

Research Article

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Transfer of nitrogen by migratory birds in the African-Western Eurasian Flyways

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Abstract: Migrating animals are known to play an important role in nutrient transfer over short distances; however, this phenomenon has not been well studied for long-distance migrants. In this preliminary study, we focused on nitrogen (N) transfer by 44 bird species that migrate from Eurasia to two regions in sub-Saharan Africa that fall into the lowest 10% quantile of global N-deposition (mean annual deposition $\leq 10.44 \text{ mg/m}^2/\text{year}$). We estimated the number of birds that die during the non-breeding season in these areas and then used N content and species-specific mass values to calculate annual N-deposition rates. For these two areas of low N-deposition, we found that bird mortality contributed 0.2 – 1.1% of total nitrogen deposition, which is a relatively small proportion. Therefore, we conclude that nitrogen transfer by long-distance bird migrants using the East Atlantic Flyway and the West Asian-East African Flyway currently has limited impact on the sub-Saharan nitrogen cycle. However, it is worth noting that this impact may have been more important in the past due to larger bird populations and lower background N-deposition (i.e., less anthropogenic impact).

Keywords: Bird migration; Bird mortality; Nonbreeding season; Nitrogen cycle; African-Eurasian flyways

1 Introduction

The movement of nutrients between ecosystems by migrating organisms has been well documented in fish [1, 2], seabirds [3] and other taxa [4, 5, 6]. For example, the deposition of nitrogen (N) and phosphorus (P) in bird guano by migrating seabirds on islands increases primary productivity, changes soil characteristics, and affects organisms throughout food webs [7, 8, 9]. Migrating animals in some ecosystems represent a vital seasonal nutritional input that sustains ecosystems throughout the year [10], and nutrient transfer by migrating species changes ecosystem functions in complex ways [6, 11, 12].

Although many studies have addressed intra-ecosystem and neighboring inter-ecosystem nutrient transfer, the role of long-distance (i.e., non-neighboring inter-ecosystem) nutrient transfer has not been well documented. For example, the autumnal Palearctic-African migration system has been estimated to include 2.1 billion passerine and near-passerine individuals [13]. In this flyway complex, population growth occurs in Eurasia during the breeding season, and mortality (with no recruitment) occurs in Africa during the non-breeding season. Thus, assuming overwintering birds are N-flux neutral (i.e., feeding and excretion during overwintering and migration periods are in balance), we suggest there is a net movement of nutrients from Eurasia to Africa each year (Fig. 1). Even if birds deposit nutrients through loss of body mass during migration, much of the migration distance is over the African continent (Fig. 1), so would still represent net movement of nutrients from northern latitudes to Africa. Considering the large number of birds migrating, this process represents a large potential transfer of nutrients from Eurasia to Africa as birds overwinter. African-Eurasian migrant populations have shown considerable declines over time [14, 15, 16], which may impact food web interactions and ecosystem function, including nitrogen dynamics.

We estimated the N-deposition rate by birds that use two African-Eurasian flyways (i.e. the East Atlantic and

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West Asian-East African Flyways) in two sub-Saharan African areas that have low total annual N-deposition rates. From these estimates, we assessed the nutrient input of migratory birds into the fraction of their non-breeding ranges that overlap with these nutrient-limited ecosystems. Our reasoning for selecting the lowest N-depositional sub-Saharan regions was that, if this phenomenon is important, it should be readily evident in these areas.

2 Methods

To determine the maximum proportional nitrogen contribution of migrating birds from Eurasian to African ecosystems, we first found the area of overlap between the two regions with the lowest N-deposition in Africa as determined by a three-dimensional chemistry/transport model (TM3) [17] and the non-breeding ranges of all bird species that migrate from Europe and Western Asia to these areas [18]. These two areas, which had N-deposition rates in the lowest 10% quantile of global nutrient areas (mean annual deposition $\leq 10.44 \text{ mg/m}^2/\text{year}$), are located in southwest South Africa/southern Namibia and northern Namibia/southern Angola (Fig. 2). We then calculated an averaged estimate for species-specific population size [18] and species-specific mass [19] of birds (Table 1). We surveyed the literature for species-specific estimates of average nitrogen content [20-26] and fit a linear regression of averaged nitrogen content for seven species by body

mass (Supplemental Fig. S1). This regression line was then used to predict nitrogen content for species of a known body mass without published data.

Overwinter mortality rate is poorly known for most migratory bird species. We estimated species-averaged overwinter survival rates using bird rings recovered from Africa [27] and methods by Kharitonov [28]. We calculated species-averaged annual survival for the two species with the most frequently returned rings: *Hirundo rustica* (0.55 – 0.61, $n = 228$) and *Pandion haliaetus* (0.77 – 0.84, $n = 475$) [27]. These estimates are consistent with published overwinter survival estimates of species with similar body masses [29, 30, 31]. Therefore, we varied the rate from 10-50%, a range that covers the minimum and maximum estimates of overwinter mortality. The nitrogen deposited by all migratory species was then calculated as a proportion of the total annual natural and anthropogenic nitrogen deposited assuming one of these two mortality rate extremes.

Many bird species partially overlap the two low N-depositional areas, so we created a “heat map” showing how these different mortality rates potentially could affect nitrogen deposition within our two select regions. In the absence of other information, we assumed spatially constant within-range densities for each species. We then apportioned overall overwinter mortality in a spatially constant manner. For example, assuming overwinter mortality of 10%, if 20% of a species’ geographic range overlapped with the low N-depositional areas, then 2% of

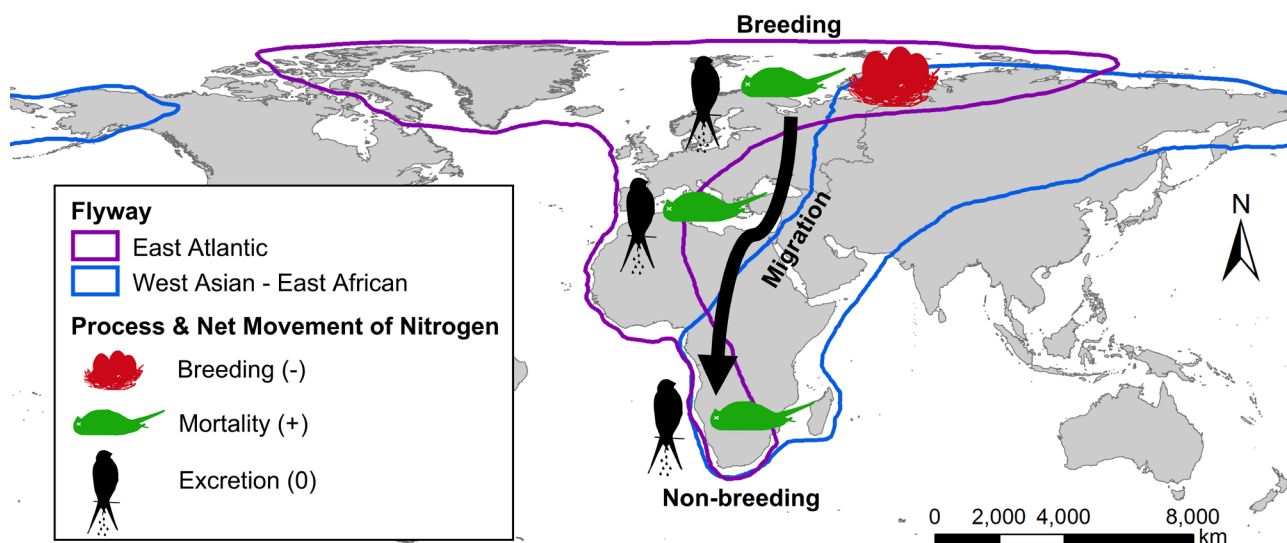


Figure 1: Schematic showing the concept of nitrogen transfer from Europe, Asia, and small parts of North America to Africa via the two flyways analyzed in this study. Large black arrow indicates the net movement of N based on our breeding, mortality, and excretion assumptions.

Table 1: Overlap between species-specific non-breeding areas [18] and two regions of Africa with the lowest background rates of N deposition [17]. Also included are the proportion of overlap between non-breeding range and low-N areas, average population estimate [18], and mass [19] for the 44 species considered.

Scientific Name	Total Non-breed- ing Area (km ²)	Area Overlap w/ Low N (km ²)	Proportion Overlap of Area	Population Estimate (N)	Mass (g)
<i>Acrocephalus arundinaceus</i>	12,930,872	157,289	0.0122	7,275,000	30
<i>Acrocephalus palustris</i>	2,257,789	186,363	0.0825	12,375,000	11.5
<i>Acrocephalus schoenobaenus</i>	16,145,361	150,132	0.0093	17,000,000	11.9
<i>Actitis hypoleucos</i>	34,941,528	978,487	0.0280	2,900,000	48
<i>Apus apus</i>	9,557,826	538,296	0.0563	130,000,000	37.6
<i>Aquila nipalensis</i>	13,722,915	64,933	0.0047	62,500	2745.5
<i>Buteo buteo</i>	9,656,998	872,836	0.0904	2,900,000	875
<i>Calidris minuta</i>	19,861,965	978,487	0.0493	1,550,000	21.1
<i>Caprimulgus europaeus</i>	6,551,248	143,886	0.0220	4,500,000	67
<i>Charadrius asiaticus</i>	8,016,415	221,284	0.0276	45,000	77.1
<i>Charadrius hiaticula</i>	23,758,435	978,487	0.0412	907,500	64.1
<i>Charadrius leschenaultii</i>	3,459,561	53,005	0.0153	245,000	74.8
<i>Chlidonias leucopterus</i>	30,226,582	903,898	0.0299	3,550,000	54.2
<i>Circus macrourus</i>	17,057,270	191,033	0.0112	24,000	388.5
<i>Circus pygargus</i>	11,936,722	85,730	0.0072	300,000	315.5
<i>Coracias garrulus</i>	14,398,581	608,578	0.0423	300,000	146
<i>Coturnix coturnix</i>	13,134,824.	337,333	0.0257	25,000,000	96.5
<i>Crex crex</i>	3,983,064	191,377	0.0480	5,000,000	155.5
<i>Cuculus canorus</i>	12,625,804	152,086	0.0120	57,500,000	111.5
<i>Delichon urbicum</i>	163413854	606,500	0.0037	30,000,000	14.5
<i>Falco naumanni</i>	15,043,484	976,629	0.0649	87,500	152.5
<i>Falco peregrinus</i>	35,961,585	545,526	0.0152	300,000	783.3
<i>Falco subbuteo</i>	11,131,952	301,658	0.0271	750,000	209.5
<i>Falco vespertinus</i>	2,712,636	262,862	0.0969	550,000	152.5
<i>Gallinago media</i>	14,251,367	109,748	0.0077	340,000	170.5
<i>Hieraaetus pennatus</i>	15,680,837	781,282	0.0498	168,500	834.5
<i>Hippolais icterina</i>	5,499,770	141,981	0.0258	12,000,000	13.2
<i>Hirundo rustica</i>	41,554,990	976,629	0.0235	388,500,000	18
<i>Lanius minor</i>	2,087,309	318,263	0.1525	2,250,000	46.5
<i>Merops persicus</i>	12,494,918	107,943	0.0086	400,000	49.3
<i>Motacilla flava</i>	20,004,222	268,710	0.0134	85,000,000	17.7
<i>Muscicapa striata</i>	11,770,534	909,510	0.0773	447,000,000	15.9
<i>Numenius arquata</i>	11,318,060	367,855	0.0325	1,072,500	805.5
<i>Oriolus oriolus</i>	8,377,172	400,099	0.0478	24,500,000	79

Table 1 continued: Overlap between species-specific non-breeding areas [18] and two regions of Africa with the lowest background rates of N deposition [17]. Also included are the proportion of overlap between non-breeding range and low-N areas, average population estimate [18], and mass [19] for the 44 species considered.

Scientific Name	Total Non-breeding Area (km ²)	Area Overlap w/ Low N (km ²)	Proportion Overlap of Area	Population Estimate (N)	Mass (g)
<i>Pandion haliaetus</i>	41,513,580	978,595	0.0236	300,000	1485.5
<i>Pelecanus onocrotalus</i>	15,438,358	631,381	0.0409	280,000	9520
<i>Pernis apivorus</i>	14,002,369	225,505	0.0161	350,000	758
<i>Phylloscopus trochilus</i>	13,292,711	709,083	0.0533	525,000,000	8.7
<i>Porzana porzana</i>	7,668,276	46,380	0.0060	750,000	87.1

that species' biomass was distributed evenly throughout the overlap area as a 'layer' in a geographic information system. We then stacked the species layers and summed the corresponding biomass distributions to estimate total biomass (and hence total N) deposition from dead birds.

3 Results

We estimated that over 43 million individual birds representing 44 species occupy the low N-depositional regions during the non-breeding season. Assuming 10-50% mortality rates for each bird species while in the non-breeding locations gives an annual average N-deposition rate of about 0.02 - 0.118 mg/m²/year. This total is only 0.2 - 1.1% of the total N deposition (natural + anthropogenic) that is presently occurring in the two low-N regions (Table 2). Although we have included a broad estimate of mortality rates, we recognize that our maximum rate (50%) is probably beyond the natural annual mortality range for most species. Local variation in bird abundance within the low-N regions, associated with differences in non-breeding ranges of individual species (11-33 species, Fig. 2A), leads to variation in N-deposition rates within the two low-N areas. Assuming an average 30% mortality rate across species in the non-breeding range, proportional N deposition ranges from near zero to a high of about 1.00%, depending on location within our low-N regions. (Fig. 2B).

4 Discussion

Our results show that N-deposition rates from mortality of migratory birds of the East Atlantic and West Asian-East African Flyways are a minor source of nitrogen input into terrestrial nutrient-poor zones of sub-Saharan Africa. This conclusion assumes equal distribution of migrants, which, as shown in our non-breeding range map, is not likely (Fig. 2). Therefore, local variation in N deposition would lead to a few areas where the overall proportion of N from bird mortality is relatively high, but still a small overall proportional contribution. However, the density of birds is likely larger outside of these low-N areas due to differences in relative primary productivity [32, 33], so our results probably over-estimate the amount of N deposition in these areas. While large numbers of these migrants are present in our selected areas, their relatively small size (i.e., mass) and subsequent small amount of N deposited through mortality events is overwhelmed by other sources of natural and anthropogenic nitrogen inputs. This pattern would be enhanced outside of our low N-depositional environments, which can have N-deposition rates orders of magnitude higher compared to our low-N regions (up to 5000 mg/m²/year) [17] and, therefore, even smaller contributions from migratory birds.

There has been a widespread decline of migratory animal populations across the globe, which, in many cases, has large effects on nutrient transfer within and

Table 2: Summary statistics for bird deaths and nitrogen (N) deposition under two annual mortality scenarios. Mortality rates are estimated per non-breeding period.

Non-breeding Mortality Rate	Number of Birds Dying (millions)	N Deposition (mg N/m ²)	Proportion N Deposition
10%	4.34	0.02	0.002
50%	21.68	0.118	0.011

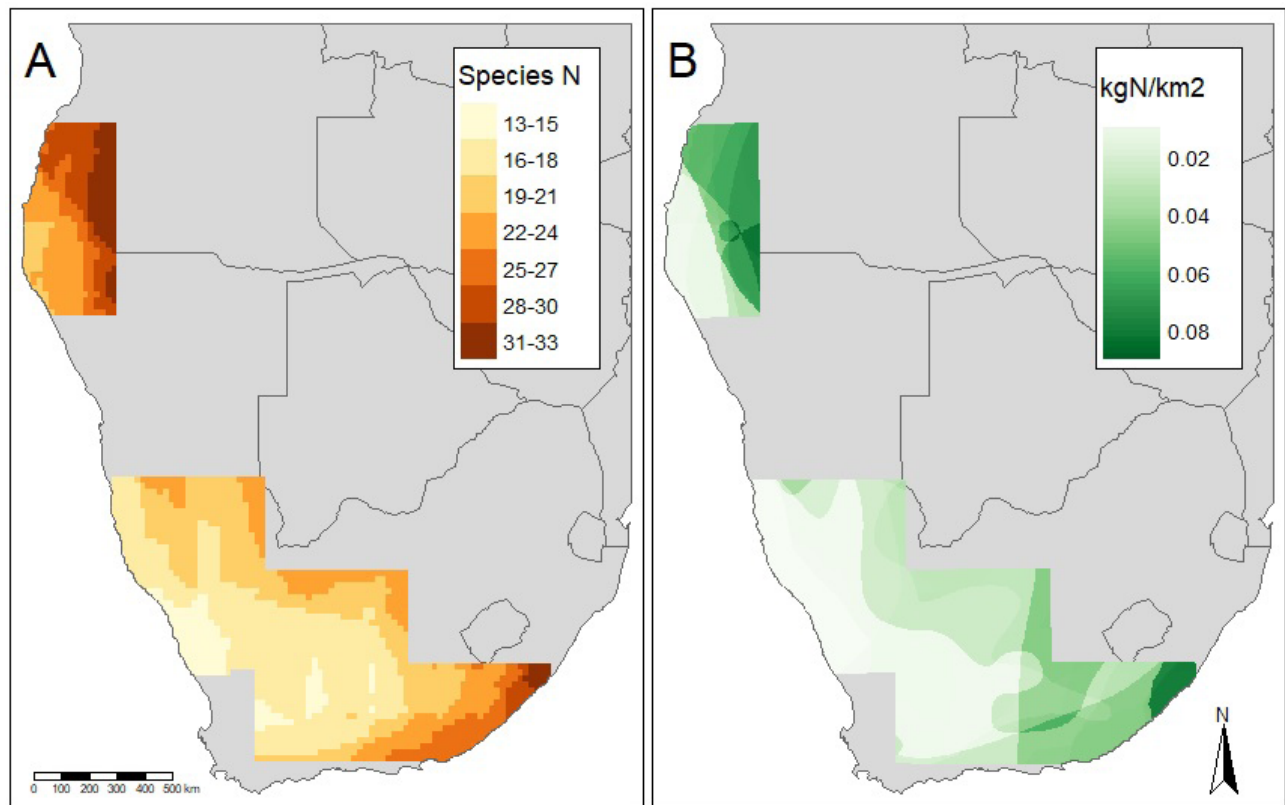


Figure 2: The two regions of Africa that receive the lowest background levels of N deposition, overlapped with a) total number of migratory bird species overwintering in those regions and b) estimated amount of nitrogen deposition due to overwintering mortality, assuming a range mortality rate of 0.30 of the non-breeding population per year.

between ecosystems [34]. The large decline of migratory birds in African-Eurasian flyways [14, 15, 16], while undoubtedly adversely affecting ecosystem services and ecological interactions (e.g., predator-prey dynamics), does not appear to be changing nitrogen cycling in appreciable ways. In the last two centuries, the nitrogen cycle has been drastically modified by human activity, increasing annual terrestrial deposition to about twice pre-industrial level [35, 36]. Therefore, in the recent past, migrating birds were likely a larger proportional contribution to total N deposition. The combination of larger past population sizes of these migrating birds and lower past N deposition would have made the African-Eurasian migration a slightly more important source of nitrogen. However, assuming a 50% decline in migrating birds in this system [16] and a doubling of N deposition due to human activity in the present, migrating bird mortality would have represented only about a 1.7% past proportional N contribution compared to pre-industrial times. Therefore, we conclude that long-distance transfer of N by migrating birds is of minimal importance to the N dynamics within the East Atlantic and West Asian-East African Flyways.

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