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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, 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°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} (m s^{-1}) at $h_c = 10$ m, and the global radiation R_g (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, 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 (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 α 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 ⁻¹)	0.246	2
functional response b_2 (g m ⁻¹)	29	3
functional response c (s m ⁻¹)	0.5	4
minimal cropping time T_{c0} (s)	0.59	5
maximal chewing rate R_{max} (g s ⁻¹)	0.032	6
metabolic energy content of grass $q \cdot e$ (J g ⁻¹)	7300	[2]
basal metabolic rate BMR (J s ⁻¹)	7.35	7
resting metabolic rate RMR (J s ⁻¹)	1.4× BMR	[17]
foraging metabolic rate FMR (J s ⁻¹)	1.9× BMR	[17]
flight speed v (m s ⁻¹)	9.44	8
flight metabolism VMR (J s ⁻¹)	114.4	9,[10]
distance from roost V_{max} (m)	3200	8

¹ average of adults in winter
² based on allometric relationship: $\log b_1 = -0.332 \log M + 0.493$ ($R^2 = 0.66$, $N = 4$)
³ based on allometric relationship: $\log b_2 = -1.49 \log M + 6.40$ ($R^2 = 0.85$, $N = 3$)
⁴ interpolation
⁵ average of other waterfowl species
⁶ based on allometric relationship: $\log R_{max} = 0.871 \log M - 4.38$ ($R^2 = 0.84$, $N = 4$)
⁷ 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
⁸this study
⁹based on allometric relationship in [10]

Thermoregulation costs

Input variables are the ambient air temperature T_a ($^{\circ}\text{C}$), windspeed u_{hc} (m s^{-1}) at 10 m height and daily sunshine duration SSD (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°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 (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

ρ (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°C)

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

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

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

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

with:

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

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

where

ε is *emissivity of the surface* of the bird (0.98) [4]

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

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

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

with:

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

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

and

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

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

where:

u (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} (W m^{-2})^{\$} 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:

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

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

ϵ_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 (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 (h day^{-1}) is *daily sunshine duration*

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

R_{emi} (W m^{-2})^{\$} 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 (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^* (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: ^{\$} [2] incorrectly gives (W) as unit; ^{\$\$} [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.