}^{-1}$ ) is *daily sunshine duration*

$DL$  ( $\text{h day}^{-1}$ ) is *daylength*

$R_{emi}$  ( $\text{W m}^{-2}$ )<sup>\$</sup> is the *radiation emitted* by the bird:

$$R_{emi} = \epsilon \cdot \sigma \cdot (T_s + 273)^4 \quad (\text{Campbell, 1977 in [4]})^{$$}$$

The wind speed  $u$  ( $\text{m s}^{-1}$ ) at the bird level is:

$$u = u^* / k_v \cdot [\ln ((h_b + z_m - pd_0 \cdot h_v) / z_m)] \quad (\text{Campbell, 1977 in [4]})$$

where:

$u^*$  ( $\text{m s}^{-1}$ ) is *friction velocity*:

$$u^* = u_{hc} \cdot k_v / [\ln ((h_c + z_m - pd_0 \cdot h_v) / z_m)] \quad (\text{Campbell, 1977 in [4]})$$

with:

$u_{hc}$  is the wind speed measured at height  $h_c$  ( $h_c = 10$  m)

$k_v$  is the *Von Karman proportionality constant* (0.41) (note:  $k_v$  cancels out in eqn  $u^*$ )

$z_m$  is *roughness length* (0.01 m) (Wieringa, 1993 in [18])

$pd_0$  is *relative displacement height* (0.78 of  $h_v$ ) (Shuttleworth, 1989 in [18])

$h_v$  (m) is *vegetation height* (m)

$h_b$  (m) is *height of the bird's centre of gravity above the ground*, from  $r$  (bird radius)

$$h_b = 1.5 \times r$$

Footnotes: <sup>\$</sup> [2] incorrectly gives (W) as unit; <sup>\$\$</sup> [4] incorrectly gives  $T_b$  instead of  $T_s$

## References

1. Ackerman, J.T., Takekawa, J.Y., Kruse, K.L., Orthmeyer, D.L., Yee, J.L., Ely, C.R., Ward, D.H., Bollinger, K.S. & Mulcahy, D.M. (2004) Using radiotelemetry to monitor cardiac response of free-living tundra greater white-fronted geese (*Anser albifrons elgasi*) to human disturbance. *Wilson Bulletin* 116: 146-151.
2. Baveco, J.M., Kuipers, H. & Nolet, B.A. (2011) A large-scale multi-species spatial depletion model for overwintering waterfowl. *Ecological Modelling* 222: 3773-3784.
3. Blaxter, K.L. (1989) *Energy metabolism in animals and man*. Cambridge: Cambridge University Press.
4. Cartar, R.V. & Morrison, R.I.G. (1997) Estimating metabolic costs for homeotherms from weather data and morphology: an example using calidridine sandpipers. *Canadian Journal of Zoology* 75: 94-101.
5. Cramp, S. & Simmons, K.E.L., eds.(1977) *The Birds of the Western Palearctic, Vol. 1*. Vol. 1. Oxford University Press: Oxford.
6. 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. *Journal of Animal Ecology* 72: 220-231.
7. Ely, C.R., Ward, D.H. & Bollinger, K.S. (1999) Behavioral correlates of heart rates of free-living Greater White-fronted Geese. *Condor* 101: 390-395.
8. Heuermann, N. (2007) Tall swards and small grazers: competition, facilitation and coexistence of different-sized grazers., in Resource Ecology. Wageningen University: Wageningen. p. 208.
9. Madsen, J. & Klaassen, M. (2006) Assessing body condition and energy budget components by scoring abdominal profiles in free-ranging pink-footed geese *Anser brachyrhynchus*. *Journal of Avian Biology* 37: 283-287.
10. McWilliams, S.R., Guglielmo, C., Pierce, B. & Klaassen, M. (2004) Flying, fasting, and feeding in birds during migration: a nutritional and physiological ecology perspective. *Journal of Avian Biology* 35: 377-393.
11. Mooij, J.H. (1992) Behaviour and energy budget of wintering geese in the Lower Rhine area of North Rhine-Westphalia, Germany. *Wildfowl* 43: 121-138.
12. Nolet, B.A. & Drent, R.H. (1998) Bewick's Swans refuelling on pondweed tubers in the Dvina Bay (White Sea) during their spring migration: first come, first served. *Journal of Avian Biology* 29: 574-581.
13. Nolet, B.A., Bevan, R.M., Klaassen, M., Langevoord, O. & Van der Heijden, Y.G.J.T. (2002) Habitat switching by Bewick's swans: maximisation of average long-term energy gain? *Journal of Animal Ecology* 71: 979-993.
14. Robinson, D.E., Campbell, G.S. & King, J.R. (1976) An evaluation of heat exchange in small birds. *Journal of Comparative Physiology B* 105: 153-166.
15. Spalinger, D.E. & Hobbs, N.T. (1992) Mechanisms of foraging in mammalian herbivores: new models of functional response. *American Naturalist* 140: 325-348.
16. Spilling, E., Bergmann, H.-H. & Meier, M. (1999) Truppgrößen bei weidenden Bläß- und Saatgänsen (*Anser albifrons*, *A. fabalis*) an der Unteren Mittelbe und ihr Einfluß auf Fluchtdistanz und Zeitbudget. *Journal für Ornithologie* 140: 325-334.
17. Stahl, J., Veeneklaas, R.M., Van der Graaf, A.J., Loonen, M.J.J.E. & Drent, R.H. (2001) Conversion factors for energetic expenditure of actively foraging brent and barnacle geese obtained by non-invasive heart rate telemetry., in Limits to the co-occurrence of avian herbivores: how geese share scarce resources, J. Stahl, Editor. PhD thesis, Rijksuniversiteit Groningen: Groningen. p. 93-120.
18. van der Graaf, A.J., Stahl, J., Bos, D. & Drent, R.H. (2001) Influence of wind exposure and temperature on energy expenditure and site choice in brent and barnacle geese., in Limits to the co-occurrence of avian herbivores. How geese share scarce resources., J. Stahl, Editor. PdD thesis, University of Groningen: Groningen. p. 121-151.
19. Van Gils, J.A., Gyimesi, A. & Van Lith, B. (2007) Avian herbivory: an experiment, a field test, and an allometric comparison with mammals. *Ecology* 88: 2926-2935.