

APPLIED ISSUES

Estimating the contribution of carnivorous waterbirds to nutrient loading in freshwater habitats

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SUMMARY

1. We estimated nitrogen (N) and phosphorus (P) loading into wetlands by carnivorous waterbirds with alternative physiological models using a food-intake and an excretion-production approach. The models were applied for non-breeding and breeding Dutch inland carnivorous waterbird populations to quantify their contribution to nutrient loading on a landscape scale.
2. Model predictions based on food intake exceeded those based on excretion by 59–62% for N and by 2–36% for P, depending on dietary assumptions. Uncertainty analysis indicated that the intake model was most affected by errors in energy requirement, while the excretion model was dependent on faecal nutrient composition.
3. Per capita loading rate of non-breeders increased with body mass from 0.3–0.8 g N day⁻¹ and 0.15 g P day⁻¹ in little gulls *Larus minutus* to 4.5–11.5 g N day⁻¹ and 2.1–3.2 g P day⁻¹ in great cormorants *Phalacrocorax carbo*. For breeding birds, the estimated nutrient loading by a family unit over the entire breeding period ranged between 17.6–443.0 g N and 8.6 g P for little tern *Sterna albifrons* to 619.6–1755.6 g N and 316.2–498.1 g P for great cormorants.
4. We distinguished between external (i.e. importing) and internal (i.e. recycling) nutrient loading by carnivorous waterbirds. For the Netherlands, average external-loading estimates ranged between 38.1–91.5 tonnes N and 16.7–18.2 tonnes P per year, whilst internal-loading estimates ranged between 53.1–140.5 tonnes N and 25.2–39.2 tonnes P and per year. The average contribution of breeding birds was estimated to be 17% and 32% for external and internal loading respectively. Most important species were black-headed gull *Larus ridibundus* and mew gull *Larus canus* for external loading, and great cormorant and grey heron *Ardea cinerea* for internal loading.
5. On a landscape scale, loading by carnivorous waterbirds was of minor importance for freshwater habitats in the Netherlands with 0.26–0.65 kg N ha⁻¹ a⁻¹ and 0.12–0.16 kg P ha⁻¹ a⁻¹. However, on a local scale, breeding colonies may be responsible for significant P loading.

Keywords: eutrophication, faeces, nitrogen, phosphorus, waterfowl

Introduction

Waterbirds produce faeces rich in phosphorus (P) and nitrogen (N) and are therefore often considered as important nutrient loaders for freshwater habitats (e.g. Leentvaar, 1967; McColl & Burger, 1976; Hoyer &

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Canfield, 1994). Especially their local aggregations during communal roosting, over-wintering flocking (Post *et al.*, 1998) and colonial breeding (Hutchinson, 1950; Bildstein, Blood & Frederick, 1992) might result in substantial inputs of nutrients into aquatic habitats.

Nutrient loading by herbivorous waterbirds, which regularly forage at terrestrial sites and excrete at wetland sites during resting (Ebbinge, Canters & Drent, 1975; Manny, Johnson & Wetzel, 1994), has received considerable attention in the literature (e.g. Post *et al.*, 1998; Kitchell *et al.*, 1999). The impact of carnivorous waterbirds on nutrient loading is more difficult to determine, partly because of their highly diverse foraging behaviour. Piscivorous species like grebes (*Podicipididae*), diving ducks (*Aythiini*) and cormorants (*Phalacrocoracidae*) often forage and excrete within the same system, hence contributing to internal loading and a more rapid cycling of nutrients by making locally fixed nutrients available for primary production (Vanni, 2002). Other species like gulls (*Laridae*), regularly feed on distant, often terrestrial resources but defecate in wetlands during breeding and roosting (Gwiazda, 1996). Therefore, they are considered as external loaders, acting as vectors for allochthonous input of nutrients.

Generally, the diet of carnivorous waterbirds, though variable, is characterized by a higher digestibility, energetic value and protein content than the diet of herbivores (Karasov, 1990). Moreover, the high protein and therefore N content in animals is associated with higher P contents (Sturner & Elser, 2002), resulting in higher N and P excretion in carnivorous birds compared with herbivorous birds of similar size (e.g. Kear, 1963; Bruinderink, 1989; Marion *et al.*, 1994). Therefore, local nutrient and notably P loading by carnivorous waterbirds may exceed those by herbivorous waterbirds and account for up to half of the total P input in certain aquatic habitats (Portnoy, 1990; Bales *et al.*, 1993).

The population sizes of many carnivorous waterbird species have greatly increased in Europe over the last three decades, e.g. by more than 20% in at least two-thirds of all breeding populations of great cormorants *Phalacrocorax carbo* (L.) and grey herons *Ardea cinerea* L. (for European species reviewed in: BirdLife International, 2004), and they may therefore be suspected to substantially impact the nutrient dynamics of wetlands. However, estimates of nutrient loading by carnivorous waterbirds are lacking despite

their need in conservation and management actions. Therefore, we estimated nutrient loading by carnivorous waterbirds on inland freshwater habitats using a modelling approach based on species-specific food requirements and faecal production. We used data on waterbird populations in The Netherlands to exemplify the potential impact of carnivorous waterbirds at a regional scale targeting: (i) the quantification of nutrients added annually by external and internal loaders, (ii) the determination of the proportion of non-breeding and breeding birds on nutrient import, and (iii) the identification of the most important species contributing to nutrient loading.

Methods

In the modelling, we distinguished between breeding and non-breeding birds. For both groups, we calculated nutrient input using two approaches. First, we developed an intake model based on nutrient concentrations of ingested food, the birds' daily energy requirements and the assumption that birds are in steady-state with respect to the focal nutrient. In the second approach – the excretion model – we used nutrient concentrations in the daily excrement productions directly. Hereafter, we use X in our notations to denote the nutrient of interest, i.e. P or N. Dry mass is used in all compositional data on food and faeces and fresh mass is used when referring to the body mass of birds.

Nutrient loading models for non-breeding birds

The daily nutrient loading contributed by a non-breeding bird (X_{nb} , g day⁻¹) is the portion A of its total nutrient release, X_{total} , which is deposited into the water:

$$X_{nb} = A \times X_{total} \quad (1)$$

For the intake model, X_{total} results from the amount of food ingested (M_{intake} , g day⁻¹) and its nutrient composition (X_{intake} , mg g⁻¹). M_{intake} was derived from the allometric relationship for body mass (M , g) dependent daily energy requirement [DER = $10^{1.0195 \pm 0.039} \times M$ (g)^{0.6808 ± 0.018} kJ day⁻¹; Nagy, Girard & Brown, 1999], the gross energy content of food (E , kJ g⁻¹) and its apparent metabolizable energy coefficient (AM). The latter gives the proportion of

utilizable energy per unit food (Karasov, 1990). Hence the complete intake model is given with:

$$X_{\text{nb-intake}} = A \times \frac{\text{DER}}{E \times \text{AM}} \times X_{\text{intake}} \quad (2)$$

In the excretion model, X_{total} is a function of the total amount of excrements produced per day (M_{excr}) and its nutrient concentration (X_{excr} , mg g⁻¹). Assuming a fixed ratio α between food intake and excretion, total excrement production could thus be calculated as:

$$M_{\text{excr}} = \alpha \times \frac{\text{DER}}{E \times \text{AM}} \quad (3)$$

and consequently, $X_{\text{nb-excr}}$ as:

$$X_{\text{nb-excr}} = A \times \alpha \times \frac{\text{DER}}{E \times \text{AM}} \times X_{\text{excr}} \quad (4)$$

For carnivorous diets, Karasov (1990) reported values for E and AM of 23.9 ± 0.46 (SE) kJ g⁻¹ and 0.76 ± 0.013 (SE) respectively. For α we assumed a value of 0.395 ± 0.039 (SE) based on herring gulls *Larus argentatus* Pon. (Nixon & Oviatt, 1973), black-headed gulls *Larus ridibundus* L. (Dobrowolski, Kozakiewicz & Leznicka, 1993) and grey herons *Ardea cinerea* L. (Marion 1988 cited in Marion *et al.*, 1994).

The proportion (A) of excrements potentially entering freshwater habitat depends on a bird's foraging strategy. For internal loaders, which forage exclusively in aquatic habitats, we assumed $A = 1$. For external loaders, which mainly forage on allochthonous, terrestrial resources, we estimated A using data of defecation rates and dropping masses of black-headed gulls and herring gulls. Table 1 provides

details on the calculation methods resulting in an estimation of $A = 0.66$ and 0.55 for black-headed gull and herring gull, respectively, of which the average [0.60 ± 0.055 (SE)] was used in all subsequent calculations of X_{nb} .

Nutrient loading models for breeding birds

The calculations of nutrient loading of breeding birds were based on family units, i.e. parents and number of offspring, over the entire breeding period from onset of incubation until fledging. Its loading consists of the amounts excreted by adults (X_{adult}) and offspring ($X_{\text{offspring}}$).

For the adults within the family we assumed one adult was continuously present at the nest ($A = 1$), hence its nutrient loading was assumed to equal that of a non-breeding bird for the duration of the nesting period (T_{nest} days; Table 2):

$$X_{\text{adult}} = X_{\text{nb}} \times T_{\text{nest}} \quad (5)$$

Total nutrient loading of a successfully raised chick was similarly calculated as that for non-breeding adults (eqns 2 and 4), with total energy requirement over the entire chick rearing period ($\text{TER}_{\text{chick}}$) calculated according to Weathers (1992) $\text{TER}_{\text{chick}}$ (kJ) = $28.43 \times M^{1.062 \pm 0.037}$, where M is body mass of adult birds (g) and AM and E equal to the 'adult' values (see above). However, $X_{\text{offspring}}$ comprises the total nutrient deposition of chicks both reaching fledging and perishing during the growth period. To approximate this problem, we multiplied $\text{TER}_{\text{chick}}$ with the species-specific mean clutch size (CS, Table 2) and a correction factor β , which we tentatively set to 0.5. The

Table 1 Estimation of the proportion (A) of faeces entering freshwater habitats for external foraging black-headed gulls *Larus ridibundus* L. and herring gulls *Larus argentatus* Pon

	<i>L. ridibundus</i>	<i>L. argentatus</i>	Source
a. Body mass (g)	275	958	Glutz von Blotzheim, 1990; Cramp, 1998
b. Daily foraging duration (h)	12	12	Gwiazda, 1996
c. Defecation rate (h ⁻¹)	2.37	3.1	Portnoy, 1990; Gwiazda, 1996
d. Dropping mass (g)	0.22	0.53	Portnoy, 1990; Gwiazda, 1996
e. Excretion rate (g h ⁻¹)	0.52	1.64	c × d
f. Daily excretion (M_{excr} , g day ⁻¹)	10.41	24.36	eqn 3
g. Excretion duration (h)	20.0	14.9	f/e
h. Retention time (h)	5.3	5.3	Hilton <i>et al.</i> , 1999; Hilton, Furness & Houston, 2000
i. Loading (A)	0.66	0.55	$1 - (b - h) / g$

Table 2 Carnivorous waterbirds considered as external and internal nutrient loaders to inland wetlands in the Netherlands. The main diet composition has been categorized as vertebrates (vert) or invertebrates and vertebrates (mix). For breeding species, average egg mass, clutch size (number of eggs per nest), breeding success (number of fledglings per nest) and nesting period (i.e. from onset of incubation until fledging in days) are given. Species abundances are given as average numbers of non-breeding birds per season (July to June; in bird days) and mean number of breeding pairs per year, both counted from 2001 to 2004 (for data sources see Methods)

Species	Scientific name	Diet composition	Body mass (g)	Egg mass (g)	Clutch size	Breeding success	Nesting period (days)	# *10 ³ (bird days)	#Breeding pairs
<i>External loaders</i>									
Mediterranean gull	<i>Larus melanocephalus</i> Tem.	mix	273	42	2.8	0.6	54	11.7	462
Black-headed gull	<i>Larus ridibundus</i> L.	mix	275	33	2.5	1.0	51	23253.2	64029
Mew gull	<i>Larus canus</i> L.	mix	387	51	2.6	0.6	55	10935.7	1086
Lesser black-backed gull	<i>Larus fuscus</i> L.	mix	792	78	2.7	1.0	63	577.3	4790
Herring gull	<i>Larus argentatus</i> Pon.	mix	958	85	2.7	0.9	74	4081.6	2027
Little gull	<i>Larus minutus</i> Pal.	mix	99					15.8	
Yellow-legged gull	<i>Larus michahellis</i> Nau.	mix	1154					2.8	
Great black-backed gull	<i>Larus marinus</i> L.	vert	1600					332.4	
<i>Internal loaders</i>									
Little tern	<i>Sterna albifrons</i> Pal.	mix	50	10	2.9	1.0	40	4.6	103
Black tern	<i>Chlidonias niger</i> (L.)	mix	74	11	2.3	1.0	42	83.9	1200
Common tern	<i>Sterna hirundo</i> L.	vert	133	21	2.8	1.0	48	666.4	7724
Purple heron	<i>Ardea purpurea</i> L.	vert	933	50	4.2	2.1	75		491
Grey heron	<i>Ardea cinerea</i> L.	vert	1433	60	4.2	2.1	75	7194.3	11669
Great cormorant	<i>Phalacrocorax carbo</i> (L.)	vert	2254	58	3.5	1.3	72	942.7	17882
Arctic tern	<i>Sterna paradisaea</i> Pon.	vert	110					0.1	
Sandwich tern	<i>Sterna sandwicensis</i> Lath.	vert	237					1.0	
Little egret	<i>Egretta garzetta</i> (L.)	mix	530					7.6	
Great white egret	<i>Ardea alba</i> (L.)	vert	1200					47.0	

resulting values of $\beta \times \text{CS}$ exceeded values of breeding success, as the number of successfully fledged chicks per nest, by 38% (median, Table 2). Moreover, nutrient excretion of growing chicks was corrected for tissue synthesis by subtracting the total amount of N and P fixed in a chick's body (X_{syn}), assuming average nutrient contents of complete bird bodies of 2.82% N and 0.46% P fresh body mass (reviewed in Dierenfeld, Alcorn & Jacobsen, 2002). Body mass increase during chick growth was calculated as the difference between body mass at hatch, which corresponded to 72% fresh egg mass (Romanoff & Romanoff, 1949; Rahn & Ar, 1974), and adult body mass (Table 2).

Thus $X_{\text{offspring}}$ for the intake and excretion models was:

$$X_{\text{offspring-intake}} = \beta \times \text{CS} \times \left(\frac{\text{TER}_{\text{chick}}}{\text{AM} \times E} \times X_{\text{intake}} - X_{\text{syn}} \right) \quad (6)$$

$$X_{\text{offspring-excr}} = \beta \times \text{CS} \times \left(\alpha \times \frac{\text{TER}_{\text{chick}}}{\text{AM} \times E} \times X_{\text{excr}} - X_{\text{syn}} \right) \quad (7)$$

Model sensitivity and uncertainty analysis

We conducted a sensitivity analysis to determine the parameter(s) most influencing the model output. Therefore, all input parameters were successively varied by $\pm 10\%$ and then, changes in model output were related to the changes in the focal input parameter by calculating the sensitivity coefficient [$\text{SC} = (R_{-10\%} - R_{+10\%})/R / (P_{-10\%} - P_{+10\%})/P$ with R the model output and P the focal parameter, Hamby, 1994]. The sensitivity coefficient (SC) gives direction and magnitude of the resulting output changes: values of $|\text{SC}| > 1$ indicate disproportionately high changes and values of $\text{SC} = 0$ indicate no effect of the considered parameter on model output.

Moreover, as the empirical estimates of all parameters varied to different magnitudes, this raised the question of how these estimation uncertainties would impact the models' nutrient loading predictions. Therefore, we conducted Monte Carlo simulations for all species where all model parameter values were randomly varied assuming a normal distribution around the mean \pm SE (or $\pm 10\%$ if SE

was not available, i.e. T_{nest} , CS, X_{intake} of mixed food, and X_{syn}). To identify the most uncertain factor within each model, we additionally simulated nutrient loadings for black-headed gull (external loader) and great cormorant (internal loaders) by consecutively setting one parameter constant and varying the remaining parameters as stated above. For each model, we ran 30 000 simulations and compared model outputs, i.e. variation of predictions in nutrient loading, by calculating coefficients of variation (CV) using square root-transformed output data.

Composition of potential diet and faeces

We reviewed published data on nutrient content of dietary items as well as faeces of carnivorous and omnivorous birds focussing on species related to aquatic habitats. Potential food species were categorized as vertebrates and invertebrates (Table 3), and dietary origin of faeces was stated whenever information was available (Table 4). Due to similar N/P ratios in vertebrates and invertebrates from different habitats (Sterner & Elser, 2002), we calculated mean N and P composition for an average vertebrate and an average invertebrate diet.

Waterbird species

For the case of the Netherlands we categorized 18 carnivorous waterbirds as external and internal loaders according to their main foraging behaviour and habitat (Table 2). For external loading we considered eight species of gulls opportunistically foraging mainly in terrestrial habitats. For internal loading we considered aquatic-omnivorous or piscivorous species (five terns, four herons and the great cormorant).

For non-breeder abundances, we used monthly counts of waterbirds in the Netherlands from July 2001 to June 2004, excluding data from the coastal regions (Wadden Sea and Schelde Delta; van Roomen *et al.*, 2003, 2004, 2005) and excluding species with fewer than 100 individuals counted per year. For breeding population size, we used estimates for the Netherlands over the years 2002–2004, subtracting numbers of birds breeding in coastal regions and omitting species with less than 100 pairs counted (van Dijk *et al.*, 2005, 2006; Willems *et al.*, 2006; SOVON Vogelonderzoek Nederland unpublished data for 2002).

All information on feeding and roosting behaviour, body mass and reproductive performance were collated from Glutz von Blotzheim, 1990; Dunning, 1993; Platteeuw & van Eerden, 1995 and Cramp, 1998.

Table 3 N and P concentrations in potential food of carnivorous waterbirds. Food is categorized as vertebrate (vert) or invertebrate (invert) and habitats are categorized as terrestrial (terr), freshwater (fresh) or marine (mar) habitats

Food		Diet	Habitat	Nitrogen (mg g ⁻¹)	Phosphorus (mg g ⁻¹)	Sources
Bream	<i>Abramis brama</i> L.	vert	fresh	106.0	27.0	Penczak & Tatrai, 1985
Brown trout	<i>Salmo trutta</i> L.	vert	fresh	106.0		Elliott, 1976
Fish	20 species	vert	fresh	112.6	24.5	Tanner, Brazner & Brady, 2000
Fish	5 species	vert	fresh	102.0	22.1	Penczak & Tatrai, 1985
Fish	17 species	vert	fresh	97.0	33.1	Davis & Boyd, 1978
Fish	11 species	vert	fresh	100.4	37.5	Lawrence 1968 cit in Tanner <i>et al.</i> , 2000
Fish	3 species	vert	mar	105.6		Hilton <i>et al.</i> , 2000
Fish	2 species	vert	mar	103.2		Mizutani & Wada, 1988
Oligochaeta		invert	terr	93.5		Mizutani & Wada, 1988
Oligochaeta		invert	terr	95.4	8.4	Penczak & Tatrai, 1985
Diptera (larvae)	Insecta	invert	terr	91.3		Mizutani & Wada, 1988
Coleoptera (larvae)	Insecta	invert	terr	86.5		Klaassen, Kvist & Lindstrom, 2000
Gammaridae	Crustacea	invert	fresh	71.1	9.7	Penczak & Tatrai, 1985
Decapoda	Crustacea	invert	fresh		10.6	Nakashima & Leggett, 1980
Trichoptera (larvae)	Insecta	invert	fresh	78.1	6.3	Penczak & Tatrai, 1985
Odonata (larvae)	Insecta	invert	fresh	111.2	6.8	Penczak & Tatrai, 1985
Chironomidae (larvae)	Insecta	invert	fresh	81.2	12.8	Penczak & Tatrai, 1985
Chironomidae (larvae)	Insecta	invert	fresh		9.3	Nakashima & Leggett, 1980

Table 4 N and P concentrations in faeces (dry weight) of carnivorous/omnivorous birds foraging in different habitat types. Habitats are categorized as terrestrial (terr), freshwater (fresh) and/or marine (mar). The main diet compositions are also given

Species	Habitat	Diet	Nitrogen Phosphorus		Reference	
			(mg g ⁻¹)	(mg g ⁻¹)		
Red-winged blackbird	<i>Agelaius phoeniceus</i> (L.)	terr	Insect/plant	96.0	13.1	Hayes & Caslick, 1984
Thrush nightingale	<i>Luscinia luscinia</i> (L.)	terr	Insect	202.5		Klaassen <i>et al.</i> , 2000
Black-headed gull	<i>Larus ridibundus</i> L.	terr/fresh	Natural mix	72.4	78.6	Gwiazda, 1996
Grey heron	<i>Ardea cinerea</i> L.	fresh	Natural mix	42.1	114.7	Marion <i>et al.</i> , 1994
Great cormorant	<i>Phalacrocorax carbo</i> (L.)	fresh/mar	Fish	32.8	143.2	Marion <i>et al.</i> , 1994
White ibis	<i>Eudocinus albus</i> (L.)	fresh/mar	Crustacean	36.0	19.0	Bildstein <i>et al.</i> , 1992
		fresh/mar	Crustacean	54.0	19.0	Bildstein <i>et al.</i> , 1992
Chicken	<i>Gallus g. domesticus</i> (L.)	fresh/mar	Fish meal	154.2	65.9	Hutchinson, 1950
Herring gull	<i>Larus argentatus</i> Pon.	fresh/mar/terr	Natural mix	12.5	15.3	Portnoy, 1990
		fresh/mar/terr	Natural mix	18.4	23.3	Portnoy, 1990
		fresh/mar/terr	Natural mix	29.6	16.2	Marion <i>et al.</i> , 1994
Black-tailed gull	<i>Larus crassirostris</i> Vie.	fresh/mar/terr	Natural mix	152.0		Mizutani & Wada, 1988
Adelie penguin	<i>Pygoscelis adeliae</i> (Hom & Jac)	mar	Crustacean	116.0		Mizutani & Wada, 1988
Black noddy	<i>Anous minutus</i> Bo.	mar	Fish	182.5	37.5	Smith & Johnson, 1995
Macaroni penguin/ king penguin	<i>Aptenodytes patagonicus</i> (Mi.) <i>Eudyptes chrysolophus</i> (Bra.)	mar	Fish/crustacean	205.0		Lindeboom, 1984
Peruvian pelican	<i>Pelecanus thagus</i> Mo.	mar	Fish	241.3	20.9	Hutchinson, 1950

Results

Nutrient content of food and faeces

In the spectrum of potential food species, vertebrates had significantly higher N and P concentrations than invertebrates (for N: $t_{14} = 3.34$, $P = 0.005$; for P: $t_{10} = 7.71$, $P = 0.001$). The nutrient content of a pure vertebrate diet was 104 ± 1.6 mg N g⁻¹ (\pm SE used throughout unless otherwise noted) and 28.8 ± 2.8 mg P g⁻¹ (Table 3). For a mixed diet consisting of equal shares of vertebrates and invertebrates nutrient concentration was calculated to 96.3 ± 7.78 mg N g⁻¹ and 19.0 ± 9.86 mg P g⁻¹ respectively.

Published values for nutrient concentrations in faeces varied considerably; for N from 12.5 mg N g⁻¹ to 241.3 mg N g⁻¹ (mean: 103 ± 19.2 mg N g⁻¹, $n = 16$) and for P from 13.1 mg P g⁻¹ to 143 mg P g⁻¹ (mean: 47.2 ± 12.7 mg P g⁻¹, $n = 12$) (Table 4).

Model results

Generally, intake models predicted higher nutrient loadings than excretion models (Fig. 1). The difference between both modelling approaches averaged 62% in N and 36% in P for bird species feeding on vertebrates and 59% in N and 1.9% in P for bird species consuming a mixed diet of vertebrates and inverte-

brates. In the following sections, lower and higher values of nutrient input refer to excretion and intake model respectively.

In non-breeding birds, the daily per capita nutrient contribution by external loaders increased with body mass from 0.32–0.76 g N and 0.15 g P in little gull (body mass: 99 g) to 2.13–5.46 g N and 0.98–1.51 g P in great black-backed gull (body mass: 1600 g). Daily per capita input by internal loaders ranged from 0.34–0.80 g N and 0.15–0.16 g P (little tern, body mass: 50 g) to 4.49–11.49 g N and 2.06–3.18 g P per individual (great cormorant, body mass: 2254 g) (Fig. 1a,b).

Nutrient loading for a family unit during the breeding season ranged from 17.6–44.0 g N and 8.6–8.7 g P in little tern to 619.6–1755.6 g N and 316.2–498.1 g P in great cormorant (Fig. 1c,d), of which offspring contributed on average 37% (range 21–54%) to the total nutrient input of the family unit. Growth effects reduced the nutrient input of chicks for N by about 12% (intake model) to 28% (excretion model) and for P by about 10% (both models).

Model sensitivity and uncertainty analysis

Model sensitivity was similar in internal/external loaders and intake/excretion models, but differed between non-breeders and breeders. For non-breeding birds, changes in body mass had disproportionately

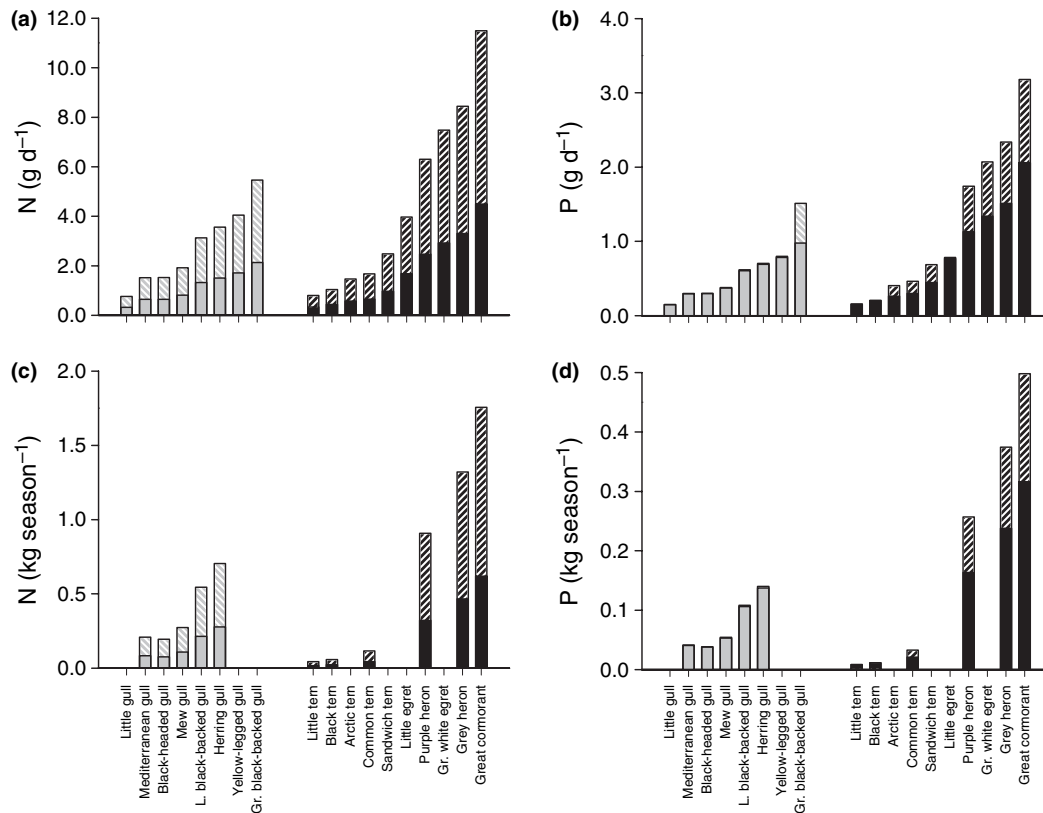


Fig. 1 Modelled external (grey bars) and internal (black bars) N and P loading by non-breeding (a & b) and breeding (c & d) carnivorous waterbirds. Loading is given as per capita rate for non-breeders and per family unit (parents and offspring) for breeders. Filled bars show nutrient loadings derived from the excretion models, dashed bars show the additional nutrient loading as predicted by the food models.

lower effects on model output ($SC = 0.68$), changes in E and AM affected model output inversely proportional (both $SC: -1.01$) and for all other parameters sensitivity coefficient was one and thus, changes in parameter values were directly reflected in model output values (positive proportional).

For breeding birds, sensitivity in intake and excretion models showed a similar pattern, with negative SC 's for E and AM in adults and offspring (range: -0.32 to -0.73) and positive SC for X_{intake} , M and DER in adults (range: 0.32 – 0.72) and X_{intake} , M , TER and offspring number ($\beta \times CS$) for chicks (range: 0.28 – 0.63). Synthesis effect (X_{syn}) was of minor negative importance (mean: -0.05). Generally, parameter sensitivity for adults decreased from little tern to cormorants, whereas for offspring the reversed pattern was found indicating a greater impact of offspring to nutrient loading in the bigger bird species.

The uncertainty in parameter estimates influenced model predictions, but according to model type,

nutrient and diet type. For non-breeders, excretion models showed similar CVs across bird species (for N: 0.11 , for P: 0.17), whereas CVs of intake models varied according to species, nutrient and diet. The CV for N increased with species-specific body mass from 0.12 to 0.25 , whereas the CV for P remained stable on a low level for a vertebrate diet (0.08 – 0.10) or on a high level under a mixed diet (0.27 – 0.28). For the breeding birds, the CV increased with species-specific body mass in all models (for N: 0.17 – 0.27 , for P: 0.11 – 0.32).

Considering blackheaded gull and cormorant as test species, the parameters causing most uncertainty in the excretion model were the proportion of nutrients in faeces X_{excr} , followed by daily energy-requirement estimations, DER and TER . If these were held constant, the CV was reduced by 33% for X_N and 44% for X_P . In DER and TER reduction of the CV amounted to 13% and 9% respectively. All other parameters caused less uncertainty in the output of the excretion models ($<6\%$).

Uncertainty in the intake models was primarily caused by the energy-requirement estimations in both the non-breeder and breeder model. If their variation was kept constant, models improved by 47% (DER for non-breeder) and by 11–25% (TER + DER in the breeder model). The second most important single parameter was X_{intake} , with a reduction in CV by 11% in both models. The remaining parameters did not affect model predictions substantially (<6% reduction in CV).

Case study – inland Dutch wetlands

Total predicted annual loading of both internal and external loaders for non-coastal Dutch wetlands ranged between 83.3–211.9 tonnes N and 39.3–52.1 tonnes P in 2001/02 and 98.8–250.7 tonnes N and 46.4–62.1 tonnes P between 2003 and 2004; 58% (excretion model) to 65% (intake model) were contributed by internal loaders (Table 5). Increased loading was attributed to the effects of non-breeding birds; the ratio of non-breeders to breeders increased from 1.7 to 2.3 and 4.3 to 5.1 for internal and external loaders respectively. Considering a total area of 3.57×10^5 ha of Dutch freshwater bodies (<http://statline.cbs.nl>), the average annual loading amounted to 0.26–0.65 kg N ha⁻¹ and to 0.12–0.16 kg P ha⁻¹.

Nutrient loading by non-breeding birds averaged 73% of the total loading but varied seasonally (Kolmogorov Z all $P < 0.01$), with peaks in January and March and dips in April and May (Fig. 2). This seasonal pattern in nutrient loading by non-breeding birds was mainly caused by the large seasonal fluctuation in external loading (CV = 0.77 compared to 0.31 for internal loading). Breeding birds contributed to nutrient loading from March to June with

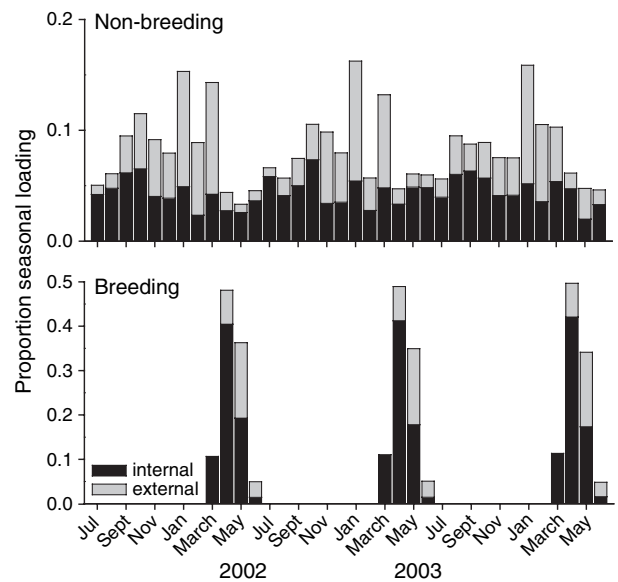


Fig. 2 Seasonal pattern of nutrient loading by non-breeding (upper panel) and breeding (lower panel) carnivorous waterbirds for non-coastal wetlands in the Netherlands from July 2001 until June 2004. Proportional loading per season (from July to June) is shown for internal (black bars) and external (grey bars) loading.

inputs from internal loaders peaking in April and from external loaders peaking in May (Fig. 2).

Non-breeding species causing most external loading were black-headed gull (47.5%), mew gull (28.2%) and herring gull (19.5%) (Fig. 3a). In breeding birds, black-headed gull (74%) and to a lesser extent black-backed gull (16%) were the most important external loaders. For internal loading two species, great cormorant (non-breeding: 89.6%, breeding: 65%) and grey heron (non-breeding: 8.6%, breeding: 32%) were of particular importance (Fig. 3b). All other species contributed less than 5% to the nutrient loading.

Discussion

Waterbirds may increase the cycling of nutrients within aquatic habitats but can also translocate nutrients among aquatic habitats as well as from terrestrial to aquatic habitats, thereby contributing to the internal and external loading. These processes result in enhanced nutrient concentrations, notably where waterbirds aggregate such as in breeding colonies and communal roosts. To date, direct measurements of bird-mediated nutrient cycling in aquatic

Table 5 Estimation of annual internal and external N and P loading by carnivorous waterbirds to inland wetlands in the Netherlands from July 2001 to June 2004. Both the lower (excretion models) and upper (intake models) estimations are given

Year	Nitrogen (tonnes)		Phosphorus (tonnes)	
	Internal	External	Internal	External
2001/02	46.8–124.5	36.4–87.4	22.3–34.8	16.9–17.4
2002/03	54.5–144.1	37.2–89.2	25.9–40.2	17.3–17.8
2003/04	57.9–152.8	40.8–97.9	27.4–42.6	18.9–19.5

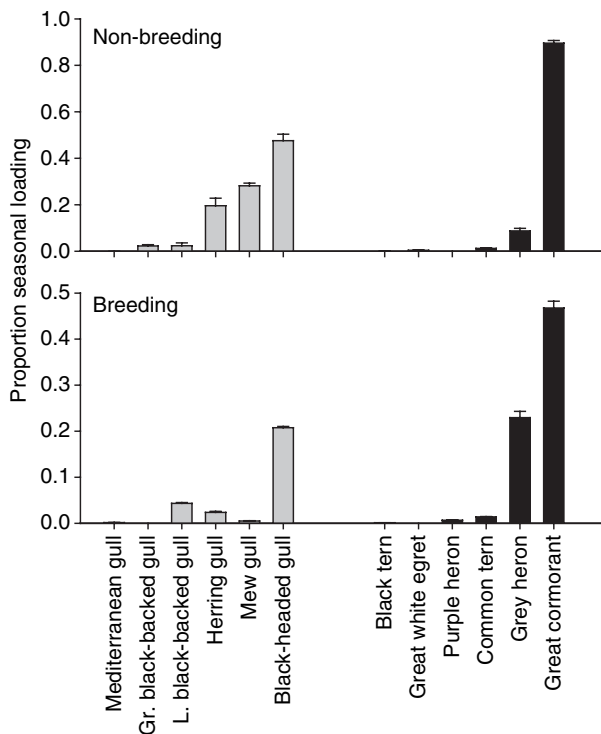


Fig. 3 Seasonal mean proportion (\pm SD) of the contribution of internal (black bars) and external (grey bars) nutrient loading into Dutch inland wetlands for both non-breeding (upper panel) and breeding (lower panel) birds. The mean seasonal proportion of each species has been calculated over the period July 2001 until June 2004.

ecosystems are lacking. Previous attempts to estimate nutrient loading by waterbirds have only employed indirect approaches, such as measurements of nutrient concentrations and primary production in focal wetlands (Leentvaar, 1967; McColl & Burger, 1976; Kitchell *et al.*, 1999), or model approaches based on local bird numbers in combination with assumptions on their metabolism (e.g. Ziemann, 1986; Marion *et al.*, 1994; Scherer *et al.*, 1995). These approaches clearly benefited from detailed knowledge of local conditions but were thereby limited in the generality of their findings. To allow generalizations and extrapolations to other species, areas and spatial scales, we developed a nutrient loading model based on simple foraging rules and literature data on energy requirements and faeces production of carnivorous and omnivorous waterbirds.

Based on the fundamental relationship of body mass and metabolic performance in birds, nutrient loading increased nonlinearly from little tern (as the

lightest species) to great cormorant (as the heaviest species). Because nutrient loading is a function of daily excretion, estimation of species-specific excrement production is crucial for all further calculations. We calculated daily excrement output from mass-faeces coefficients and reported dropping intervals in gulls (Table 1) yielding lower values than obtained in earlier studies, mainly because these assumed continuous 24 h defecation (e.g. Portnoy, 1990; Gwiazda, 1996). Hence, the shorter time at least gulls required to empty their digestive tract resulted in lower nutrient loading than previously assumed. In our models, we assumed adult birds to be in steady state with respect to N and P. However, in periods of production, e.g. moult or egg formation, nutrient requirements of birds may increase (Murphy, 1996), resulting in lowered daily nutrient excretions (e.g. Fox & Kahlert, 1999). However, N required for feather synthesis during a complete moult equalled approximately 1% of total body mass (after Turcek, 1966) and consequently should only marginally influence nutrient loading.

The excretion models generated much lower predictions for N loading than the food models. The question is whether the excretion model underestimates or the food model overestimates nutrient loading. Uncertainty analysis showed that predictions of the excretion model were highly dependent on the input values for excremental N concentration; these were also the values that varied the most in the published literature (Table 4). A comparison of the faeces-processing and N-extraction methods in these studies suggests that a greater part of them might have measured uric acid and urea but neglected ammonia. Although it is known for a few bird species only, ammonia can constitute 20–30% of total N excretion (Preest & Beuchat, 1997; Tsahar *et al.*, 2005) but will be lost before collection and/or if excrements are simply air- or oven-dried before N measurements. Due to ammonia-excretion, the food model might also slightly overestimate N loading because it assumes that 'all what goes in, will go out', which might overestimate nutrient (particularly N) loading if birds do not directly defecate into the freshwater or if a significant proportion of N is lost into the atmosphere by ammonia volatilization. Consequently, in our opinion, the food model therefore gives a reliable upper boundary or worst-case scenario estimate. Finally, the estimated proportion of faeces produced

by external loaders and imported into wetlands, α , has to be considered as a tentative estimate only; the estimation of α was based on two field studies only (Portnoy, 1990; Gwiazda, 1996). In carnivorous waterbirds food retention time is longer (Table 3) and daily excretion rate is lower (e.g. Gould & Fletcher, 1978) than in herbivorous waterbirds; moreover gulls frequently use aquatic sites for resting and comfort behaviour during the day. So, it is very likely that a higher proportion of their faeces (60% in our model) enter a focal wetland than in herbivorous waterbirds (<20%, Ebginge *et al.*, 1975; Manny, Wetzel & Johnson, 1975).

Case study: Dutch inland wetlands

When incorporating seasonal abundance of waterbirds at landscape scale our loading model suggests that carnivorous waterbirds are only of minor importance for N loading into Dutch freshwaters. The estimated total annual amount of 260–650 g N per hectare for both external and internal loaders is negligible compared to estimated N input from agriculture, precipitation and point emissions ranging between 5 and 5000 kg N ha⁻¹ a⁻¹ (van Puijenbroek, Janse & Knoop, 2004). Even similar estimates of allochthonous N input by herbivorous waterbirds (Hahn S. *et al.*, unpubl. data) exceeded external carnivorous loadings by 1.6–4 times.

However, a different picture appears for P loading. Phosphorus loading from agriculture and other external sources is estimated to be between 0.15 and 390 kg P ha⁻¹ a⁻¹ (van Puijenbroek *et al.*, 2004). Because the diet and faeces of carnivorous waterbirds contained a relatively high P concentration, and carnivorous and herbivorous waterbirds can use the same freshwater habitats, their joint P contribution may significantly affect the primary production of the often P-limited wetlands impacting wetland nutrient budgets at a landscape scale (Karl, 2000; Wassen *et al.*, 2005). On a local scale the effects may even be more dramatic and not only with respect to P but also N. We calculated that one-fourth of the annual loading is concentrated around breeding colonies, especially colonies of great cormorants and black-headed gulls. The fertilizing effect of such concentrations for a particular lake will clearly depend on lake size and depth, regular water mixing within the annual cycle as well as the magnitude of nutrient loading from other sources.

For instance, in shallow lakes with a euphotic zone down to the bottom an immediate response of phytoplankton is very likely. Besides such a direct and immediate impact on lake productivity, avian contributed nutrients may also enter the sediments and be released over longer time periods (McColl & Burger, 1976; Bales *et al.*, 1993). Additionally, colonies of waterbirds almost always persist over many years leading to an accumulating fertilizing effect and a potentially delayed effect of avian nutrient loadings (Hobara *et al.*, 2005; Ellis, Farina & Witman, 2006).

Our results showed that the loading effect of non-breeders was higher than that of breeding birds, amounting to 68% and 83% of the internal and external loading respectively. In extreme cases roosting gulls contribute up to 60% of total P input (Bales *et al.*, 1993). Non-breeding birds, being much less restrictive in their habitat choice than breeding birds, can use almost all larger waterbodies for resting and roosting, leading to a less aggregated pattern of nutrient release at a landscape scale than for breeding birds.

The most numerous carnivorous waterbird species, which profited from recent agricultural and urban developments, were also largely responsible for the external loading, especially black-headed gull and mew gull with their high affinity for pasture feeding habitats (e.g. Honza & Modry, 1994). For internal loading, both breeding and non-breeding great cormorants appeared to be of considerable importance. However, albeit qualified as internal loaders, these birds may be responsible for a considerable translocation of nutrients between freshwater bodies. Great cormorant populations have increased markedly over the last three decades; from 4470 to 23 325 breeding pairs in the Netherlands alone (van Eerden & Gregersen, 1995; van Dijk *et al.*, 2006). This has also resulted in a considerable lengthening of feeding trips, and distances of up to 30 km between feeding and breeding sites are not unusual (Platteeuw & van Eerden, 1995), often connecting different freshwater systems.

Our loading model verified the potentially significant role of carnivorous waterbirds for nutrient loading, in particular that of P. The model can easily be applied to a range of species and spatial scales. To improve model estimations, we suggest obtaining additional data of species-specific excretion performances and related nutrient composition of faeces in future empirical studies. Furthermore, such studies

should pay particular attention to phenology and long-term development of roosts of non-breeding birds. Hitherto, most attention has been paid to the nutrient loading by breeding birds, whereas our calculations also indicate the potentially important role of non-breeding birds.

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