

Nutrient cycling at the landscape scale: The role of diel foraging migrations by geese at the Bosque del Apache National Wildlife Refuge, New Mexico

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Abstract

Wildlife refuges are sites of dense aggregations of wintering waterfowl. Refuge managers are concerned about local water-quality effects and the amount of birdborne nutrient load that might cause eutrophication in roosting ponds and/or be exported to downstream systems. We initiated this research effort to test the hypothesis that daily feeding migrations by geese represented a significant source of nutrients to wetland systems at the Bosque del Apache National Wildlife Refuge in the middle Rio Grande River valley of New Mexico. We documented the role of geese in translocating nutrients through a combination of time budget and mass balance models for birds, bioassays of phytoplankton growth, and stable isotope methods that trace the source of nitrogen to food webs. Geese increased the nutrient loading rates in some wetland ponds by up to 40% for total nitrogen and 75% for total phosphorus. Bioassays revealed that nitrogen was consistently limiting to primary production by algae in the ponds. Chlorophyll levels increased in proportion to bird densities. Fish and crayfish from the ponds intensively used by birds had very low stable nitrogen signatures relative to those from the Rio Grande River. This result derived from the low ¹⁵N in alfalfa and corn, which were the primary forage for birds, and accumulated through food webs in proportion to bird use of individual ponds as roosting areas. In general, the wetland ponds functioned efficiently in retaining the birdborne, allochthonous nutrient load and only modest amounts of the total nitrogen or phosphorus were exported downstream.

*Does the wild goose, reconnoitering the farmer's cornfield,
bring something more than wild music from the lake, take some-
thing more than waste corn from his field?*

Aldo Leopold

Lakes in relation to terrestrial life patterns

Each autumn, hundreds of thousands of waterfowl migrate to winter refuges in southerly latitudes. In the southwestern U.S. winter months are spent near large river systems such as the Rio Grande. The riparian corridors in arid regions

focus ecological interactions at their ecotones and provide sharp boundaries for landscape-scale processes (Decamps and Naiman 1990). Historically, migratory waterfowl spent winter foraging in floodplain areas and roosting on natural islands within the river system. Managed flows and reduced water volumes have diminished those habitats to a small fraction of their former extent.

As human populations have grown in the southwest, demand for alternative water uses has risen with the growth of agriculture and urbanization. Water is an essential and limiting resource for both economic and ecological processes in this region. In the context of multiple stressor issues raised in this symposium, water is the common resource that must be sparingly shared among users. Some of those uses have profound impact on water quality (e.g., sewage treatment, urban runoff, agricultural runoff, irrigation uses, etc.). The human communities downstream have a strong and growing interest in the quantity and quality of water received from upstream sources.

Water is also the essential requisite for an assemblage of wildlife refuges established along the Rio Grande. These refuges were developed as an alternative to the wetland habitats lost when the river system came under intensive human use. Water quantity and quality are important considerations for refuge management because outbreaks of disease such as avian cholera and type C botulism are often associated with poor water-quality conditions (Wobeser 1981). Dense aggregations of migratory waterfowl may exacerbate those concerns through their addition of allochthonous nutrients to refuge ponds and the flushing of ponds that can carry those nutrients downstream.

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Approximately 5,000 geese wintered at the Bosque del Apache National Wildlife Refuge during 1967–1968 (Post et al. 1998). Controls on hunting and habitat improvements over the next two decades brought that number to 60,000 geese during winter 1985–1986. Since then, joint management of the system of state and federal refuges in the middle Rio Grande valley has maintained densities at Bosque del Apache at 35,000–55,000 geese each winter. This refuge also plays a vital current and future role in survival of whooping cranes (*Grus americana*) raised by their sandhill crane (*Grus canadensis*) surrogate parents because they accompany those parents in their seasonal migrations between nesting areas in Idaho and wintering grounds in New Mexico. Increases in crane and goose populations continue and, logically, raise concerns about the carrying capacity of aquatic systems in the winter refuges where water and its management are key components of habitat quality.

A recent symposium volume (Kerekes 1994) presents a diversity of examples of the role of birds in aquatic ecosystems. The role of geese has been the focus of several major studies (e.g., Bazely and Jeffries 1989; Manny et al. 1994) and the central issue of controversy about negative ecological effects due to continuing increase in goose populations (Warren and Sutherland 1992; Srivastava and Jeffries 1996). One particularly provocative recent review argued that goose densities are now excessive and should be aggressively reduced (Ankney 1996).

There is rapid growth in the general view of the importance of mobile consumers and their contribution to local nutrient cycles (Kitchell et al. 1979; Carpenter and Kitchell 1993). Recent reviews emphasize the potential effects that can derive from aggregations of birds and their contribution to nutrient loading (Oliver and Legovic 1988; Bildstein et al. 1992). The extensive effects of snow geese on vegetation in nesting areas near Hudson Bay can be discerned from satellite images (Kerbes et al. 1990; Srivastava and Jeffries 1996). At the continental scale, winter refuges have played a key role in enhancing the populations of migratory waterfowl. As an example, snow goose populations in North America have increased approximately fourfold in recent decades (Ankney 1996). Thus, the effects of conditions in the winter refuges are expanded to the landscape scale proximate to the refuge, which includes the radius of daily foraging flights (up to 50 km), and to the continental scale that includes the entire annual migration.

Animal aggregations, such as those that occur seasonally in waterfowl refuges, provide “best evidence” opportunities for assessment of the relative contribution of nutrient inputs due to higher order consumers. At the landscape scale, daily foraging away from the refuge followed by returns to roost at the refuge site create a vector of nutrient transport which can serve to subsidize local ecosystem processes. For the resident forms, including avifauna that remain on the refuge and components of the aquatic food web, some nutrient addition could produce a positive feedback that enhances local primary and secondary production processes to ultimately yield greater carrying capacity at the site. By extension, eutrophication due to excessive nutrients can inhibit these processes and diminish carrying capacity.

One general expectation is that the shallow pond systems

in waterfowl refuges would function as wetlands. They would serve as nutrient sinks and nitrogen limitation would be the major regulator of productivity (DeLuane et al. 1986). Birdborne nutrients would alter productivity and nutrient cycling processes in these ecosystems. We do not know the magnitude of those effects, but we can imagine that they would be locally variable. Higher order consumers such as fish provide one means for tracing the nutrient subsidy because they accumulate the net effects of nutrient loading and cycling (Kitchell et al. 1979; Schindler et al. 1993). The magnitude of export to downstream ecosystem processes is also unknown.

We reasoned that migratory birds would translocate nutrients and produce a discernible change in both nutrient budgets and nutrient cycles of refuge ponds at the Bosque del Apache National Wildlife Refuge. In this paper, we document those effects through a combination of time budget and mass balance models for snow geese, the most abundant bird species (Post et al. 1998), and the effects of their nutrient additions as derived from measures of nutrient concentrations, bioassays of phytoplankton growth, and stable isotope methods that trace food webs. We demonstrate that geese substantially increased the nutrient loading in some ponds and that their effects were readily apparent in stable isotope results for top consumers (fish and crayfish) in the local food webs. The ponds functioned efficiently in retaining added nutrients and only modest amounts of the total loads were exported downstream.

Methods

The study site—The Bosque del Apache National Wildlife Refuge is within the riparian zone of the Rio Grande River ~30 km south of Socorro, New Mexico. This site is a component of the Sevilleta LTER site and is operated by the U.S. Fish and Wildlife Service. The refuge has an extensive network of canals, dikes, and ditches that fill or drain shallow wetland ponds and irrigate agricultural areas within the refuge, dozens of which are used in any given year (Fig. 1). This system is aggressively and intensively managed to maximize wading bird and waterfowl use. This includes crop management (through partnerships with local farmers) on adjacent agricultural lands which provides food (alfalfa and corn) primarily for geese and cranes. Fertilizers applied to these fields can enter aquatic food webs through runoff and through the direct transport of daily bird migrations. Water levels and flushing rates of the individual pond systems are designed to yield maximum habitat values for waterfowl and wading birds. Some wetland units are managed to encourage pioneer vegetation on moist or flooded soils which provides a favored food resource for many birds (Fredrickson and Taylor 1982); others are allowed to develop secondary succession communities dominated by sedges (*Carex* spp.) willows (*Salix* spp.), and cattail (*Typha* spp.) that provide preferred habitat to other species. Fire, bulldozers, and graders are among the tools regularly employed by refuge managers. Control of pond flushing rates reduces stagnation and minimizes conditions that might promote diseases (Wobeser 1981) or blooms of toxic cyanobacteria (Codd 1995) which

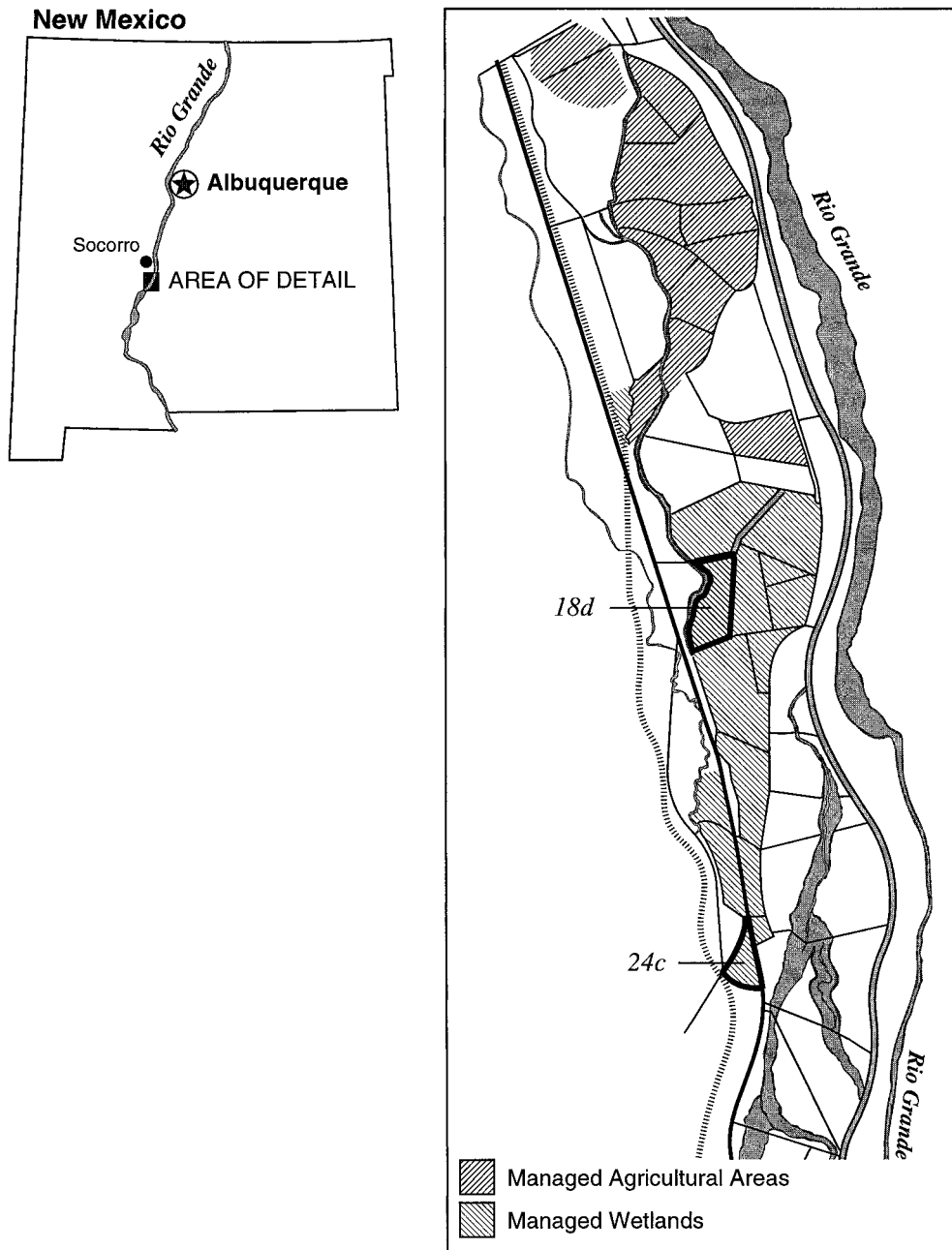


Fig. 1. Map of Bosque del Apache National Wildlife Refuge. Water levels can be managed for each of the units denoted by light border lines. Heavy dark lines identify the inflow and outflow canal systems. Agricultural systems are denoted by the ladder line and managed wetlands by hatching. Pond 18d (50.2 ha) is the major roosting site for geese (high bird density); Pond 24c (25 ha, low bird density) was sampled as a reference system.

can have devastating effects at the high bird densities observed each winter. Aggressive water management practices are employed in refuge wetland systems, as described in greater detail by Taylor and Kirby (1990) and Taylor (1992).

Aquatic communities in the pond systems are largely derived from the autumnal filling process as water is drawn through canals from the Rio Grande. With the exception of the birds, pond food webs are dominated by adventitious omnivores such as mosquitofish (*Gambusia affinis*) and cray-

fish (*Procambarus* and *Cambarus* spp.) plus miscellaneous representatives of the river community and invertebrates characteristic of pond environments in the southwestern U.S. Much of this biomass is exported when ponds are drained in spring and returns to the river through the effluent canal system of the refuge.

Foraging activities by resident birds (e.g., snow geese and sandhill cranes) can include several forays each day to local fields or can involve a single, day-long foraging migration

that takes them substantial distances away from the refuge. A recently published study (Post et al. 1998) describes the interactions of weather effects and management practices in regulating diel foraging migrations. Briefly restated, refuge managers change the availability of corn in response to local weather conditions and bird densities. State and federal refuge managers coordinate their activities to encourage dispersal of birds during periods when densities are deemed too high or when severe weather will restrict access to distant sites. Typically, birds engage in two diel migration and foraging bouts during the early and late periods of their season at the refuge. A single, longer foraging bout is more common during midwinter.

After foraging, birds return to the refuge ponds to rest while digestion, egestion, and excretion proceed. These behaviors recruit nutrients from the surrounding terrestrial landscape which are deposited as guano and incorporated in local aquatic nutrient cycles. Other birds (ducks and wading birds) may migrate short distances from the refuges or remain to forage there throughout the diel cycle. They can benefit from enhancement of local production processes due to the migratory components of the avifauna. Assessing the extent and importance of these nutrient subsidies is the key component of our research interest.

Post et al. (1998) developed the data and models required to estimate nutrient loading rates due to the feeding and diel migratory behavior of geese—the most abundant large birds. That study combined energetics models with time budget studies to calculate the kinds of foods (alfalfa or corn) consumed and the amounts of time spent foraging, in flight, or roosting on ponds. Rates of digestion and temperature or wind effects on flight frequencies were used to estimate the daily foraging behavior and amount of guano deposited in Pond 18d, which is the most commonly used roosting area at the refuge. The nutrient composition of alfalfa, corn, and guano was used to estimate the amount of nitrogen and phosphorus deposited per unit time. This study complements that of Post et al. (1998) by providing evidence of the ecological effects of those nutrients on the pond systems and an estimate of the nutrient retention by ponds heavily used by migratory birds.

Management practices and responses of birds to them define the scale of nutrient transport. But those are variable, so there is no way to explicitly define dimensions for the landscape involved. At its daily minimum, the landscape scale includes two adjacent habitats: the ponds and the managed agricultural sections of the refuge (<2 km, see Fig. 1). At the intermediate scale of each winter, the landscape scale extends from the ponds to other agricultural areas up to 50 km from the refuge. At the maximum or annual scale, the landscape extends to regions in the northern states and in Canada where these birds spend their summer breeding period. Thus, the result of providing well-managed winter refuges is expressed in bird populations and their ecological effects at the continental scale.

Field and laboratory methods—We focused our analyses on “white geese” because they represent more than half of the migratory bird biomass at the refuge. Their foraging behaviors are well known and their flocking behavior creates

substantial local densities. Estimates of white goose abundance include the lesser snow goose (*Chen caerulescens caerulescens*), which is usually 95% of white goose abundance, and Ross' goose (*Chen rossii*) which forage and roost together, although the latter is much less abundant (about 5% of total). Other goose species are present at the refuge, but are much less abundant. Other abundant waterfowl (e.g., ducks) forage primarily on the wetlands and recycle nutrients but play a lesser role in importing them. The other large component of the bird biomass (cranes) may migrate to distant sites and spend extended, variable periods of days or weeks away from the refuge (Post et al. 1998).

Goose abundance was estimated each week from counts provided through the standard methods used by wildlife biologists at the refuge. The number of geese in each field and wetland unit was estimated by first counting several subsets of the geese in a field or wetland (e.g., groups of 50 or 100). With an impression of group size and a standard rate of scanning the fields, the number of groups of 50 or 100 geese was counted to obtain quick and relatively accurate estimates of the total number of geese. Estimates of the number of geese on each field and wetland were added to obtain the estimate for the size of the goose population at the refuge during a given week.

Water from the Rio Grande River enters the refuge canal system from the north end (Fig. 1) and is distributed to individual ponds through a flowthrough system regulated by gate levels at the inlet and outlets of each pond. After passing through the wetland units, water is collected in a common canal and carried back to the Rio Grande River. We selected two refuge pond systems for intensive study. During 1995–1996, Pond 18d (high bird density) was intensively managed to attract roosting birds. This pond had shallow water depths, high flowthrough rates, and no emergent vegetation. It regularly served as the roosting site for the majority of geese on the refuge. Pond 24c (low bird density) also received river water from the canal system but water level was maintained at greater depths and that discouraged use by geese. Ponds are flooded at the beginning of the migration season, then drained at the end (Taylor 1992). Nutrient data presented for the beginning and end dates of our study approximate the initial and final concentrations for pond waters while those for the inlet to Pond unit 18d represent changes in water quality of the Rio Grande River.

Nutrient limitation was determined through a regular series of analyses and bioassay studies. Water samples were taken weekly in the high bird and low bird ponds and bi-monthly in the inflow and outflow canals. Water was collected from the outflow of the high bird and low bird ponds and from the center of the inflow and outflow canals by filling one 20-liter water container from each wetland unit. The water was quickly transported back to the Sevilleta Field Research Station where it was subsampled. For samples from each wetland unit, 100 ml was frozen and later transported to the University of New Mexico campus in Albuquerque for contract analysis of total (inorganic and organic) nitrogen and phosphorus concentrations.

Initial chlorophyll *a* concentrations were obtained by filtering 250 ml through each of three 0.45- μ m Gelman fiber filters, which were wrapped in aluminum foil to prevent pho-

todegradation and immediately stored in a freezer. Later, chlorophyll was extracted by the methanol method and analyzed using standard fluorometric techniques as described by Carpenter and Kitchell (1993). Water from the bulk sample was used to set up a nutrient limitation bioassay where 12 cubitainers were each filled with 1 liter of the water sample. Three were saturated with an inorganic nitrogen solution, three with an inorganic phosphorus solution, three with a solution of nitrogen and phosphorus at the Redfield ratio, and three served as unmanipulated controls. For nitrogen additions, we used $580.1 \text{ mg N liter}^{-1}$, in the form of NH_4NO_3 and inoculated 1 liter of the water sample with 1 ml of the stock solution. For phosphorus additions we used $81.02 \text{ mg P liter}^{-1}$, in the form $\text{Na}_2\text{HPO}_4 \cdot 7\text{H}_2\text{O}$ and inoculated 1 liter of the water sample with 1 ml of the stock solution. A 1-ml inoculation of each stock solution was added to the three remaining 1-liter samples as test for co-limitation effects. All 12 cubitainers were allowed to incubate for three full days at ambient temperatures and light conditions outside the laboratory. Then, 250 ml of the water in each cubitainer was filtered and analyzed as for those of the initial water samples.

The stable isotope of nitrogen (^{15}N , Peterson and Fry 1987) was measured from tissues of adult mosquitofish (*G. affinis*) and crayfish collected from the nearshore areas of the inflow canal, high bird and low bird ponds, and the outflow canal. These samples were collected once each month. The *Gambusia* and crayfish were collected with a benthic insect sweep net, transferred to airtight vials, and frozen. In addition, we collected *Gambusia* from the fire control pond at the Sevilleta Field Research Station. This pond was filled with groundwater and had a natural assemblage of local biota. Alfalfa, corn, and goose guano were also sampled to determine N, P, and ^{15}N concentrations in each. Later, the samples were thawed and dried at $45\text{--}50^\circ\text{C}$, then removed from the vials and ground into a fine powder in a Wiley mill. Samples were shipped in airtight vials to the University of Alaska-Fairbanks for contract analysis of isotope concentrations required to calculate the $\delta^{15}\text{N}$ data. Isotope ratios were determined using a Europa 20-20 continuous flow mass spectrometer with reproducibility of 0.2 per mil. Replicate samples were analyzed to provide a measure of variability and estimate confidence intervals.

Results

The seasonal changes in abundance of geese at Bosque del Apache are presented in Fig. 2A. Abundance peaks in mid-late November as birds arrive from their migration. Abundance declines during midwinter as some birds continue south and some disperse to other refuges in the Rio Grande valley. In late winter, abundance increases as birds aggregate and stage for the northerly migration.

The results of the Post et al. (1998) study set the stage for this analysis and are briefly recanted here. More than 90% of the geese at Bosque del Apache roost on 10% of the wetland area. Pond 18d (50.2 ha) holds most of those geese each evening. During early and late winter periods, geese make two foraging flights each day: one at dawn and the

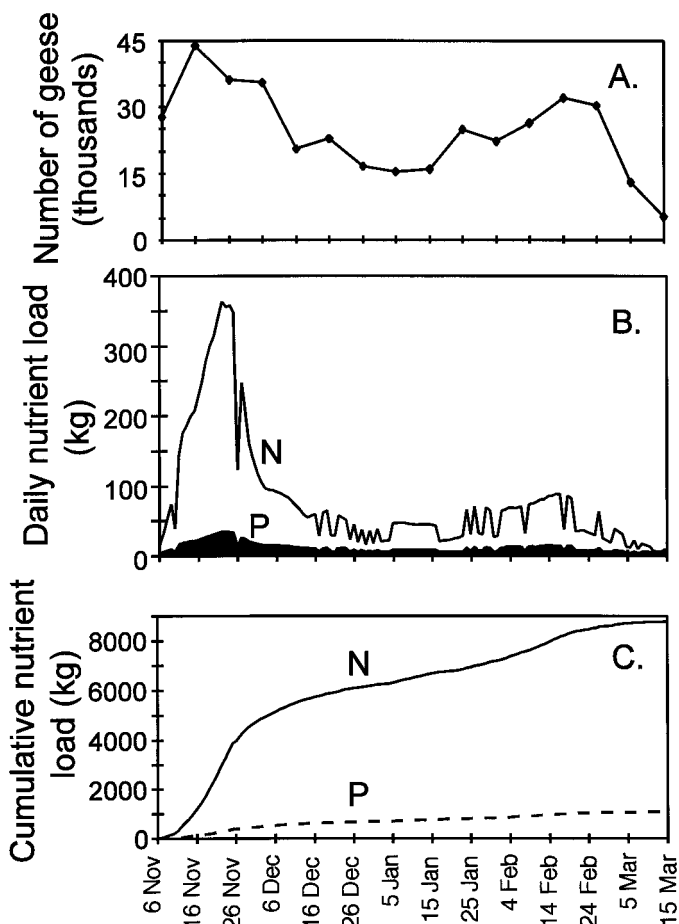


Fig. 2. A. Number of geese (in thousands) in the Bosque del Apache National Wildlife Refuge during winter 1995–1996 as estimated from weekly surveys. B. Estimated daily nutrient load (kg) of nitrogen and phosphorus deposited by geese in wetlands of the refuge. Nutrient loading estimates were obtained from a nutrient loading model combined with goose behavioral data. C. Cumulative nitrogen and phosphorus loading to wetlands of the refuge due to diel migrations by snow geese during winter 1995–1996 (from Post et al. 1998).

other before sunset. Most of those return to roost on Pond 18d during midday. In midwinter periods when air temperatures are $<10^\circ\text{C}$ and winds are strong, geese make a single morning flight to feeding areas and remain there for the full day before returning to the refuge. During early winter, geese feed heavily to compensate for the energy lost during migration. They first focus their foraging on wetland systems where moist soil pioneer vegetation (e.g., sedges, *Cyperus* spp., and smartweed, *Polygonum* spp.) has grown during summer and then move to alfalfa fields after the native vegetation resources are depleted. Although corn is available, the geese avoid it because they cannot see predators in standing corn. During winter, refuge managers knock down standing corn in adjacent agricultural areas and do so in proportion to their estimate of the energy needs of the birds (i.e., they offer access to more corn during cold periods). Geese alternate between cornfields and alfalfa for that period. As

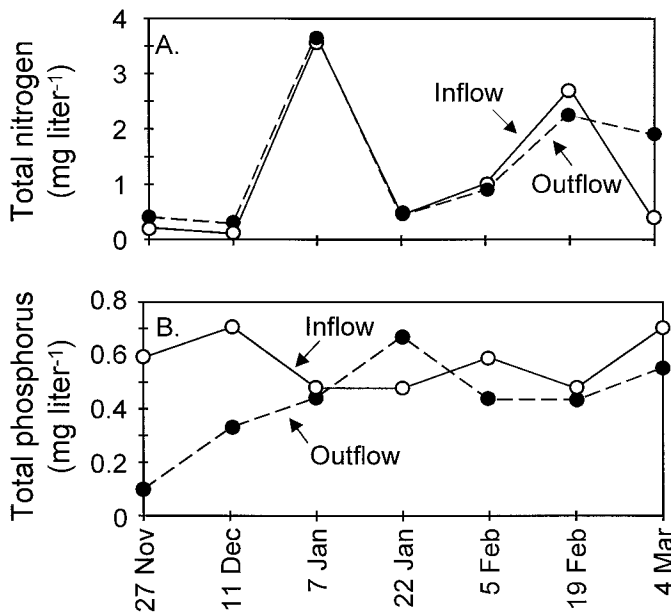


Fig. 3. Total nitrogen (A) and phosphorus concentrations (B) in the inflow and outflow canals of the Bosque del Apache National Wildlife Refuge system at bimonthly intervals during winter 1995–1996.

winter ends, geese feed more heavily on corn and store energy in preparation for their northerly migration.

In aggregate, geese excreted about 60% of their consumed nutrients while in the refuge wetland systems. This excretion supplied about 40% of the nitrogen and 75% of the phosphorus added to the wetland system (Pond 18d) most intensively used for roosting. Although areal loading rates are variable due to changes in bird behavior, our estimate of peak rates were 350 kg N d⁻¹ and 35 kg P d⁻¹ for the wetland system as a whole. If all of that were deposited in Pond 18d, it would produce peak loading rates of ~7 kg N ha⁻¹ d⁻¹ and 0.7 kg of P ha⁻¹ d⁻¹ or 0.7 g N m⁻² d⁻¹ and 0.07 g P m⁻² d⁻¹. The allochthonous nutrient loading rates in this system were among the highest recorded for wetlands in the temperate zone (Post et al. 1998).

The seasonal pattern of nutrient loading to the entire 494 ha of wetland systems in this refuge (Fig. 2B) demonstrates the intense feeding behavior immediately following arrival in the refuge and is followed by lower loading rates due to midwinter changes in foraging and diel migratory behavior. The ratio of nitrogen to phosphorus loading changes with feeding behavior because alfalfa has an N:P of 10.4 while that for corn is 5.3. Early in the season, the greater consumption of alfalfa accelerates the rate of nitrogen addition relative to phosphorus. A second increase in loading rates develops in late winter as goose density increases. The cumulative loading of nitrogen and phosphorus is depicted in Fig. 2C.

Total nitrogen concentrations in the inflow and combined outflow canals of the entire refuge were variable but similar through winter (Fig. 3A). Total phosphorus concentrations were higher in the inflow waters early in the season, but increased to levels comparable to those of the outflow by

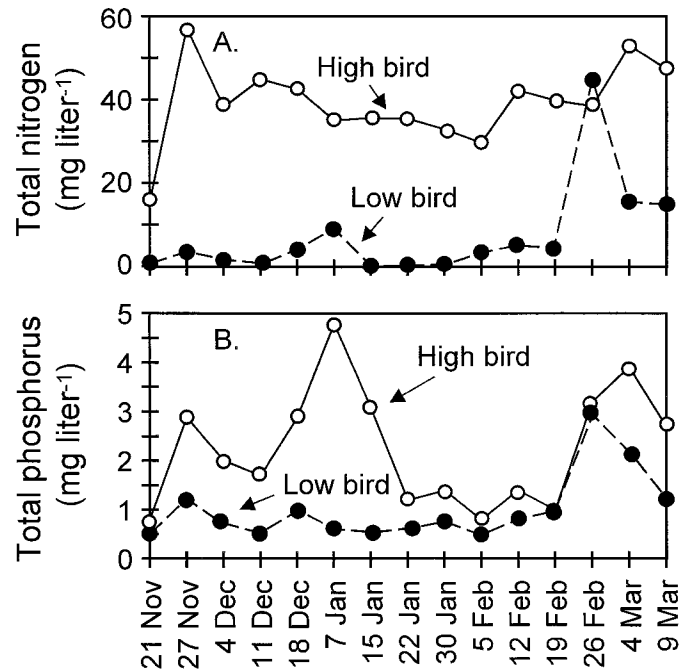


Fig. 4. Total nitrogen (A) and phosphorus concentrations (B) in water samples from ponds with high or low bird densities at the Bosque del Apache National Wildlife Refuge. Data based on weekly bird surveys and nutrient samples during winter 1995–1996.

the end of the period (Fig. 3B). Hence, the nutrients added by birds made little change in waterborne nutrient budgets for the entire system. Either local assimilation and recycling by the wetlands was very efficient in retaining the additional nutrient load or the nutrients in guano were not very soluble and represented no real enhancement.

Results presented in Fig. 4 demonstrate that nutrients imported by the birds did enhance the local concentrations. The high bird densities in Pond 18d produced several-fold greater concentrations of both total nitrogen and total phosphorus than those observed in the waters of Pond 24c where bird densities were very low. While individual ponds reflected the nutrient loading of birds, the combined effects of low density on most ponds and the assimilative capacity (nutrient recycling and conversions) of the wetland systems produced little or no net export of nutrients to the canals carrying water downstream from the refuge. In fact, the refuge wetlands actually retained a portion of the phosphorus brought in with Rio Grande River water (Fig. 3B).

Guano from geese did increase local algal production as indicated by the contrast of chlorophyll concentrations from ponds where bird densities were high vs. low (Fig. 5). Chlorophyll concentrations in Pond 24c (low bird densities) were low and less variable than those in Pond 18d (high bird densities) which showed bimodal peaks corresponding with seasonal changes in goose feeding behaviors. Chlorophyll concentrations peaked during the early and late periods of winter when geese were making two foraging flights per day and roosting on the pond during the midday period and at night. This foraging behavior roughly double the nutrient loading rates, and chlorophyll concentrations indicate that the algae

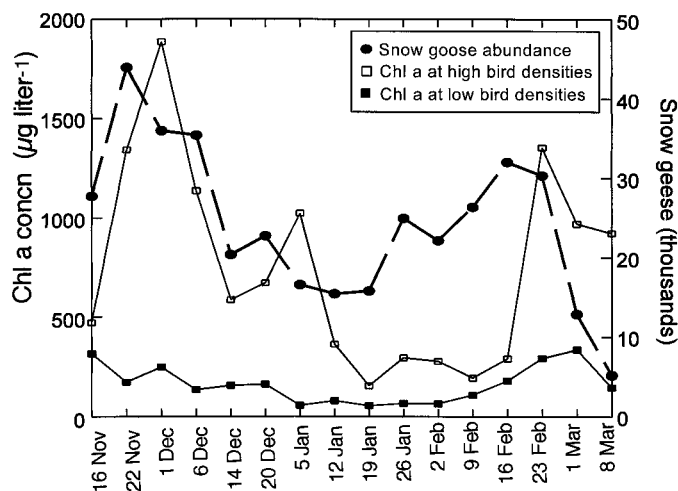


Fig. 5. Chlorophyll *a* concentration in water samples from ponds with high or low bird (goose) densities at the Bosque del Apache National Wildlife Refuge. As for Fig. 4, data are from weekly samples during winter 1995–1996.

responded to those nutrient additions. Chlorophyll was consistently higher in the pond that had high bird densities, but lowest during the period when birds were making a single flight, spent the midday in fields, and imported fewer nutrients (Fig. 5).

Nutrient addition bioassay results correspond with the general patterns of data observed in pond nutrient and chlorophyll concentrations (Fig. 6). In both pond systems, algal growth (relative to controls) responded strongly to nitrogen additions and exhibited co-limitation to the combined addition of nitrogen and phosphorus. Neither system responded strongly to the addition of phosphorus alone, a result consistent with the observation that phosphorus concentrations in the inflow waters were high—regularly between 400 and 600 $\mu\text{g liter}^{-1}$. The strongest bioassay responses occurred toward the end of the midwinter period when cumulative loading by birds had dropped as a result of the single-bout feeding behavior. That limitation decreased in the high bird ponds with the late season increase in bird densities.

The stable isotope data provide particularly powerful, integrative evidence of the role of birds in adding nutrients. We initially reasoned that birdborne nutrients would be low in ^{15}N because the geese were feeding on a nitrogen fixer (alfalfa) and on corn which was enhanced by commercial fertilizer applications; both would have very low levels of ^{15}N . The $\delta^{15}\text{N}$ results for alfalfa, corn, and goose guano (when feeding on alfalfa) averaged 0.8, 5.8, and 2.5, respectively. As birds carried that nitrogen to the pond system where it was incorporated in local food webs, we expected that the apex consumers (*Gambusia* and crayfish) in these ponds would be very different from those in the inflow canals where the local food webs were heavily influenced by intense recycling of nitrogen in the Rio Grande River upstream. Food webs there would have a much higher background concentration of ^{15}N . That hypothesis was strongly supported by the data (Fig. 7). Crayfish and *Gambusia* in the inflow canal had high concentrations of the heavy isotope. Those from the pond where bird densities were low

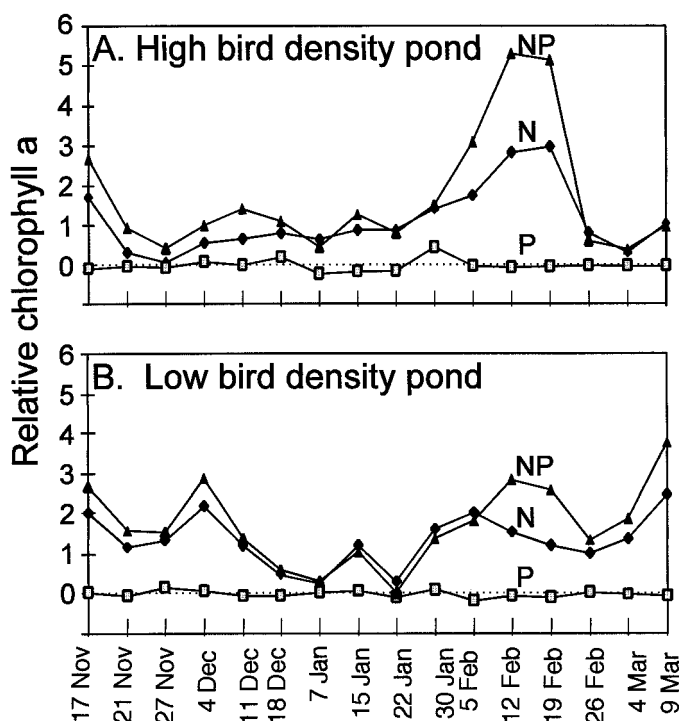


Fig. 6. Chlorophyll *a* concentration relative to controls for nutrient limitation bioassays performed on water sampled from ponds with high bird densities (A) and low bird densities (B) at weekly intervals during winter 1995–1996. Test samples were inoculated with high concentrations of nitrogen (N), phosphorus (P), and their combination (NP).

showed some reduction in ^{15}N relative to that from the upstream site. Those from the pond where bird densities were high and those in the outflow canals (most of which were probably emigrants from the ponds) had $\delta^{15}\text{N}$ levels indicative of a strong dilution effect due to loading of nitrogen by birds. Peterson and Fry (1987) indicate that trophic levels differ by about 3–4 $\delta^{15}\text{N}$. The animals in the outflow and high bird pond had $\delta^{15}\text{N}$ levels that were the equivalent of one trophic level (*Gambusia*) or nearly two trophic levels (crayfish) different from those in the inflow canal habitat. These differences were not due to changes in trophic levels of the fish because diets of *Gambusia* in all samples indicated similar foraging behavior and were dominated by littoral Cladocera (e.g., Chydoridae) and chironomids. Instead, the differences in $\delta^{15}\text{N}$ levels reflect the relative importance of sources of nitrogen entering local food webs. Fish and crayfish from the food webs where bird densities were high gave an unequivocal response to the addition of nitrogen low in ^{15}N . Nitrogen translocated from agricultural areas by geese enhanced the local concentration with a low ^{15}N source which then ascended through the food web.

We had an accidental but informative test of our hypothesis regarding dilution of the stable nitrogen signal in *Gambusia*. At the beginning of our study, we sampled *Gambusia* from the small pond at the Sevilleta Field Research Station. Analysis of their stable nitrogen isotope produced a result of average $\delta^{15}\text{N} = 8.0$, which is about the level expected for an insectivorous and zooplanktivorous fish. Samples taken

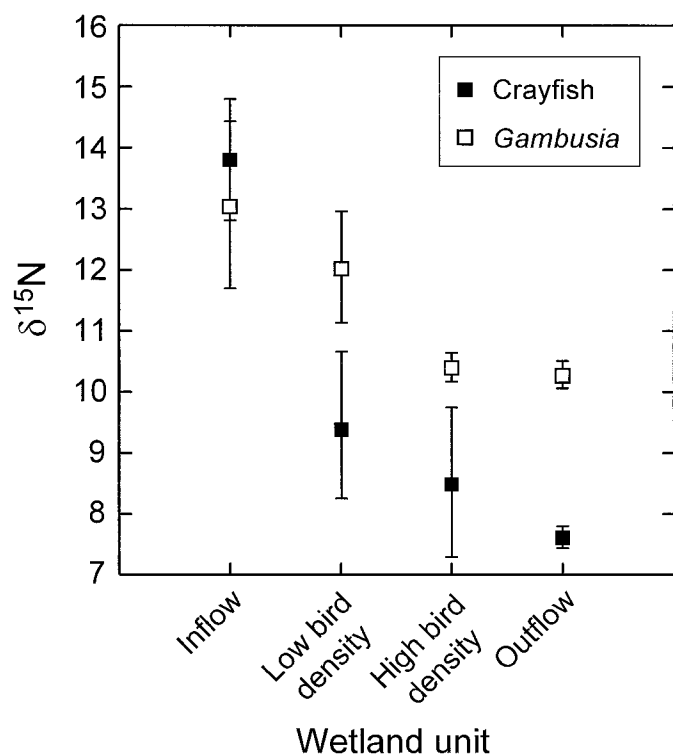


Fig. 7. Average nitrogen stable isotope signature ($\delta^{15}\text{N}$) from crayfish and fish (adult *Gambusia affinis*) sampled once each month during winter 1995–1996 in the inflow canal, ponds with low or high bird densities, and the outflow canal. Bars indicate standard errors of each mean.

late in the study period produced an average $\delta^{15}\text{N} = 0.5$. Inquiring about the cause of this change, we learned that the station manager had sought to invigorate the *Typha* stands in the pond margin by liberal application of plant fertilizer sticks to soils where cattail was rooted. This source of nitrogen diluted that accumulated in the pond food web and appeared as a strong signal in the apex consumer. Its effects were analogous to those we posited would occur in proportion to the nitrogen transported from alfalfa and corn through bird feeding and migration.

The lessons learned from using stable isotope methods in our study reinforce the need for knowing the relative importance of sources of nitrogen to a particular food web and, therefore, the inferences that can be built when stable isotope data are used to test for alternatives. In this case, we observed very large differences in $\delta^{15}\text{N}$ results for a fish (*Gambusia*) that occupied a similar trophic position in each of several different food webs. Those differences allowed us to discern the relative importance of nutrient translocation by geese by contrasting that result with those from food webs where recycling was intense (Rio Grande River water at the inlet) with that from a pond where a recent addition of commercial fertilizer had occurred (Sevilleta Research Station).

Discussion

Every line of evidence supports the hypothesis that daily feeding migration by geese is a major source of nutrients to

wetland systems in the Bosque del Apache Wildlife Refuge. The combination of modeling and behavioral data presented by Post et al. (1998) demonstrates that nutrient loading is proportional to bird densities and that birdborne nutrients could account for 40% of the nitrogen input and 75% of the phosphorus input to these systems during winter (Fig. 2). Direct measures of nutrient (Fig. 4) and chlorophyll concentrations (Fig. 5) demonstrate that local nutrient cycles are augmented by the addition of nitrogen and phosphorus in guano. Bioassay results identify nitrogen as the primary limiting nutrient and that its addition allows local algae to evidence rapid growth until phosphorus is limiting (Fig. 6). Stable isotope results from fish and crayfish (Fig. 7) demonstrate that the nitrogen transported by geese is incorporated in the pond food webs. It provides a cumulative indicator that corresponds with the modeling results—birds nearly double the nitrogen load to refuge ponds where high roosting densities develop.

Refuge managers are concerned that high levels of nutrient loading may create water-quality conditions detrimental to these wetland pond systems and possibly create a major problem by loading nutrients to the downstream systems. We have no means for evaluating the prospect of their greatest concern—disease outbreaks—but we can offer the conclusion that effects are local and proportional to bird densities. Refuge managers have extensive experience in manipulating bird abundances (Fredrickson and Taylor 1982; Taylor and Kirby 1990). Our general results indicate that nutrient loading rates peak early in winter and are much higher than would be expected from simple knowledge of bird densities because geese are very actively feeding on high nitrogen foods and translocating much of that to the roosting ponds. If local water-quality problems are a growing concern, that is the period when aggressive management of aggregation behavior and pond or wetland flushing rates would be most beneficial.

Although those ponds where bird densities are high do have higher nutrient levels, the net effect of dilution by other units in the refuge and the efficient retention of nutrients by these wetlands produces little or no net export from the refuge system as a whole. At the larger scale, we must recognize that the primary determinant of nutrient status in these systems is the water quality of the Rio Grande River. Its nutrient levels are high (Fig. 3). Unless remedial measures are established, those nutrient concentrations will likely increase in proportion to growth in the upstream urban and agricultural areas.

One management alternative would involve passing Rio Grande River water through one or more of the heavily vegetated wetland units before routing it to the units managed to encourage bird roosting. Similarly, effluent water could be routed through a downstream unit before re-entering the canal system that returns it to the Rio Grande. In that case, water quality could be improved as it enters and as it leaves the refuge system. The nutrient reduction mechanisms are those of lower flow velocities and increased recycling by microbial and algal communities in the wetland systems. Cumulative eutrophication effects in ponds can be offset by sustaining or expanding the current practice of draining the intensively used ponds at the end of each season followed

by removal of accumulated sediments and tillage practices that aerate the dried soils, accelerate denitrification, and improve phosphorus retention. The residents of downstream communities and the reservoirs of the lower Rio Grande (Elephant Butte and Caballo) could see modest but immediate benefits from these practices. Further, the entire river ecosystem would probably be less negatively affected through dilution of the currently high nutrient concentrations in the Rio Grande. There is some trade-off due to greater evaporative water loss as water is slowed and spread in its passage through the refuge wetland units, but that is reduced by the low temperatures and the fact that most of the wetland vegetation is quiescent during this time of year.

At the scale of continents of states, bird densities are very low. Therefore, we can safely assume their role in nutrient cycling is of local importance and primarily in those sites where aggregations occur. Feeding aggregations during migration can have large ecological effects (Bazely and Jeffries 1989; Kerbes et al. 1990). That is certainly the case in winter refuges for migratory waterfowl elsewhere and deserves research attention beyond that we present for this refuge. Although each refuge may be unique and different, the approaches presented by Post et al. (1998) and those herein offer some tools that can help address similar issues at other sites.

The multiple stressors theme of this symposium applies in a direct way to the results presented above. In the Rio Grande valley, water quality and quantity are central concerns. Both can be degraded by the interacting stressors of urban and agricultural water uses and, locally, by nutrient translocation due to diel migrations and aggregation of foraging waterfowl. Water quality in the upstream Rio Grande will be improved in proportion to human efforts at remediation through expanded sewage treatment facilities and reductions in non-point loading such as those due to agricultural practices. That is the dominant component in determining water quality in the river because the volume of water diverted to use in the wildlife refuges is a modest proportion of total annual flow. Winter refuges such as the Bosque del Apache can be managed to reduce the local effects of birds and they may be managed to actually make some improvement in water quality as it passes through the refuge system. The net effect of aggressive and effective management of refuge systems such as that practiced at Bosque del Apache can benefit both the water users downstream and the natural resource of bird populations that overwinter there. Each spring, as the birds begin their migration to more northerly breeding grounds, those results are carried to the continental scale.

Earlier in this century, the rapid loss of wetland habitat in North America caused Leopold (1949) to write a eulogy for sandhill cranes. He expected them to go the way of the passenger pigeon. Reversal of that trend and effective development of winter refuges have combined to yield substantial increases in the populations of sandhill cranes and those of some other migratory waterfowl such as snow geese. Leopold would probably be pleased to learn that his prediction

was wrong. He would repeat his assertion that the calls of geese and cranes offer encouragement for continued improvements in the restoration and management of wetlands.

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