Geese as vectors of nitrogen and phosphorus to freshwater systems

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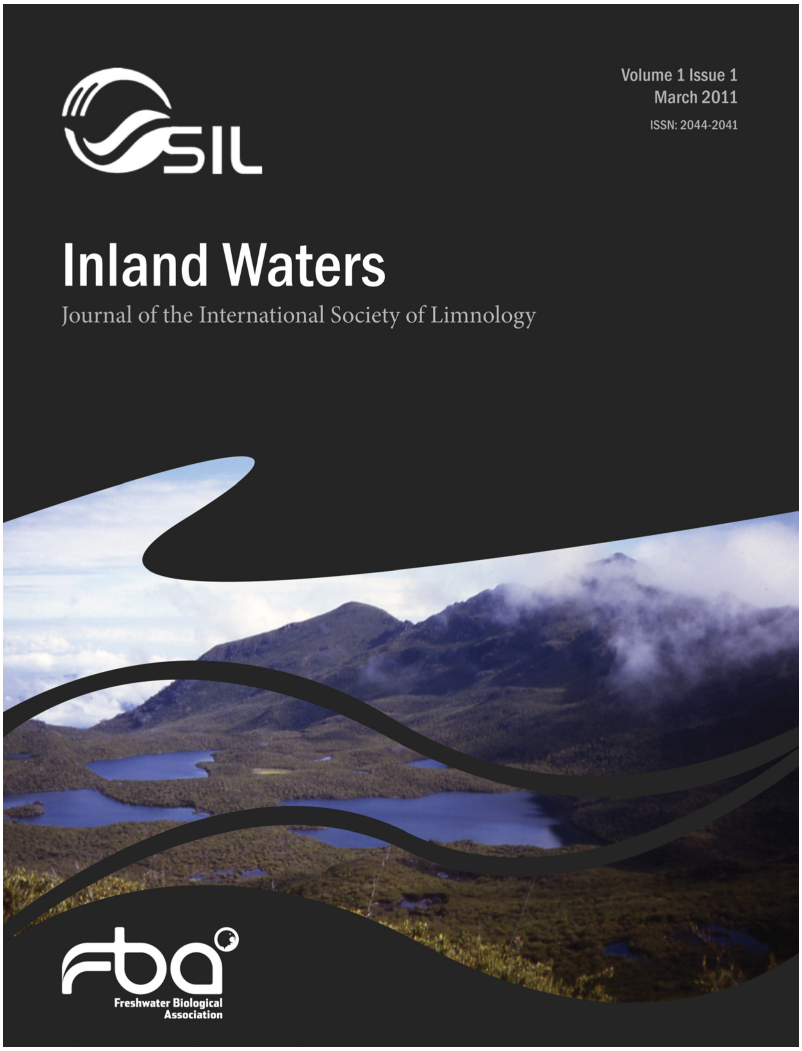
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Article

Geese as vectors of nitrogen and phosphorus to freshwater systems

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Abstract

Many goose populations have increased dramatically over the past decades, which may influence inland waters used as roost sites. We reviewed the role of geese in the influx of nitrogen and phosphorus to freshwater systems. Several methods have been used to estimate guanotrophication impacts of geese. Water and sediment analysis have been conducted in areas of high and low geese presence; however, productive wetlands tend to attract more birds, and the causality is therefore ambiguous. Faecal addition experiments have attempted to estimate the impacts of droppings on water chemistry, sediments, algal growth, or invertebrate densities. The most common method of estimating goose guanotrophication is by extrapolation, usually based on multiplication of faecal production and its nutrient content. Based on such studies and those including information about daily migration patterns, we developed an approach to improve estimates of the nutrient contribution of geese. The relative role of geese in wetland eutrophication is also affected by the influx from alternative sources. The greatest guanotrophication impacts are likely found in areas with few alternative nutrient sources and with large goose flocks. Limited inflow and outflow of a freshwater system or a scarcity of wetland roosts may also increase problems at a local scale. Although several studies have looked at the impacts of geese on, for example, water chemistry or soil sediments, the effects are often smaller than expected, in part because no study to date has assessed the ecosystem response by including impacts on all levels, including water nutrient levels, nutrient sedimentation, chlorophyll content, and zooplankton response.

Key words: *Anser*, *Branta*, *Chen*, eutrophication, goose, guanotrophication, nutrient

Introduction

Freshwater ecosystems are strongly affected by nutrient input, and many inland waters in agricultural areas have become eutrophied as a result of excess nutrient runoff. Many of these cultivated areas have also seen a sharp increase in goose populations, which roost on the wetlands and thus act as nutrient vectors.

Geese are large herbivorous waterfowl in the family Anatidae of the order Anseriformes (Clements et al. 2013). They occur on all continents, but many species in the genera *Anser*, *Branta*, and *Chen* disproportionately breed in arctic or temperate regions of the northern hemisphere and undertake long-distance migrations to lower latitudes in winter (Del Hoyo et al. 1992). Goose populations have displayed 2 striking trends in the northern hemisphere in recent decades. The first is a dramatic population increase in several species, notably pink-footed goose (*Anser brachyrhynchus*), barnacle goose (*Branta leucopsis*), and graylag goose (*Anser anser*) in Europe; snow goose (*Chen caerulescens*) in North America; and Canada goose (*Branta canadensis*) on both continents (e.g., Fox et al. 2010). The second trend, which has a longer history, is that wintering and staging geese have increasingly abandoned natural foraging habitats in favour of man-made crop land and lawns/parks (Jefferies et al. 2004). These processes have led to a sharp increase in the presence of geese in proximity to humans.

Faecal littering by geese can profoundly affect the terrestrial systems where they feed and nearby wetlands where they roost. Geese are potentially significant vectors of microbes, nutrients, and trace elements within each

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system from terrestrial to aquatic, especially in areas where large numbers of geese occur for an extended time. Although the impact of microbes and other contaminants from goose faeces on the health of humans, livestock, and wildlife has not been comprehensively reviewed, Mathis and Kevern (1975) showed goose faeces contained high levels of cadmium and lead, which they deduced contributed to contamination of aquatic systems. Nutrients in faeces can lead to algal blooms and reduce habitat quality for many animal groups (Havens 2008).

Defecation, grubbing, and trampling by feeding geese may increase nutrient turnover and outflow from terrestrial ecosystems. More importantly, staging and wintering geese generally return from foraging areas to a freshwater roost site at least once a day to rest, transporting nutrients from terrestrial to aquatic systems (Kitchell et al. 1999). Most studies of nutrient transport by geese have been conducted in areas where agriculture is the main land use and where many wetlands are already eutrophied (Fig. 1). In areas dominated by oligotrophic wetlands, however, waterbirds may add nutrients that are in short supply and may therefore be essential to maintaining primary production. Based on fossil diatom records, Linnman (1983) maintained that waterfowl may have caused seasonal eutrophication in otherwise nutrient-poor environments. Nutrients (Mallory et al. 2006) and bacterial production and diversity (Mindl et al. 2007) have also been shown to increase in nutrient-poor wetlands in the arctic when geese are present. These studies highlight the positive aspects of geese as nutrient vectors providing an ecosystem service (Green and Elmberg 2014).

Despite early concerns about the effects of waterfowl on wetland eutrophication, which predate the recent strong increase in goose populations (Kalbe 1982), the topic has not been comprehensively reviewed. The aim of this study

Fig. 1. Distribution of studies covered by this review.

Figure 1 is based on the following references: [1]Brandvold et al. 1976, [2]Chaichana et al. 2010, [3]Chaichana et al. 2011a, [4]Davies 1973, [5]Dessborn 2005, [6]Don and Donovan 2002, [7]Gremillion and Malone 1986, [8]Hahn et al. 2008, [9]Hallström et al. 2002, [10]Harris et al. 1981, [11]Huang and Isobe 2012, [12]Kear 1963, [13]Kitchell et al. 1999, [14]Lerner 2000, [15]Lerner 2006, [16]Lürling and van Oosterhout 2013, [17]Manny et al. 1994, [18]Manny et al. 1975, [19]Mindl et al. 2007, [20]Moore et al. 1998, [21]Olson et al. 2005, [22]Pettigrew et al. 1998, Özbay 2015, [24]Post et al. 1998, [25]Rip et al. 2006, [26]Rönicke et al. 2008, [27]Rutschke and Schiele 1978, 28Sanderson and Anderson 1981, 29Scherer et al. 1995, 30Tobiessen and Wheat 2000, [31]Unckless and Makarewicz 2007 [32]Van Geest et al. 2007, [33]Velander and Mocogni 2001, [34]Wambach and Mallin 2001.

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was to synthesize and evaluate previous research on the role of geese in the transfer of nitrogen (N) and phosphorus (P) to freshwater systems to provide a more useful algorithm for estimating nutrient flux by geese to wetlands. This algorithm is based on defecation rates, faecal weights, faecal N and P contents, and estimates of how much is likely to enter the roost wetland.

Methods

To review existing peer-reviewed literature, we searched the databases Natural Sciences Collection (http://search.proquest.com), Web of Science (https://apps.webofknowledge.com), and Google Scholar (https://scholar.google.com) using combinations of the search terms: goose, geese, *Anser*, *Branta*, *Chen*, eutrophic*, guanotrophic*, feces, faeces, dropping, nitrogen, and phosphorus. We also searched Google with the same search strings to cover some of the nonscientific literature as well as the domestic Swedish search engine Artikelsök. The last access date for these searches was 11 November 2015. Search outputs were scanned for relevant entries by looking at titles and abstracts. All papers thus found were examined for relevance, and reference lists in relevant articles were in turn examined for additional studies.

Previous studies on geese as possible nutrient vectors to freshwater ecosystems have been conducted in various ways. Many are not directly comparable, and therefore a synthesis of study type, geographical area, wetland status, and time of year was performed to obtain an overview of data availability and quality.

Studies on goose faeces in terrestrial systems were not included; however, many of these terrestrial studies served as a foundation for subsequent studies on eutrophication by geese in wetlands. In addition, our searches showed that many studies on the transfer of nutrients to aquatic systems were based on data on defecation rates, food passage, and faecal nutrient content from earlier studies, many of which did not look specifically at eutrophication, but at other aspects of goose digestion and ecology. For our review, we included the background information from these terrestrial studies, summarized the data, and compared goose species, diet, and time of year. Because the cited studies used as a basis for guanotrophication processes varied greatly in sample size, the value for each study was weighted by sample size according to the following formula to obtain a representative average value:

$$\text{Weighted mean: } \frac{\sum x_i n_i}{\sum n_i}, \tag{1}$$

where x_i is the average value of study i, and n_i is the sample size in study i.

For studies that did not provide sample size, we used the average sample size of the analysed studies. In other cases, sample size referred to various things (e.g., sampling events or droppings), which means these sample sizes were not comparable with those of other studies. In these cases, arithmetic means were used and studies were assigned the same weight. The statistical tests and equation estimates (Fig. 2; best fit) were carried out using Excel 2011.

Results

Distribution of goose nutrient flux studies

Although geese have a worldwide distribution, most studies relevant to this review were conducted in agricultural areas of Europe and North America (Fig. 1). The focus on these locations may be partly due to accessibility, but because they are also where geese naturally congregate in large flocks during staging, wintering, and migration, they coincide with much of the human–goose-related conflict. Of the studies in our review, 14 of 32 were conducted in agricultural areas. Other land uses or biotopes included urban areas (6 papers), agricultural/forest mixes (4), arid grasslands (4), forest (1), tundra (1), and glacial valley (1). Almost all studied waterbodies were eutrophied lakes of various sizes (17). Oligotrophic lakes (2) and other wetland types (4) are underrepresented in the research. Studies are fairly evenly distributed among seasons (Table 1). The majority of studies assessed impacts of mixed waterfowl communities (15 papers); however, studies that did not specifically mention geese were excluded from our review (Table 2).

Among the various methods used to measure or estimate nutrient input by geese on a wetland (Table 1), the most common was to count the number of birds and extrapolate using data on defecation rates and faecal nutrient content. Our review reveals that many of the nutrient flux studies were based solely on bird counts and did not include original data on defecation rates or faecal content, but instead made extrapolations based on one or several previous studies. The studies chosen as reference for extrapolation were not always the most relevant or recent (e.g., Terres 1987). More problematic still, in several assessments, other waterbird species or domestic geese were used as a reference for extrapolation instead of the species under study (e.g., Sanderson and Anderson 1981). We concluded that for this reason alone, some previous studies had limited value in this review and were excluded from the synthesis; they are, however, included in the summary of studies (Table 1) and were used in the estimates that follow.

Table 1. Studies investigating nutrient contribution by geese to inland waters. The authors used different methods to estimate impacts (left column). See Fig. 1 for reference code.

	Wetland trophic status		**Season**				
Study type	**Eutrophic/ hypertrophic**	**Oligotrophic**	**Spring**	**Summer**	**Autumn**	**Winter**	**Total**
Bird counts	2, 5, 7, 15, 16, 17, 18, 20, 25, 29, 30, 34		2, 5, 6, 8, 10, 14, 15, 17, 18, 20, 21, 24, 25, 28, 29, 30, 34	2, 5, 6, 7, 8, 10, 17, 18, 20, 25, 29, 30, 34	2, 5, 6, 10, 14, 15, 17, 18, 20, 24, 29, 30, 34	2, 5, 6, 8, 10, 11, 13, 15, 16, 17, 18, 24, 25, 28, 29, 30, 34	**22**
Faecal production	14, 18, 27		12, 14		27	18	**4**
Faecal density survey	5, 26	32	5	5, 32	5	5, 26	**3**
Faecal nutrient analysis	5, 9, 14, 15, 16, 17, 18, 26, 27		5, 12, 14	5, 30, 31, 32	5, 27	5, 9, 12, 15, 16, 18, 26	**12**
Water quality analysis	2, 3, 7, 16, 25, 26, 29, 30, 34		2, 3, 4, 16, u 25, 26, 29, 30, 33	2, 3, 7, 10, 16, 21, 25, 26, 29, 30, 33	1, 2, 3, 4, 10, 16, 29, 30, 33	1, 2, 3, 4, 13, 16, 25, 26, 29, 30, 33	**16**
Sediment analysis	3		30		1, 4	1, 4, 16	**4**
Analysis of aquatic organisms						13	**2**
Faecal addition experiments	9	19		2, 19, 30, 31		9	**4**
Bioenergetics model estimates			8, 24	8	24	8, 13: 24	**3**
Dropping rate model estimates			8	8		8	**1**
Isotope analysis						13	**1**
Total	**17**	**2**	**23**	**28**	**29**	**24**	

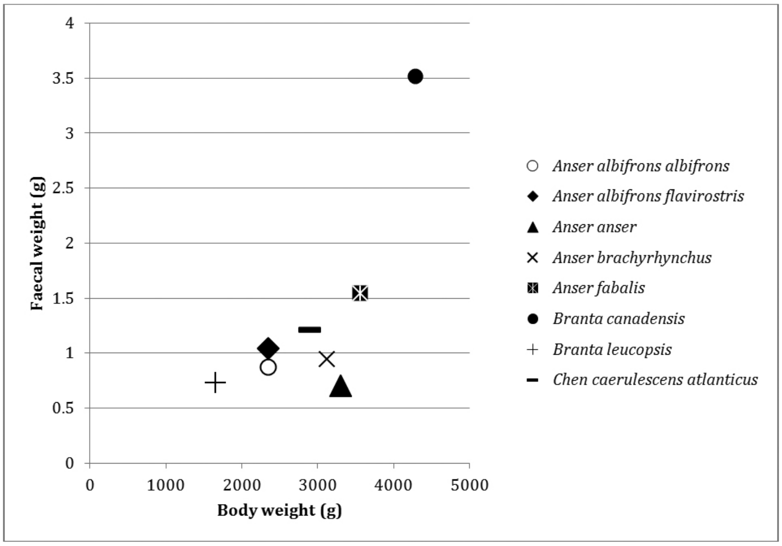

Fig. 2. Dropping size (g dry weight) based on weighted means in relation to body weight (g) in 8 goose species ($y = 0.2758e^{0.0005x}$, $R^2 = 0.5773$; Helm 1951, Kear 1963, Ebbinge et al. 1975, Manny et al. 1975, Owen 1975, Madsen 1985, Paterson 1987, Bédard and Gauthier 1989, Manny et al. 1994, Fox and Kahlert 1999, Lerner 2000, Therkildsen and Madsen 2000). Bird weights are based on values in Del Hoyo et al. (1992).

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Table 2. Number of studies of nutrient contribution by geese to inland waters, by species and continent. Numbers in parentheses refer to studies on domestic geese.

	North America	Europe	Australasia
Anser albifrons	0	3	1
Anser anser (domestic goose)	(1)	6	(1)
Anser brachyrhynchus	0	2	0
Anser fabalis	0	5	1
Branta canadensis	9	6	1
Branta leucopsis	0	4	0
Chen caerulescens	2	0	0
Chen rossii	1	0	0

Uncertainties in nutrient fluxes from geese to inland waters

Faecal contribution to roost

Accurate estimates of faecal production of geese should consider (1) time spent at the roost, (2) maximum contribution of droppings during a stay at the roost, (3) goose species (especially body size), and (4) defecation rate. The defecation rate, in turn, depends on diet, time of year, and important life-history events.

Geese generally have separate feeding and roost sites. Feeding sites are often freshwater wetlands to which they return in predictable daily migrations that may change between seasons. Andrikovics et al. (1982) estimated that graylag geese spent 38% of the time in the water during the nonbreeding season but only 8% during the breeding season. During the summer and fall, many geese make 2 trips to the roost in a day, in midday as well as in the evening (e.g., Post et al. 1998, Kitchell et al. 1999), but as winter days get shorter in the northern part of the range, only one feeding trip is made, and geese often stay on the feeding grounds throughout the day (e.g., Kitchell et al. 1999, Therkildsen and Madsen 2000). The number of daily feeding trips from a roost can also be affected by weather; low temperatures and strong winds both tend to reduce feeding mobility (Post et al. 1998). Feeding cycles may also be strongly influenced by the lunar cycle; geese are capable of feeding almost exclusively at night and resting during the day (Ebbinge et al. 1975), which might also influence the number observed or actual daily trips and, in turn, the estimated faecal transport by geese to the roost. The potential contribution to a roost wetland will also depend on the amount of time that geese spend feeding. In a time budget study by Therkildsen and Madsen (2000), pink-footed geese spent more time feeding while on pastures than on winter wheat. The feeding time can also be influenced by other factors such as disturbance or day length (Post et al. 1998).

The contribution of goose faeces on the roost site can be assessed several ways, most based on estimates of dropping rates or intestinal passage times. Documented defecation rates are often based on observations of individual birds, which can be achieved by various methods such as feeding caged wild birds selected food items (Rutschke and Schiele 1978), observing individual birds in the wild, or recording faecal density after a flock of counted geese have been on a site for a given period of time (Manny et al. 1975, 1994, Rönicke et al. 2008). The wide variation observed in defecation rate (Table 3) is partly due to nutrient and cellulose contents of the food; as the fibre content increases throughout the summer, more droppings are produced (Table 3). Events in the annual cycle of geese may also strongly influence digestion and therefore defecation rate, independent of the quality of food. Fox and Kahlert (1999) found that graylag geese feeding on *Puccinellia maritima* had 455 s (7 min 35 s) between droppings prior to moult, which changed to an average of 985 s (16 min 25 s) during moult. Similarly, increased passage times are observed during incubation (Prop and Vulink 1992).

Estimating the amount of faeces deposited on the roost site requires knowing the time needed for food to pass the bird's alimentary system. Roost sites often have piles containing 10–12 droppings, subsequently estimated as the number required to empty the alimentary canal (Ebbinge et al. 1975, Dessborn 2005), assuming individual geese settle and remain in one place once they get to an overnight roost, which is unlikely. Another way to estimate roost site load is by counting the faeces left by a known number of geese. This method led Ebbinge et al. (1975) to conclude that, on average, 24.4 droppings per individual were produced during the night by resting barnacle geese, an estimate supported by the largest pile found at the study site consisting of 25 droppings. In comparison, geese in captivity had an elevated production during their resting phase (33 droppings; Ebbinge et al.

Table 3. Time between droppings in geese (in seconds), expressed as weighted means, which considers the sample size of the included studies. Because the values are based on weighted means, no standard deviation could be calculated. Summer is not included due to important life-history events (such as incubation and moult) that influence digestion, leading to wide variations among studies. The table is based on data from Kear 1963, Ebbinge et al. 1975, Ydenberg and Prins 1981, Madsen 1985, Bédard and Gauthier 1986, Bédard and Gauthier 1989, Bazely et al. 1991, Paterson 1991, Prop and Vulink 1992, Lerner 2000, Therkildsen and Madsen 2000.

	Spring (sec)	Staging and wintering (sec)
Natural vegetation	253	244
Pasture and improved grasslands	466	232
Agricultural crops	509	274

1975). These findings clearly indicate that estimating the faecal production based on the average pile size (10–12) will underestimate the contribution to the roost wetlands.

Another way to estimate the contribution of faeces to a roost site is to estimate faecal passage time. Using dye or food items as markers, passage time was 9910 s ± 1400 (1 h 24 min, n = 10 studies including Cape Barren goose, graylag goose, barnacle goose, red-breasted goose, lesser snow goose, and Canada goose; Marriott and Forbes 1970, Mattocks 1971, Owen 1975, Burton et al. 1979, McWilliams 1999). Initial passage time, or the time to produce the first dropping after initiating feeding, has been analysed in several studies but is not relevant for estimating the contribution to the roost because the time needed to fill the gut is less important than the time needed to empty it. These data are, however, the best available information for passage times. When geese fed on natural and pasture vegetation, the initial passage time was 3155 ± 249.5 s (52 min ± 4 min SE; n = 6; Mattocks 1971, Ebbinge et al. 1975, Burton et al. 1979, Madsen 1985), but when the geese fed on agricultural crops, the passage time was significantly longer at 7640 ± 1174.8 s (127 min ± 20 min SE; n = 6; *t*-test: $p = 0.012$; Mattocks 1971, Prop and Vulink 1992).

Yet another method to calculate faecal passage time is based on the length of the digestive tract, the length of droppings, and the time lapse between defecations (Prop and Vulink 1992, Lerner 2000). Digestive tract length naturally varies among goose species for allometric reasons but may also vary within species between seasons. For example, in spring the intestines may become shorter during times of fat build-up, as suggested by Prop and Vulink (1992). The easiest way to estimate roost dropping load, however, is probably by using the estimates of Ebbinge et al. (1975) of 24 droppings per goose, particularly for lengthy stays at the roost when geese are likely to empty their alimentary canal before leaving.

Faecal production is a result of defecation rate and faecal size. We found no significant correlation between body size and defecation rate in the investigated dataset ($R^2 = 0.08$, Pearson's $r = 0.28$, $p = 0.59$, n = 6 species; body weights from Del Hoyo et al. 1992). Larger birds produce larger droppings (Fig. 2), however, meaning that larger geese species are likely to contribute more faecal material to an aquatic system.

Faecal nutrient content

Fourteen of the reviewed studies conducted a nutrient analysis of faeces, but because many used different laboratory analyses methods, the results are not readily comparable. For N, Kjeldahl total nitrogen (TN) was the most commonly used measure (Table 4); however, uric acid, organic N, urea, ammonia, and other N compounds have also been studied. Similarly, total P (TP; Table 4) was most commonly used for measuring P, but some studies measured phosphate, soluble reactive P, or orthophosphate instead. Again, because these inconsistencies hamper comparison among studies, we limited our synthesis to those that measured TN and TP. Kear (1963) observed that the nutrient content of goose diet closely reflected that of the faeces. In other words, faeces produced after feeding on a nutrient-enriched field where P fertilizer had been applied contained more P than faeces produced after feeding on land with plants with low P levels. The role of fertilizer is not clear in the present synthesis, however, because the values of P and N are not greater in droppings from agricultural crops than from natural vegetation, but rather the opposite. The vegetation type did not seem to impact the amount of N in the faeces, but the interaction between vegetation and time of year was marginally different ($F_{6,39} = 2.4$, $p < 0.5$), as was the time of year ($F_{3,39} = 3.5$, $p < 0.5$); however, when 4 spring outliers were removed (2 from natural vegetation, 1 from grass, and 1 from crops), no statistical significance could be detected.

Water flow and sediment analysis

Chemical analyses of nutrient influx caused by geese can either directly indicate the input by measuring the nutrient content of faeces or indirectly by measuring the nutrient content in water or sediment of wetlands where geese have been. In indirect measurements, impact can be estimated by comparing (1) the available nutrients between 2 sites in similar watersheds but with varying

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Table 4. Averages of total nitrogen (TN) and total phosphorus (TP) measured as a % of dry weight. Nitrogen is given as averages, weighted by sample size, which means that no standard deviation can be given. For P, the sample size was not consistently documented in the different studies and therefore standard averages (not weighted) are presented. Standard deviation is included for P values (Bazely and Jefferies 1985, Dessborn 2005, Fox and Kahlert 1999, Helm 1951, Kear 1963, Lerner 2000, 2006, Rutschke and Schiele 1978).

	Spring		Summer		Autumn		Winter	
Vegetation	TN	TP	TN	TP	TN	TP	TN	TP
Natural vegetation	2.76	0.50*	1.99	—	—	—	5.87*	—
Grass	2.87	0.57 ± 0.21	2.45	0.51 ± 0.07	2.70*	0.43 ± 0.04	2.17	0.56 ± 0,04
Agricultural crops	2.13	0.43*	—	—	2.04	1.02 ± 1.06	1.71	—

* Only one study

degrees of waterfowl use (e.g., Brandvold et al. 1976), (2) the nutrient levels in inflow versus outflow of a wetland frequented by geese (e.g., Olson et al. 2005), or (3) nutrient levels over time as bird numbers change, either over several years (e.g., Tobiessen and Wheat 2000) or seasonally (e.g., Davies 1973, Scherer et al. 1995). These 3 types of studies may illustrate a correlation between elevated nutrient levels and goose utilization but do not necessarily demonstrate a causal link. One way to elucidate the origins of nutrients is by isotope analysis. Kitchell et al. (1999) was the only study found that investigated stable isotopes in relation to N contribution in geese. Goose faeces had low levels of $\delta^{15}N$ compared to the background levels; thus, a comparison between inflow and outflow in the studied system provided strong evidence of goose N contribution to the system.

Faecal addition experiments

Another way to estimate the impact of faecal nutrients is by experimentally adding faeces to observe the response in the ecosystem. Effects of faecal additions can be estimated by measuring (1) soluble N and P (Unckless and Makarewicz 2007), (2) response in chlorophyll content (Hallström et al. 2002), or (3) change in zooplankton densities (Pettigrew et al. 1998).

Most studies show a limited response to addition of faeces (e.g., Unckless and Makarewicz 2007), and the strongest response was found in nutrient-poor habitats fed by glacial runoff (Mindl et al. 2007). The limited observable effect in some of the studies was hypothesized by Davies (1973) to be due to a tendency for the nutrients in bird faeces to sink to the bottom as sediments, which has also been confirmed in experiments by Unckless and Makarewicz (2007). Another reason for limited response in measureable water nutrients or chlorophyll levels may be a rapid increase in zooplankton and other grazers such as *Daphnia*, in other words a strong top-down effect (Pettigrew et al. 1998, Van Geest et al. 2007). No study to date has investigated the effects of faecal additions on the ecosystem as a whole (measuring nutrients in water and sediments, chlorophyll levels, and invertebrates). Such a study is critical to better understand the role of geese and other waterbirds in wetland eutrophication.

Energetics and defecation models

Three studies (Table 1) used models to estimate nutrient contribution by geese and other waterbirds. Hahn et al. (2008) developed 2 models: an intake model that assumes birds excrete as much N and P as they consume, and a dropping model that includes estimated faecal production and nutrient content. Post et al. (1998) used models based on bioenergetics, which are dependent on bird weight and daily temperature. These studies extrapolated faecal production by adjusting for the bird's body size; however, this method does not always take into account that different diets pass through the gut at different rates and contain different amounts of nutrients. Bédard and Gauthier (1989) found that geese feeding on grass defecated twice as often as geese feeding on grain, and Kear (1963) found that the nutrients in the diet tend to reflect that of the food source. The strong influence on metabolism and nutrient absorption by energy-demanding annual events such as incubation and moult (Fox and Kahlert 1999) is also often ignored in such models.

The energetics model developed by Post et al. (1998) and later used by Kitchell et al. (1999) is based on energy requirements extrapolated across taxa. Similarly, the model developed by Hahn et al. (2008) made assumptions about digestive performance across avian taxa, and the relative contribution of nutrients was calculated for different species adjusting for size and energy requirement; however, this did not take into account the differences in feeding ecology and important life history events of species included in the model. Hahn et al. (2008) also developed a defecation model based on digestive performance, faecal production, and nutrient concentrations.

These models can provide tools for estimating nutrient contribution by geese. We developed a similar, easy to use tool based on the reviewed literature.

A suggested protocol for estimating nutrient contribution by geese to wetlands

The following extrapolation can be a useful tool for managers because it synthesizes the available data and can be used to estimate the maximum number of geese a wetland can hold until the nutrient load becomes unacceptably high.

For this analysis we use a hypothetical wetland with a flock of 10 000 autumn-staging geese, 40% Ross’s and 60% Canada geese, feeding on crops in a nearby field. There is no significant difference between defecation rates of goose species, but the faecal weight differs between species; therefore, we calculated an average faecal weight for our flock. Canada goose droppings weigh on average 3.5 g (dry weight), but because no average value for Ross’s goose droppings was available, we used the exponential estimates for the curve (Fig 2). Assuming that a Ross’s goose weighs on average 1429 g (Del Hoyo et al. 1992), the average dropping dry weight can be estimated to be ~0.56 g ($y = 0.2758e^{0.0005x}$). The average dropping weight in the flock as a whole was therefore 3.5 g × 0.6 + 0.56 g × 0.4 = 2.3 g.

Our imaginary flock of geese was observed to return to the roost during midday and in the evenings and stay there the entire night. During night, the total number of droppings was 24.4 per individual goose based on the study by Ebbinge et al. (1975), which equates to 2.3 g × 24.4 droppings/night = 56 g/night. The midday roost visit lasts for ~1.5 h. The average passage time for natural vegetation and pasture is 52 min but is considerably longer for crops (127 min). We can therefore assume that the geese will continue to produce faeces during their midday stay at the roost. The time between droppings in our case was on average 232 s (3 min 52 s; Table 3) over the duration of the midday stay (90 min), meaning that 23 droppings at 2.3 g average weight will be produced, totalling 53 g per individual. Accordingly, the midday and overnight stays together will generate 109 g per individual per day. Our flock of 10 000 birds will therefore produce 1090 kg of faeces in 1 day. The TN and TP contents will be on average 2.0% (N) and 1.0% (P), respectively (Table 4). Specifically, the daily nutrient input to the wetland in this example would be 22 kg of N and 11 kg of P.

Synthesis

Are geese important vectors of nutrients to freshwater systems?

The relative impact of geese for a wetland’s nutrient status relies on estimates and assumptions about alternative sources, which are often site-specific and difficult to measure. The most important factors that influence nutrient influx to inland waters is usually land use (Fig. 3). Geese are most likely to contribute significantly to nutrients of waterbodies with limited alternative input sources, including limited surface runoff (e.g., 73% of P and 64% of N; Chaichana et al. 2010) or where the water input is from nutrient-poor sources such as groundwater, direct rainwater, or glacial runoff. The export of nutrients from a system is also important when assessing the overall impact of geese as nutrient vectors. Lakes or other aquatic systems that lack outflow are more likely to show a strong eutrophication response to geese (Harris et al. 1981). The importance of geese as a vectors of nutrients will also vary seasonally or annually, particularly in arid or semi-arid areas where allochthonous input correlates to seasonal rainfall. In a study by Moore et al. (1998), the watershed supplied ~18 times more P than did geese during average rainfall, but during drought, the P from geese exceeded the watershed’s contribution by 7 times. The contribution of birds may also be exacerbated in arid areas where a crowding effect occurs in wetlands that remain during drought (75% of P and 40% of N; Post et al. (1998).

Several of the reviewed extrapolation studies were conducted in agricultural areas where the contribution by geese is insignificant compared to other sources (<5%; Lerner 2000, Don and Donovan 2002, Dessborn 2005); however, geese may still contribute significantly when they aggregate in large densities or when smaller flocks aggregate on few or small wetlands (Manny et al. 1975, Hahn et al. 2008). Rönicke et al. (2008) estimated high relative P contributions from birds (88–92% of the allochthonous annual load), but because the lake was already eutrophied, the annual contribution by birds was only ~10% of existing nutrient pools. Hallström et al. (2002) estimated the amount of P from agriculture to be equivalent to 90–270 geese staying for 4 months, whereas the local sewage plant only represented about 3–9 geese staying for 4 months. The effects of geese in relation to urban settlement and sewage plants will vary by wastewater treatment regulations and technical advancements, but an estimate based on a reviewed literature was presented by Beaulac and Reckhow (1982; Fig 3). In urban wetlands, the relative contribution by geese seems

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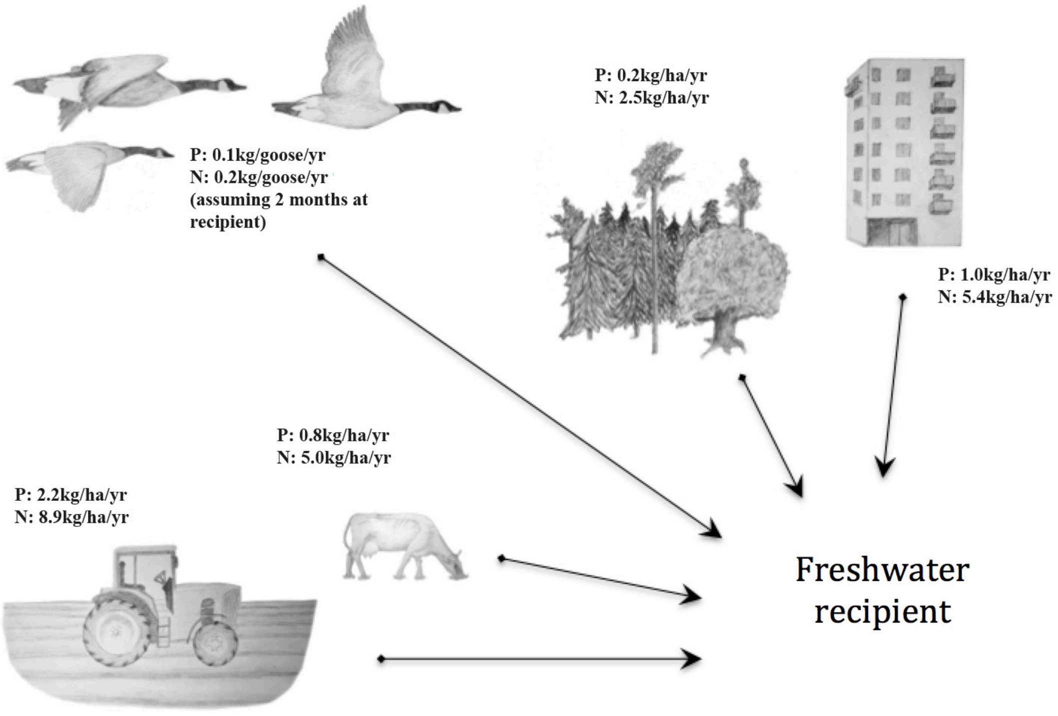

Fig. 3. A conceptual diagram illustrating alternative sources of P and N to a freshwater recipient. The estimate of goose contribution is based on the suggested protocol in this manuscript, based on the following assumptions: (1) the goose species is Canada goose that visits the roost twice a day (at night and for 90 min during the day); and (2) the geese use the roost for 2 months per year. The other nutrient estimates are based on a review by Beaulac and Reckhow (1982). The areal units refer to terrestrial areas in the catchment.

to be slightly larger than in agricultural areas (7–8% of the annual P; Gremillion and Malone 1986), possibly because soil runoff is limited and waterbodies and watersheds are generally smaller.

By measuring nutrient levels in inflow and outflow of a wetland frequented by geese, Davies (1973) and Velander and Mocogni (2001) found elevated nutrient levels and concluded they were at least partly due to goose input to the wetland. Olson et al. (2005) found that primary productivity was limited by both P and N in the inflow, but only N was limited in the outflow water of their study lake, indicating a goose-mediated change in the ecosystem because goose faeces contribute a larger proportion of P than N compared to surface runoff. Comparing inflow and outflow can be problematic, particularly when estimating the impact of geese temporarily on a wetland. Olson et al. (2005) found that geese contributed 85–93% of P and 33–44% of N to the wetland, and their impact extended long after their stay ended, evidenced by a gradual export of nutrients from the lake. Gradual export of nutrients means that a comparison between inflow and outflow may not reflect nutrient input at the time of the study but may instead reflect a combination of current input, historical loads, and/or build-up by sedimentation. This delay may also explain why Scherer et al. (1995) could find only a weak correlation between waterbird use and P levels when comparing seasonal use. A likely explanation for the delayed response is that nutrients in faecal material quickly reach the sediments. Phosphorus tends to build up in the sediment and stay adsorbed to the organic material in the faeces, as shown by an experimental study by Unckless and Makarewicz (2007). The N in bird faeces contains uric acid, which also tends to sediment (Davies 1973). Eutrophication effects may therefore be delayed until the nutrients are released from the sediment by disturbance (such as foraging geese) or a change in water chemistry or temperature.

Ecosystem impacts

Geese are potentially important vectors of nutrients; however, they may also impact aquatic systems in shallow lakes and wetlands by stirring the sediments, increasing the likelihood that P and N are released (Fanning et al. 1982). Geese can change the macrophyte cover by browsing, grubbing, and trampling (Chaichana et al. 2011b) and thus maintain a turbid state. Reduced macrophyte cover and increased turbidity can create or maintain a system dominated by algae. Once an aquatic system becomes turbid, it is often difficult to increase macrophyte cover, even when grazing is prevented (Rip et al. (2006). The algae-dominated state typical of eutrophied freshwater systems can therefore be difficult to alter.

Some studies illustrated a positive correlation between bird density and chlorophyll levels (i.e., algal abundance; Kitchell et al. 1999, Tobiessen and Wheat 2000), despite rapid sedimentation of nutrients. Some studies that did not find a change in chlorophyll levels due to goose eutrophication concluded that the lack of an observed response was due to an increase in consumers (e.g., microcrustaceans and cladocerans), and the limited response of producers to increasing nutrient levels could therefore be explained by a strong top-down effect (Pettigrew et al. 1998, Van Geest et al. 2007). Sedimentation and top-down effects are both likely to interfere with clear ecosystem responses, such as measureable nutrient or chlorophyll levels.

Conclusions

Many of the reviewed studies base their estimates of nutrient and faecal productions on previous studies, which we subsequently used to estimate faecal production and content. This overlap of data introduces a bias toward older studies, and because land-use, fertilizer application, and farming methods may change over time, more contemporary studies would likely yield different results. Because faecal passage times and nutrient contents vary among sites and seasons, future studies should use site- and time-specific values instead of basing estimates on previous literature with data of different provenance. TN and TP levels must also be presented so that the total nutrient input can be estimated and compared to other study areas; TN and TP include most soluble and nonsoluble forms and therefore provide an indication of the impact of geese over time.

The bulk of studies on geese as nutrient vectors concern contribution to eutrophication in already nutrient-rich systems, and although the role of geese in nutrient-poor systems remains largely unstudied, the few studies that have addressed the topic indicate that geese may play an important and positive role in shaping these ecosystems (Linnman 1983, Mindl et al. 2007).

A valuable next step in goose guanotrophication research would be an experimental ecosystem approach, tracing the N and P from goose faeces to determine to what extent they end up in the sediment, water column, primary producers, and consumers. An experimental approach would also allow manipulation of temperature, UV-light, and stirring to simulate different environmental settings, allowing us to go beyond estimating nutrient contribution to predicting the impacts of geese on different wetland environments.

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