

APPLIED ISSUES

Quantification of allochthonous nutrient input into freshwater bodies by herbivorous waterbirds

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SUMMARY

1. Waterbirds are considered to import large quantities of nutrients to freshwater bodies but quantification of these loadings remains problematic. We developed two general models to calculate such allochthonous nutrient inputs considering food intake, foraging behaviour and digestive performance of waterbirds feeding in terrestrial habitats: an intake model (IM), mainly based on an allometric relationship for energy requirements and a dropping model (DM), based on allometric relationships for defaecation.
2. Reviewed data of nitrogen (N) and phosphorus (P) content of herbivorous food varied according to diet type (foliage, seeds and roots), season and fertilization. For model parameterization average foliage diet contained 38.20 mg N g⁻¹ and 3.21 mg P g⁻¹ (dry weight), whereas mean faeces composition was 45.02 mg N g⁻¹ and 6.18 mg P g⁻¹.
3. Daily allochthonous nutrient input increased with body mass ranging from 0.29 g N and 0.03 g P in teals *Anas crecca* to 5.69 g N and 0.57 g P in mute swans *Cygnus olor*. Results from IM differed from those of DM from ducks to swans by 63–108% for N and by –4 to 23% for P. Model uncertainty was lowest for the IM and mainly caused by variation in estimates of food retention time (RT). In DM food RT and dropping mass determined model uncertainty in similar extent.
4. Exemplarily applying the models to Dutch wetlands resulted in mean annual contribution of herbivorous waterbirds to allochthonous nutrient loading of 382.8 ± 167.1 tonnes N a⁻¹ and 34.7 ± 2.3 tonnes P a⁻¹, respectively, which corresponds to annual surface-water loadings of 1.07 kg N ha⁻¹ and 0.10 kg P ha⁻¹.
5. There was a distinct seasonal pattern with peak loadings in January, when bird abundances were highest. Lowest inputs were in August, when bird abundance and nutrient content in food was low and birds foraged less in terrestrial habitats. Three-quarters of all nutrient input was contributed by greater white-fronted goose *Anser albifrons*, greylag goose *Anser anser*, wigeon *Anas penelope* and barnacle goose *Branta leucopsis* alone.
6. We provide general, easy to use calculation methods for the estimation of allochthonous nutrient inputs by waterbirds, which are applicable to a range of waterbird species, a variety of potential diets and feeding behaviours, and across spatial scales. Such tools may greatly assist in the planning and execution of management actions for wetland nutrient budgets.

Keywords: eutrophication, loading, nitrogen, phosphorus, waterfowl

Introduction

Freshwater habitats may receive nutrients from external sources via precipitation, surface runoff, groundwater inflow and migrating animals. The first two are directly affected by human activity, e.g.

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enhanced atmospheric pollution results in increased nitrogen (N) and phosphorus (P) concentrations in precipitation (Bergstrom & Jansson, 2006) and nutrient-rich runoff from agriculture caused by intensive application of fertilizers (e.g. Schweigert & van der Ploeg, 2002; Hirt, Hammann & Meyer, 2005). Excrements from animals that feed outside the system but rest and/or breed in wetlands are a natural source for N and P. Where waterbirds are numerous, their excreta can occasionally represent a major external nutrient source (Portnoy, 1990; Manny, Johnson & Wetzel, 1994), especially if the wetland is a favoured roost for migratory birds (Post *et al.*, 1998).

In contrast to piscivorous waterbirds, which are nearly exclusively tied to aquatic systems, many species of herbivorous waterbirds frequently forage in terrestrial habitats but breed and rest in lakes and wetlands. They may thus be responsible for considerable reallocation and concentration of allochthonous nutrients in freshwater bodies. Over the past decades many herbivorous waterbirds, notably geese (*Anser* and *Branta*), have increased in numbers in the western world (Madsen, Cracknell & Fox, 1999) with a current annual wintering population in north-western Europe of approximately 9.3×10^6 birds (van Eerden *et al.*, 2005). An important driving force for these population trends are modern agricultural practices providing high-quality food throughout the year, thereby enlarging the carrying capacities of terrestrial habitats (van Eerden *et al.*, 1996). Waterbirds have subsequently adapted their foraging behaviour, feeding frequently in terrestrial agricultural habitats, especially during winter (Mayes, 1991; Gill, 1996). As they continue roosting on safe wetland sites, the increased numbers of waterbirds will presumably increase nutrient input to these systems.

Despite the obvious potential for herbivorous birds to mediate allochthonous nutrient input to freshwater bodies, few detailed studies have investigated this role (e.g. Manny *et al.*, 1994; Marion *et al.*, 1994; Gwiazda, 1996; Post *et al.*, 1998). Although these studies considered only a limited number of species and local conditions their results have been generalized and widely applied for other study systems (Scherer *et al.*, 1995; Moore *et al.*, 1998; Andersen *et al.*, 2003; Olson *et al.*, 2005; Rip, Rawee & de Jong, 2006). However, a general framework for

calculating nutrient contributions of waterbirds is lacking.

The effect of waterbirds on the nutrient budgets of lakes or wetlands is difficult to measure directly. However, the seasonal occurrences of potentially contributing waterfowl species (Family *Anatidae*) and their behaviour are often well documented, which should allow indirect assessment of their effect. We thus developed a modelling framework for the calculation of allochthonous nutrient input to freshwater bodies. Considering the birds' foraging behaviour, energy requirements, metabolic constraints and the nutrient concentrations in food we developed two alternative approaches. To parameterize these models we reviewed data on chemical composition of faeces and various herbivorous diets to provide a sound basis for further model applications, e.g. to different habitats and regions. Finally, we exemplarily applied the models to waterbird populations in Dutch lakes and wetlands as one of the largest, most uniform, and important landscapes for wintering waterbirds in Europe.

Methods

Nutrient input models

We developed two approaches to quantify allochthonous N and P input by herbivorous waterbirds. The first is based on mass-specific energy requirement and daily food intake (intake model, IM). The second approach focused on daily faecal output and digestive performance (dropping model, DM). In their basic considerations both models assumed a simple daily routine of the birds, with one continuous foraging bout in terrestrial habitats and the remaining time being spent on a wetland or lake (i.e. a typical foraging pattern when daylight is limited during winter). For the application the models are parameterized according to waterbird species, their food and season (see Model parameters). Hereafter, we will use *X* in our notations to denote the nutrient of interest, i.e. N or P. All presented data of energy density, mass of food and faeces (as well as their elemental composition) refer to dry mass. Furthermore, we use the term defaecation in the broader sense combining defaecation and excretion of renal products, because all are finally mixed in the cloaca of birds.

Intake model

We assumed all birds to be in steady state with respect to N and P. Thus, for all birds the daily amount of N and P defaecated corresponded to the amount ingested. Hence defaecation of N and P depended on daily food intake and its elemental concentration (X_{food} ; mg g^{-1}).

Daily terrestrial food intake (DFI_t ; g day^{-1}) was calculated using the allometric relationship of daily energy requirement (DER ; kJ day^{-1}) to body mass (M ; g , $\text{DER} = 10^{1.0195} \times M^{0.6808}$, after Nagy, Girard & Brown, 1999), the energy content of the terrestrial diet (E ; kJ g^{-1}), the apparent metabolizable energy coefficient (AM) (Table 1) and the species and season-specific proportion of energy obtained from terrestrial food relative to the total amount of energy required (f_t) (see below and Table S1):

$$\text{DFI}_t = f_t \times \text{DER} / (E \times \text{AM}) \quad (1)$$

When returning to the wetland after feeding, waterbirds excrete a certain fraction of their daily faecal output at this roosting site (Ebbinge, Canters & Drent, 1975; Manny, Wetzel & Johnson, 1975). Assuming the elemental concentration in faeces to be constant throughout the day, N and P defaecation at the roost and thus the allochthonous input into a freshwater body (X_{ai} ; g day^{-1}), should correspond to

N and P intake. To calculate X_{ai} we assumed the digestive tract of waterbirds to be completely filled when feeding ceases and birds fly to the roost. The fraction of all droppings produced at the roost can be calculated as the ratio of retention time (RT) and total foraging time T_f (Fig. S1), where RT is defined as the average time for food to pass a bird's digestive tract. Consequently, combining RT/T_f with food intake and N and P content of the food yields the allochthonous nutrient input:

$$X_{\text{ai}} = \text{RT}/T_f \times \text{DFI}_t \times X_{\text{food}} \quad (2)$$

Published values for feeding times varied between 9.6 and 14 h (Owen, 1972; Ebbinge *et al.*, 1975; Owen & Thomas, 1979; Mayhew, 1988; Therkildsen & Madsen, 2000b); therefore, we set $T_f = 12$ h for all species. Additional validation of T_f came from barnacle geese *Branta leucopsis* (Bech.) and Canada geese *Branta c. canadensis* (L.) which released 15.25% and 15.86% of daily droppings at their roost (Ebbinge *et al.*, 1975; Manny *et al.*, 1994), corresponding to T_f of 13.6 and 15.0 h.

Dropping model

Alternatively, the allochthonous nutrient input from droppings produced during roosting was directly calculated using the following parameters

Table 1 Parameters included in Monte-Carlo simulations given as means and SE

Trait	Mean	SE	A	SE _A	B	SE _B	References
DER			1.0195	0.0393	0.6808	0.0182	22
E	20.78	1.13					See Results
AM	0.36	0.0236					13
N_{food}	38.2	1.1					See Results
N_{drop}	45.0	1.6*					4; 11; 15; 16; 31
RT			-0.3196	0.2803	0.2020	0.0844	5; 7; 12; 17; 18; 20; 21; 23; 25
DrM			-3.0650	0.2783	0.8901	0.0816	2; 6; 8; 9; 14; 15; 19; 23; 27-30
DrR			2.1299	0.1722	-0.3065	0.0524	1; 3; 5; 6; 8; 9; 10; 19; 23; 24; 25; 26-29

Linear regression for DER and digestive performances was $\log(\text{Trait}) = A + B \times \log(\text{body mass})$.

SE, standard error; DER, daily energy requirement (kJ day^{-1}); E, gross energy content of food (kJ g^{-1}); AM, apparent metabolizable energy coefficient; N_{food} and N_{drop} , nitrogen concentration in food and droppings (mg g^{-1}); RT, retention time (h); DrR, dropping rate (h^{-1}); DrM, dropping mass (g).

*Calculated from arithmetic mean.

(1) Bazely, Ewins & McCleery, 1991; (2) Bazely & Jefferies, 1985; (3) Bedard & Gauthier, 1986; (4) Bruinderink, 1989; (5) Bruinzeel *et al.*, 1997; (6) Brunckhorst, 1996; (7) Burton, Hudson & Bragg, 1979; (8) Ebbinge *et al.*, 1975; (9) Fox & Kahlert, 1999; (10) Fox *et al.*, 1998; (11) Gwiazda, 1996; (12) Hassall & Lane, 2005; (13) Karasov, 1990; (14) Kear, 1963; (15) Manny *et al.*, 1994; (16) Manny *et al.*, 1975; (17) Marriott & Forbes, 1970; (18) Mattocks, 1971; (19) Mayhew, 1988; (20) Mayhew & Houston, 1993; (21) McWilliams, 1999; (22) Nagy *et al.*, 1999; (23) Owen, 1975; (24) Prins & Ydenberg, 1985; (25) Prop & Vulink, 1992; (26) Summers & Critchley, 1990; (27) Therkildsen & Madsen, 2000b; (28) van Eerden, Slager & Soldaat, 1997; (29) Ydenberg & Prins, 1981; (30) J. van Gils, unpubl. data; (31) G. Eichhorn, unpubl. data.

on digestive performances: food RT (h), dropping mass (DrM, g), dropping rate (DrR, numbers of droppings h⁻¹), elemental concentration in droppings (X_{drop}, mg g⁻¹) and the proportion of droppings originating from terrestrial food (f_t):

$$X_{ai} = f_t \times RT \times DrM \times DrR \times X_{drop} \quad (3)$$

For between-model comparisons, we calculated N and P input for all target species (see below) assuming fully terrestrial feeding (f_t = 1) and average foliage diet from fertilized habitat (Table 2).

Test of model uncertainty

As all model parameters inherently contain errors to a varying degree, the question arises how these errors affect the models' ultimate results. Therefore, we conducted an uncertainty analysis for the calculation of allochthonous N input using Monte-Carlo simulations. In the IM, we varied the parameters for the calculation of RT, DER, E, AM and X_{food}, and in the dropping model, we varied RT, DrM, DrR and X_{drop}. In the Monte-Carlo analyses, the value for each parameter was drawn from a normal distribution (mean ± SE, Table 1). Nitrogen inputs were calculated for a 'typical' duck, goose and swan with body masses of 800, 2200 and 9800 g respectively. A total of 30 000 runs were conducted per simulation. We determined the factor with the greatest impact on model uncertainty by consecutively setting SE of individual parameters to zero. All models were compared by calculating

coefficients of variation (CV) using square-root transformed output data.

Model parameters

Digestive performance We analysed published data on digestive performance of herbivorous waterbirds, e.g. RT, DrM, DrR in relation with species-specific body mass to derive general allometric relations.

Composition of herbivorous diet and faeces We reviewed published data on energy and nutrient content of dietary items and faeces of herbivorous waterbirds from temperate climates of the northern hemisphere. Diets were categorized as seeds (from *Poaceae*), roots and rhizomes (including sugar beet), and foliages of grass and herbs. We extracted the following dietary parameters: gross energy content (kJ g⁻¹), AM, which is the metabolized energy content divided by the gross energy content of the food (Karasov, 1990), and N and P content (mg g⁻¹). Additionally, we checked for seasonal variation (spring, summer and winter; see below for definition of these seasons) as well as the influence of fertilizer application on N and P content of the food. For faeces, N and P content (mg g⁻¹) data were only available from studies carried out in fertilized habitats (Bruinderink, 1989; Manny *et al.*, 1994; Gwiazda, 1996; G. Eichhorn, unpubl. data).

Waterbird species and numbers For the estimation of N and P input of waterbirds on a landscape scale, we parameterized both models with published data of monthly counts of herbivorous waterbirds in

Table 2 Composition of herbivorous diet of terrestrial feeding waterbirds

Diet	E	n	AM	n	Water	N	Fertilized				Unfertilized			
							N _{food}	n	P _{food}	n	N _{food}	n	P _{food}	n
Seeds	18.79	4	0.67	6	11.6	3	18.62	5						
Root	14.91	3	0.56	3	81.5	3								
Sugar beet	13.96	2	0.84	1			11.36	3	2.15	2				
Foliage														
Spring							40.13	24			27.13	3		
Summer							33.70	23	3.18	12	22.60	25	1.70	10
Winter							41.23	23	2.50	8	32.60	13	2.95	2
Average	20.78	18	0.36	31	75.5	31	38.20	73	3.12	34	26.31	42	1.91	12

Data are given for gross energy content (E, kJ g⁻¹), apparent metabolizable energy coefficient (AM) and water content of fresh food (%). Nitrogen (N_{food}, mg g⁻¹) and phosphorus (P_{food}, mg g⁻¹) contents of the various food categories are provided for fertilized and unfertilized habitats. Additionally, the annual and seasonal means for foliages are depicted. The number of studies is given by n; for a detailed list of sources see Appendix S1.

wetlands of the Netherlands from July 2001 to June 2004 (van Roomen *et al.*, 2003, 2004, 2005). Only species with more than 100 individuals counted per year were included in the analysis. In total, we considered 26 herbivorous waterbird species potentially foraging in terrestrial habitats during at least part of the year (Table S1). Because many species show seasonally varying foraging behaviour, we scored the proportion of food obtained from terrestrial habitats (f_t) in five levels (0, 0.25, 0.5, 0.75 and 1), where $f_t = 0$ indicates no terrestrial and $f_t = 1$ fully terrestrial foraging, distinguishing three seasons: (i) winter (October–February); (ii) spring (March–April) and (iii) summer (May–September). If, for example, a species would take one-quarter of its daily food from an aquatic habitat, its f_t score would be 0.75 and thus, three of four from terrestrial sources. All f_t scores as well as body mass and data on migration behaviour were derived from central and north-west European populations given by Glutz von Blotzheim (1990); Dunning (1993) and Cramp (1998). We categorized all species according to systematic order and body mass into: (i) dabbling ducks (*Anatini* including Egyptian goose *Alopochen aegyptiacus* (L.) and Eurasian coot *Fulica atra* L.; $n = 8$ species); (ii) geese (*Anser* and *Branta*, $n = 14$ species) and (iii) swans (*Cygnus*, $n = 4$ species).

For nutrient input on a landscape-scale, we considered seasonal variation in nutrient composition of foliages as well as increased N requirements in migrating species during spring pre-migratory fattening for the IM calculations. Because 1 g body storage contains 0.09 g protein, corresponding to 0.0144 g N g⁻¹ wet mass (Klaassen, 1996; Jenni & Jenni-Eiermann, 1998), the deposition of body stores leads to decreased N excretion. In consideration of this effect we assumed a 10% increase of body mass over the month preceding departure and subtracted the corresponding N requirement from the IM results over that month.

Results

Model parameters

Digestive performance Both food RT and DrM increased with body mass: $RT = 10^{-0.3196} \times M^{0.2020}$ ($R^2 = 0.21$, $P = 0.03$, $n = 24$) and $DrM = 10^{-3.065} \times M^{0.8901}$ ($R^2 = 0.87$, $P = 0.001$, $n = 20$) (Fig. 1a,b),

whereas DrR decreased with increasing body mass with $DrR = 10^{2.130} \times M^{-0.3065}$ ($R^2 = 0.58$, $P = 0.001$, $n = 27$, Table 1 & Fig. 1c).

Composition of herbivorous diet and faeces Gross energy content of foliage was highest, followed by seeds and roots (Kruskal–Wallis: $\chi^2_{2,24} = 7.67$, $P = 0.02$, Table 2). These differences in gross energy content were counteracted by a significantly lower AM of foliage compared with seeds and roots ($F_{2,39} = 10.71$, $P = 0.001$; Table 2). Within foliage, neither gross energy

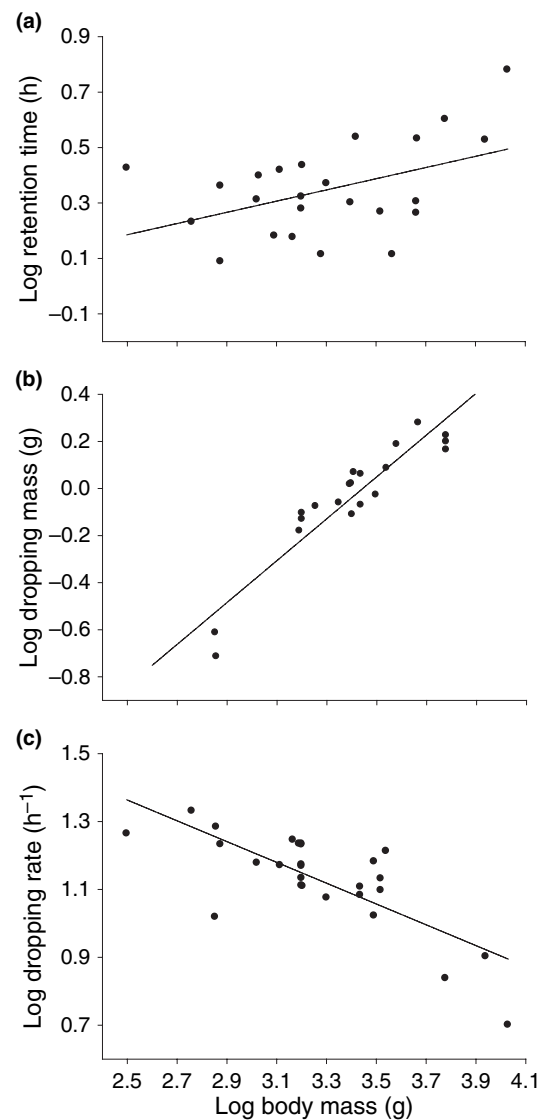


Fig. 1 Relationships of (a) food retention time (RT), (b) dropping rate (DrR) and (c) dropping mass (DrM) to species-specific body mass of waterbirds feeding on foliage diet. Data were log–log-transformed before linear regression; for references see Table 1.

content (Mann–Whitney U -test = 5.00, $P = 0.12$, $n = 18$) nor their AM differed significantly ($t_{29} = -1.22$, $P = 0.23$) of grass and herbs.

Nitrogen content of diets differed significantly ($F_{2,148} = 11.20$, $P = 0.001$), with less N in seeds and sugar beet than in foliage (Table 2). Similar patterns appeared for P, with foliage values 1.4 times higher compared with sugar beet (no data for seeds, very few data for beet, Table 2). N content of foliage was highly dependent on fertilizer application ($F_{1,111} = 28.37$, $P = 0.001$) and season ($F_{1,111} = 11.80$, $P = 0.001$, interaction: $P = 0.68$). In general, fertilization enhanced N content by 45% and reduced seasonal fluctuations (range in fertilized diets: 2.7–18%, in unfertilized diets: 16.7–30.7%, Table 2). Fertilizer application also resulted in 63% higher P-values ($F_{1,38} = 13.33$, $P = 0.001$). Seasonal variation in P content ranged between 15% and 33%, with lowest values during winter ($F_{2,26} = 4.44$, $P < 0.02$; no data for food from unfertilized habitats). Generally, P content in foliage was positively related to N content, with $P = 0.150 \times N - 1.064$ [reduced major axis regression (RMA): $R^2 = 0.25$, $P = 0.001$, $n = 44$]. In faeces, weighed mean N and P contents amounted to 45.02 mg g^{-1} ($n = 546$, seven studies) and 6.18 mg g^{-1} ($n = 495$, four studies) respectively. Insufficient data prevented the detection of potential variations in faecal N or P across seasons and food types.

Nutrient input models

Both IM and DM predicted an increase of nutrient excretion with increasing body mass. Compared with the DM, the IM yielded 63%, 79% and 108% higher N excretions for a typical duck, goose and swan respectively. The mean predicted daily N input ranged from $0.29 \pm 0.08 \text{ g N day}^{-1}$ for common teal *Anas crecca* L. (body mass: 315 g) to $5.69 \pm 2.84 \text{ g N day}^{-1}$ for mute swan *Cygnus olor* (Gmel.) (body mass: 10750 g) (Fig. 2). For P, IM and DM predictions differed by -4%, 6% and 23% for the average duck, goose and swan, respectively; the mean daily P input ranged from $0.03 \pm 0.003 \text{ g P}$ in the common teal to $0.57 \pm 0.087 \text{ g P}$ for mute swans (Fig. 2).

Both models were afflicted with considerable uncertainties as revealed by Monte–Carlo simulations with increasing CV values from ducks to swans by 18% (Fig. S2a,b). However, uncertainty in IM was significantly lower than in DM [repeated measure

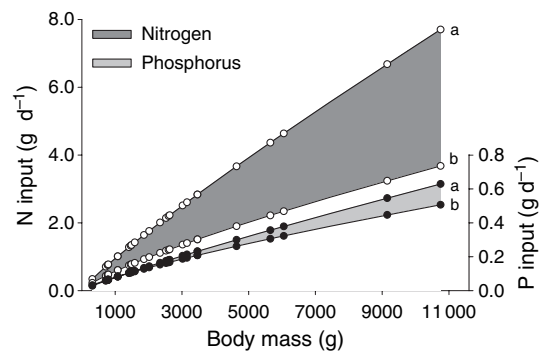


Fig. 2 Daily nitrogen and phosphorus input of waterbirds feeding exclusively on terrestrial foliage. Results from intake model (IM) and dropping model (DM) are marked with a and b respectively.

(RM) ANOVA: $F_{1,5} = 396.0$, $P = 0.003$]. In IM the major source of uncertainty resulted from RT, e.g. if RT variation was set to 0, CV of N input decreased by 80% (Fig. S2c). Neither DER nor the combination of E, AM and X_{food} significantly affected CVs compared with the fully randomized model (RM ANOVA: $F_{3,11} = 413.2$, $P = 0.001$, Bonferroni t -test full RM versus RT: $P = 0.001$, full randomized model versus DER and E, AM, X_{food} : both $P > 0.05$). In DM, uncertainty mainly resulted from RT and DrM, which decreased CVs by 26% and 25%, respectively, when set constant (Fig. S2d); DrR had less (9%), and X_{drop} no effect (RM ANOVA: $F_{4,14} = 349.9$, $P = 0.001$, Bonferroni t -test full randomized model versus RT, DrM, DrR: all $P = 0.001$, full randomized model versus X_{drop} : $P > 0.05$).

Effect of diet on nutrient input In IM exclusive feeding on sugar beet resulted in 81% and 56% lower N and P input, respectively, compared with a foliage diet given similar RT. When waterbirds fed only on seeds RT increased 58% on average compared with a foliage diet (mallard *Anas platyrhynchos* L.: 3.6 h – 89%, cited in Karasov, 1990, greylag goose *Anser anser* (L.): 3.7 h – 26%, Storey & Allen, 1982). However, because of high E and AM, the per capita input was 54% below X_{ai} of feeding on foliage.

In the DM, an increasing RT is accompanied by decreasing DrR as both are functionally related to body mass (substitution of RT into equation of DrR, if $M = \text{constant}$). Hence, nutrient input of ducks and geese feeding exclusively on seeds showed a 21% decrease compared with a foliage diet, given a similar faeces composition to foliage feeders.

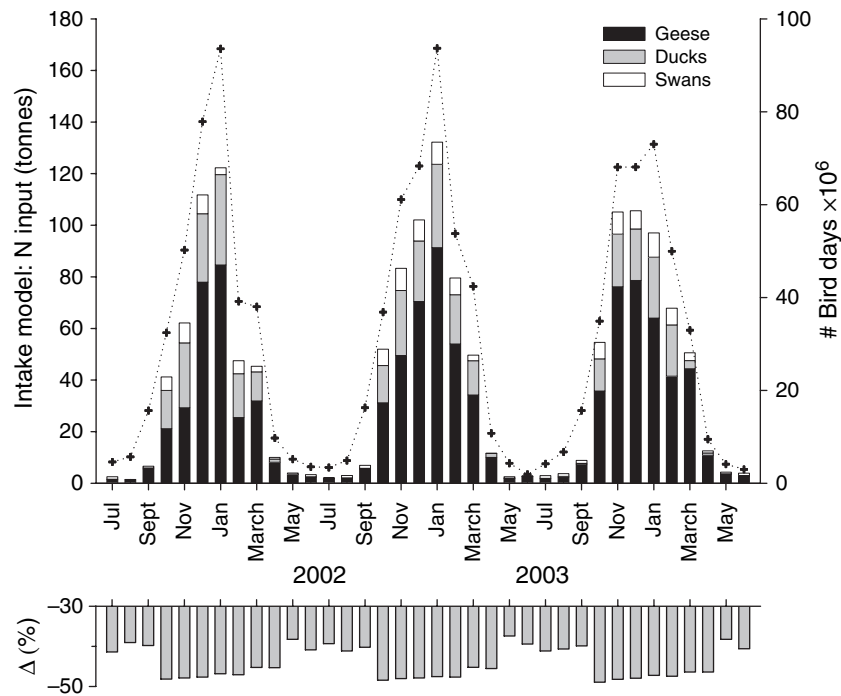


Fig. 3 Seasonal pattern of nitrogen input into Dutch lakes and wetlands by geese (black), ducks (grey) and swans (white). Nitrogen input is given in metric tonnes per month, calculated from the intake model (IM, upper panel). Crosses mark monthly abundance of waterbirds from 2001 to 2004. Differences between IM and dropping model are given as % IM in the lower panel (see text for model details).

Model application – waterbird input in Dutch lakes and wetlands

There was a distinct seasonal pattern in nutrient input according to waterbird abundance with the highest values in January (mean of IM, DM: 89.5 tonnes N month⁻¹) and lowest input during mid-summer (mean in August: 2.2 tonnes N month⁻¹) (monthly differences: Kruskal–Wallis: $H = 33.24$, $P = 0.001$, d.f. = 11, Fig. 3).

The predicted annual N input into Dutch freshwater bodies ranged between 243.5 tonnes (DM) and 527.7 tonnes (IM, Table 3). Consideration of body reserve accumulation in preparation for spring migration decreased the predicted values only slightly, by 0.22%. The estimated P input per year ranged

Table 3 Total allochthonous nutrient input into Dutch lakes and wetlands by herbivorous waterbirds

Year	Nitrogen (tonnes)		Phosphorus (tonnes)	
	IM	DM	IM	DM
2001–02	458.1	243.5	30.3	33.4
2002–03	527.7	278.3	34.7	38.2
2003–04	517.2	272.3	34.3	37.4

Estimations (in metric tonnes) were derived from two model calculations based on species specific energy requirements (intake model, IM) and species specific digestion parameters and excretion rates (dropping model DM).

between 30.3 tonnes (IM, lower values due to low P content in winter) and 38.2 tonnes (DM, see Table 3 for annual ranges). Relating this to a total surface area of 3.57×10^5 ha of Dutch freshwater (<http://statline.cbs.nl>) yields a N and P input of 0.74–1.40 kg N ha⁻¹ year⁻¹ and 0.09–0.10 kg P ha⁻¹ year⁻¹ (these values double if the IJsselmeer, the largest Dutch freshwater body of which only the fringes are used by roosting herbivorous waterbirds, is excluded).

Geese were the most important nutrient contributors, with a mean monthly contribution of 71.9% (range: 46.4–92.9%), followed by ducks (mean: 16.4%, range: 1.4–41.8%) and swans (swan: 11.7%, range: 0.5–36.1%). On a species level, four waterbird species were responsible for 75% of the total annual input, with greater white-fronted goose *Anser albifrons* (Sco.) leading (25%) followed by greylag goose (21%), wigeon *Anas penelope* L. (15%) and barnacle goose (14%). Each of the remaining 22 species contributed <7% to the total nutrient input.

Discussion

Nutrient input models

Herbivorous waterbirds seasonally forage in terrestrial habitats, but visit freshwater sites for roosting.

Although they have, therefore, been acknowledged as contributors to the nutrient budgets of freshwater habitats, the magnitude of their contribution has remained speculative (e.g. Unckless & Makarewicz, 2007). The few empirical studies that have measured the actual input have resulted in highly variable estimates, ranging from <1% and 7% of annual N and P load, respectively (Marion *et al.*, 1994) to 40–75% of N and P loading during winter (Post *et al.*, 1998). Generalizations have been deterred by the diversity of potentially important factors, including the abundance of contributing bird species, their seasonally varying foraging behaviour and time budgets, and the nutrient concentrations in different food types, as well as their seasonal and local variations. Therefore, we aimed to develop general yet robust models for the calculation of allochthonous nutrient inputs that are universally applicable for most temperate habitats, to almost all herbivorous waterbird species and across many spatial scales.

Earlier attempts to calculate the nutrient input of herbivorous waterbirds focused on specific local situations (Marion *et al.*, 1994; Gwiazda, 1996; Post *et al.*, 1998; adapted by Kitchell *et al.*, 1999; Olson *et al.*, 2005), and often relied on parameter estimates from very few and different species (Manny *et al.*, 1975, 1994; Marion *et al.*, 1994). Moreover, the proportion of nutrients entering a certain freshwater habitat (X_{ai} in our model) seemed very difficult to measure empirically and, consequently, was often roughly assumed (Table 4).

To overcome the species-specific and site-specific constraints we made the following generalizing assumptions, which are supported by empirical findings: first, herbivorous waterbirds are functionally and ecologically similar such that all are constrained by a fibre-rich, low energy food which governs digestion performance (Karasov, 1990). Secondly, their food requirement, and therefore digestive performance, scales allometrically with body size (Nagy *et al.*, 1999). Thirdly, birds follow a simple daily routine, with continuous foraging during daylight hours and spending the night on a freshwater roosting site; a typical situation during the winter season for most geese and swans (e.g. Ebbsing *et al.*, 1975; Rees, 2006).

Our dual approach, of IM and dropping model, allows application to a wide range of species, habitats and spatial scales because they can be parameterized

with a variety of published or measured data, either on diet composition or dropping composition. However, the quality of parameter estimates clearly determines the quality of model predictions. Model uncertainty in IM was smaller than in DM, rather caused by different model structures than by different inaccuracy in parameter estimates. As we have shown in the uncertainty analyses, outputs of both models essentially rely on food RTs as crucial parameter, of which empirical estimates varied greatly across species (Fig. 1a) and diet compositions (Karasov, 1990, see below). Hence, for a general improvement of model accuracy experimental and field measurements of RTs of different food are urgently needed.

Generally, DM predicted lower nutrient input than IM, especially for N. However, it is not clear if DM and IM under- or overestimate the real loadings; based on data of food composition IM should predict the maximum possible loading values. Such discrepancy between N input as predicted by intake or defaecation models is not restricted to herbivorous waterfowl, but also occurred in similar calculations for carnivorous birds (Hahn, Bauer & Klaassen, 2007). A potential explanation is the excretion of a certain portion of N in the form of ammonia (Tsahar *et al.*, 2005). DM predictions will underestimate total N deposition because ammonia will be lost before collection and/or if excrements are simply air- or oven-dried before N measurements.

Nutrient input will be further underestimated if birds make more than one return flight a day between foraging and roosting site. The magnitude of such underestimation would depend on the duration of the intermittent rest, and the RT and DrR of the bird. Short escapes of a few minutes caused by disturbance at feeding sites, e.g. in coots, have only a negligible effect on nutrient loading. Furthermore, the principal contributors for nutrient input are wintering geese. Their foraging on often distant terrestrial sites is mostly constrained by daylight, thus, justifying our assumption of a single daily foraging trip (Ebbsing *et al.*, 1975; Therkildsen & Madsen, 2000a). In contrast to our expectations, alterations in terrestrial diets were only of minor importance for nutrient input. Although switching from foliage to temporarily highly-preferred alternative food types like seeds or roots (Owen, 1976; Owen & Thomas, 1979; Amat, Garcia-Criado & Garcia-Ciudad, 1991) can almost double RTs (Karasov, 1990), the higher energy contents and AM

Table 4 Synopsis of published data on allochthonous nutrient input (X_{ai}) by herbivorous waterbirds

Species	X_{ai}						Reference
	BM (g)	Process	Method	Proportion (%)	N_{input}	P_{input}	
Lesser snow goose	2630	In	O, A	60*	1.89*	0.27*	Post <i>et al.</i> , 1998
Canada goose	2560	Df	O	No data	1.43–1.57	0.44–0.49	Manny <i>et al.</i> , 1975 Manny <i>et al.</i> , 1994 Manny <i>et al.</i> , 1994
Dabbling duck	1178	Df	A	No data	0.72	0.23	Moore <i>et al.</i> , 1998
Mallard	1080	Df	A	100	1.24	0.50	Scherer <i>et al.</i> , 1995
Mallard	1080	M	A	(100)	0.79	0.40	Andersen <i>et al.</i> , 2003 Marion <i>et al.</i> , 1994
Canada goose	3630	Df	A	50		0.61	Moore <i>et al.</i> , 1998
Canada goose	3630	Df	A	(50)		0.76	Scherer <i>et al.</i> , 1995
Mallard	1140	Df	O	(80)		0.38	Scherer <i>et al.</i> , 1995
American wigeon	750	Df	A	(50)		0.16	Scherer <i>et al.</i> , 1995
European wigeon	716	Df	A	<25		0.13	Klein, 1993

For earlier studies, the process considered to calculate X_{ai} is indicated with the following: Df, defaecation; In, intake; M, mixture of food intake and defaecation; the method to estimate the proportion X_{ai} from daily excretion and/or food intake are denoted with O, observations/measurements or A, assumptions. Proportion gives values of particular nutrient input compared to total daily nutrient release by a single specimen. Predictions of N and P input (g day^{-1}) from these studies are compared with results using our approaches (this study).

Data in brackets did not refer explicitly to the allochthonous origin of nutrients.

*Median values.

of these alternatives thereby reduce daily food requirements and, thus, counteract the effect of longer RTs (contrary to Post *et al.*, 1998).

Comparison of species-specific predictions of our models to earlier studies showed a high degree of similarity to the range of published data for local N input (Table 4), but an 'under-prediction' of the data for P. The latter difference probably resulted from the fact that the earlier studies assumed a much higher proportion (25–100%, Table 4) of the daily faeces production to be released on the roosts, while in our model this proportion ranged only between 12% and 26%. Our more conservative estimates are supported by empirical observations on wintering geese releasing 15–16% of their faeces at the roost (Ebbinge *et al.*, 1975; Manny *et al.*, 1994).

Model application – waterbird input in Dutch lakes and wetlands

Waterbirds in north-west Europe show a clear seasonal abundance pattern, with maximum numbers reached in mid-winter, followed by a steep decrease in spring as many species commence migration to their breeding grounds and a minimum in mid-summer. Not surprisingly, the temporal pattern in nutrient input paralleled this abundance pattern (Fig. 3). Yet, it was also affected by changes in feeding behaviour of resident breeding populations, which switched from terrestrial to freshwater habitats and from a herbivorous to an omnivorous diet (van den Wyngaert *et al.*, 2003, Table S1). Another factor exacerbating this pattern was the seasonal change in N content of foliage, which reached peak values in winter and spring and troughs in summer. Although the use of fertilizers in modern agricultural practice augmented protein and thus N content in foliages, and flattened the amplitude of seasonal fluctuations (e.g. Sedinger, 1997), N concentrations still reach a low during summer. If the birds feed in unfertilized habitats, such as Arctic tundra, allochthonous nutrient inputs will probably decrease, as indicated by 50% lower nutrient concentrations in goose faeces collected in the 1950s (20.7 mg N g⁻¹ and 4.4 mg P g⁻¹, Kear, 1963). Less important were also processes in the life-cycle of birds that entail changes in their physiology. Accumulation of body stores in preparation for spring migration and consequently, reduced defaecation, lowered nutrient input by only 0.22%. Molt might

be another activity with increased energy and/or nutrient demands and thus, decreased N and P excretion (Fox, Kahlert & Ettrup, 1998; Fox & Kahlert, 1999). However, molting waterbirds are flightless and therefore feed almost exclusively in safe wetlands and hence should not contribute to allochthonous loading.

Assessing the overall importance of waterbirds for the nutrient budget of a wetland highly depends on the size and depth of the wetland, its surrounding habitat and other nutrient emitters (Janse, 1997). Lakes that are not excessively used for roosting waterbirds contributed <1% to the total annual nutrient budget (Gwiazda, 1996; Schernewski, 2003). Even in lakes harbouring large breeding and wintering populations bird-mediated nutrient input was of minor importance (<3% N, <7% P) compared with import from the catchment (Marion *et al.*, 1994) or from wastewater treatment plants (Andersen *et al.*, 2003). However, massive concentrations of waterbirds at relatively small freshwater bodies can result in relatively high nutrient inputs, especially if the density of suitable resting habitat for waterbirds is low and other sources of allochthonous nutrients are small (Post *et al.*, 1998; Kitchell *et al.*, 1999).

In the case of the Netherlands, the bulk of the nutrients in surface waters originates from extensive farming; input from agricultural runoff and point emissions into Dutch lakes are estimated to range between 5 and 5000 kg N ha⁻¹ a⁻¹ and between 0.15 and 390 kg P ha⁻¹ a⁻¹ (van Puijenbroek, Janse & Knoop, 2004). Compared with such human-induced nutrient emissions, the estimated average nutrient input by herbivorous waterbirds of 0.74–1.40 kg N ha⁻¹ a⁻¹ and 0.09–0.10 kg P ha⁻¹ a⁻¹ seems to be of minor importance at a landscape scale. However, as waterbirds tend to aggregate local effects may be considerable especially if such concentrations persist over longer periods: recent nutrient loading of 13 Dutch lakes amounted to 35.5 kg N ha⁻¹ month⁻¹ and 0.625 kg P ha⁻¹ month⁻¹ (median annual nutrient load of 13 Dutch lakes from 1990 to 1996, averages were 2–2.8 times higher, Portielje & van der Molen, 1998). These monthly loadings would correspond to bird densities of 1885 (323) ducks ha⁻¹ month⁻¹ for N (P) or 800 (139) geese ha⁻¹ month⁻¹ for N (P) – densities that can be easily reached during peak times of migration.

Finally, the role of waterbirds for nutrient loading will depend on the topography of the freshwater

habitat, e.g. lake area and depth, sediment type as buffer, water retention, vicinity to other potential roosting habitats and period of time considered. Therefore, the proposed models provide useful, widely applicable tools to quantify the contribution of waterbirds within specific freshwater systems relative to other external sources (an interface for calculation of nutrient input by waterbirds is downloadable: <http://www.nioo.knaw.nl/CL/PDI/index.htm>).

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Supplementary material

The following supplementary material is available for this article:

Fig. S1 Basic model of feeding (solid line) and excretion pattern (dotted line) of waterbirds performing a single foraging trip per day.

Fig. S2 Uncertainty analyses of intake model (left) and dropping model (right) using Monte-Carlo simulations with parameter values drawn from normal distributions.

Table S1 Common species of herbivorous waterbirds that potentially act as vectors for allochthonous nutrient transport to waterbodies in the Netherlands.

Appendix S1. References of diet compositions (see Table 2).

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2427.2007.01881.x>

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