

UvA-DARE (Digital Academic Repository)

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

Nolet, B.A.; Kölzsch, A.; Elderenbosch, M.; van Noordwijk, A.J.

DOI 10.1111/1365-2664.12698 Publication date 2016

Document Version Other version

Published in Journal of Applied Ecology

Link to publication

Citation for published version (APA):

Nolet, B. A., Kölzsch, A., Elderenbosch, M., & van Noordwijk, A. J. (2016). Scaring waterfowl as a management tool: how much more do geese forage after disturbance? *Journal of Applied Ecology*, *53*(Special Feature: Model-assisted monitoring of biodiversity), 1413-1421. https://doi.org/10.1111/1365-2664.12698

General rights

It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: https://uba.uva.nl/en/contact, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.

UvA-DARE is a service provided by the library of the University of Amsterdam (https://dare.uva.nl)

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 ($T = 86,400 \text{ s d}^{-1}$) is split into time spent resting, foraging T_f , s d⁻¹), and flying (T_ν , 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 .

$$MEI = q \cdot e \cdot IIR \cdot T_f \tag{eqn 1}$$

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:

 $DEE = (T - T_f - T_v)RMR + T_f \cdot FMR + T_v \cdot VMR$ (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

$$T_{f}^{*} = \frac{(T - T_{v})RMR + T_{v} \cdot VMR}{q \cdot e \cdot IIR - (FMR - RMR)}$$
(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]:

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

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:

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

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 (°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]:

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

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:

$$T_{h(S)} = T_c + \frac{1}{R_{\text{max}}}S$$
 (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]:

$$T_{c(L)} = T_{c0} + cL$$
 (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*:

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

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 <i>BMR</i> (J s ⁻¹)	7.35	7
resting metabolic rate <i>RMR</i> (J s ⁻¹)	$1.4 \times BMR$	[17]
foraging metabolic rate FMR (J s ⁻¹)	$1.9 \times BMR$	[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

 Table S1. Parameter values for white-fronted geese

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 (°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.

 $HMR = H \cdot 4\pi \cdot r^2$ (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

 $\rho (g m^{-3}) \text{ is the density of dry air as a function of } T_a:$ $\rho = 1292 - (5 \cdot T_a) + (0.01567 \cdot T_a^{-2}) \text{ (Monteith 1973 in [14])}$ $cp \text{ is specific heat of air (1.010 J g^{-1} °C^{-1})}$ $T_b \text{ is body temperature (40 °C)}$ $T_{es} \text{ is standard operative temperature (°C) (see below)}$ $r_p \text{ is plumage resistance (867 s m^{-1}) [18]}$ $r_e (s m^{-1}) \text{ is equivalent outer resistance:}$ $r_e = (r_r \cdot r_a)/(r_{r+}r_a) \qquad [14]$

with:

 r_r (s m⁻¹) is radiation resistance: $r_r = (\rho \cdot cp) / [4. \varepsilon \cdot \sigma \cdot (T_a + 273)^3]$

where

ε is *emissivity of the surface* of the bird (0.98) [4] σ is the *Stefan-Boltzmann constant* (5.67 10⁻⁸ W m⁻² °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: $r_{fr} = 820 [2 . r / (T_s - T_a)]^{\frac{1}{4}}$

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:

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

where:

 T_e (°C) is equivalent temperature: $T_e = T_a + (R_{abs} - R_{emi}) \cdot r_e / (\rho \cdot cp)$ (Campbell, 1977 in [4]) in which:

 R_{abs} (W m⁻²)^{\$} is the *radiation absorbed* by the bird: $R_{abs} = \alpha \cdot A_{ratio} \cdot R_g + \varepsilon_s \cdot \sigma \cdot (T_a + 273)^4$ (Campbell, 1977 in [4]) where:

α is absorbtivity 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 (W m⁻²) = R_a . (Aa + Ba . (SSD / DL))

where:

 R_a (W m⁻²) is the *extra-terrestrial radiation* calculated according to <u>http://www.supit.net</u>

Aa and *Ba* are *Ångström-Prescott constants* (calculated with tool on <u>http://www.supit.net</u>) *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: $R_{emi} = \varepsilon \cdot \sigma \cdot (T_s + 273)^4$ (Campbell, 1977 in [4])^{\$\$}

The wind speed u (m s⁻¹) at the bird level is:

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

where:

 $u^* (m s^{-1})$ is friction velocity: $u^* = u_{hc} \cdot k_v / [\ln ((h_c + z_m - pd_0 \cdot h_v) / z_m)]$ (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 tule 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 freeliving Greater White-fronted Geese. *Condor* 101: 390-395.
- 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 brachyrynchus*. *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.
- 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) Mechamisms 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 Mittelelbe 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.