ELSEVIER

Contents lists available at SciVerse ScienceDirect

Journal of Great Lakes Research



journal homepage: www.elsevier.com/locate/jglr

Quantification of cormorant litter and nutrient deposition to Great Lakes island ecosystems



Scott A. Rush ^{a,*}, Tammy Dobbie ^b, Aaron T. Fisk ^c

^a Department of Wildlife, Fisheries & Aquaculture, Mississippi State University, Mississippi State, MS 39762, USA

^b Point Pelee National Park, 407 Monarch Lane, RR 1, Leamington, Ontario N8H 3V4, Canada

^c Great Lakes Institute for Environmental Research, University of Windsor, Windsor, Ontario N9B 3P4, Canada

ARTICLE INFO

Article history: Received 18 October 2012 Accepted 18 January 2013 Available online 3 April 2013

Communicated by Craig Hebert

Index words: Ammonia Cormorant management Nitrate Phosphorus Phalacrocorax auritus

ABSTRACT

Ornithogenic nutrients derived from waterbirds such as the double-crested cormorant (Phalacrocorax auritus, Lesson) have been linked to habitat change within nesting colonies. For the islands of Lake Erie, where increasing cormorant populations and subsequent habitat change have spurred management activity, estimates of the quantity and chemical characteristics of avian-derived contributions are lacking. To evaluate the quantity and chemical characteristics of ornithogenic litterfall beneath a double-crested cormorant colony on a western Lake Erie island we investigated the mass of material and nutrient composition (PO_4^{3-} , NO_3^{-} and NH_4^{+}) reaching the forest floor under three nest densities (Low: 1-96 nests ha⁻¹; Medium: 97-255 nests ha⁻¹ and High: >255 nests ha⁻¹). As expected, litterfall (total mass) input differed among nest densities with the most substantial input (225.05 g/m² week⁻¹) measured under High nest density conditions. Nutrient concentrations also showed increases with nest density to a point, where mean PO_4^{3-} and NH_4^+ concentrations showed no differences between Medium and High nest density sites. As well, NO₃⁻ concentrations were highest under Medium density, with no differences in this nutrient observed between Low and High density. Collectively, litterfall nutrient composition was similar to those linked to habitat changes in other waterbird colonies. Similarities in the concentrations of several nutrients between Medium and High nest density categories suggest that management actions aimed at reducing allochthonous nutrient contributions should try to sustain nest density at or below 96 nests ha⁻¹.

© 2013 International Association for Great Lakes Research. Published by Elsevier B.V. All rights reserved.

Introduction

Allochthonous materials transported by waterbirds such as the double-crested cormorant (Phalacrocorax auritus, Lesson) reflect a connection between their aquatic feeding areas and terrestrial breeding environments (Ellis et al., 2006). Subsidies of avian-derived nutrients such as the deposition of guano and other materials have been implicated in the alteration of biochemical nitrogen cycling in many littoral ecosystems (Hebert et al., 2005; Hobara et al., 2001; Mizota, 2009). On islands, the effects of avian-derived materials have been connected to vegetative decline and changes in the biological and functional diversity of altered ecosystems (Kolb et al., 2012; Osono et al., 2002; Rippey et al., 2002). These impacts, among others, have fostered efforts to lower local cormorant populations to levels at which ecosystem impacts are minimized. However, in establishing management targets for protecting island ecosystems, the composition and quantity of avian-derived contributions underlie the ability to predict the response of littoral forest ecosystems.

Materials deposited at waterbird colonies include food items, carcasses (e.g., egg, chick and adult), vegetation debris and metabolic

* Corresponding author. Tel.: +1 662 325-0762.

waste products (Sanchez-Pinero and Polis, 2000). Owing to their nutrient-rich diet, guano likely reflects the important nutrient source for most nest colony ecosystems where avian-derived nitrogen (N) and phosphorus (P) contributions may exceed those from other sources by several orders of magnitude (Furness, 1991). The principal form of N in fresh guano is uric acid (Bird et al., 2008). Under aerobic conditions, uric acid is hydrolyzed to ammonium (NH₄⁺) and gaseous ammonia (NH₃) which can spread and exert influence on surrounding ecosystems (Smith, 1967). Other major compounds in guano include nitrate (NO₃⁻), (Lindeboom, 1984; Schmidt et al., 2004), with phosphate (PO_4^{3-}) typically providing the greatest contribution of total P (Lindeboom, 1984; Smith and Johnson, 1995). Although nutrient mobility can differ among compounds, with higher mobility typically associated with nitrate relative to ammonium and phosphorus (Barber, 1984), the leaching of ornithogenic nutrients from soils can create non-linear effects between materials deposited and concentrations measured in recipient ecosystems, including both spatial and temporal differences (Hobara et al., 2005). Because nutrients can be transformed or transported from an ecosystem, measurements of soil based concentrations may provide only a coarse representation of ecosystem loading.

Over the last 40 years the number of double-crested cormorants nesting within the Laurentian Great Lakes has increased substantially

E-mail address: srush@cfr.msstate.edu (S.A. Rush).

^{0380-1330/\$ -} see front matter © 2013 International Association for Great Lakes Research. Published by Elsevier B.V. All rights reserved. http://dx.doi.org/10.1016/j.jglr.2013.03.002

(Wires and Cuthbert, 2010). Concomitant with this population increase have been changes in plant communities associated with some nesting colonies (Boutin et al., 2011; Hebert et al., 2005). Changes in the plant communities and the potential loss of unique habitats have in part, prompted the development of cormorant management plans (Parks Canada, 2008; USDA, 2006). While habitat conservation through cormorant management is predicated on density and distribution of nesting cormorants little information exists on the quantity and composition of contributions that can occur under various nest densities. Thus, the aims of this study were to investigate the quantity and chemical characteristics of litterfall beneath various cormorant nest densities. Drawing relevance to a nearby island, where active cormorant population monitoring and management have been enacted, we broaden the scale of our study to identifying mean contributions for this additional island ecosystem.

Methods

Study area

Field components of this study took place on Middle Sister (4 ha in size) and Middle Island (18 ha) in western Lake Erie (Fig. 1). Cormorants first colonized Middle Island in 1987 and Middle Sister Island in 1999, with nesting colonies experiencing substantial subsequent growth (Hebert et al., 2005). Following colonization, the vegetative communities of these islands have experienced significant changes, including loss of biological and structural diversity (Boutin et al., 2011; Hebert et al., 2005). At present, major habitat types on both islands include unvegetated rocky shoreline as well as wet and mesic forests (Kamstra et al., 1995). Cormorant nesting activity on Middle Sister and Middle Island occurs annually from late March



Fig. 1. Map of western Lake Erie showing the locations of two study sites, Middle Sister Island and Middle Island. The bottom panel illustrates the density of double-crested cormorant nests on Middle Island during June 2010.

through early September. Although migrating or loafing cormorants may be present on or around the islands for a longer period, their activities are concentrated primarily on the shoreline as opposed to the interior forest habitat where nesting occurs.

Deposition quantification

In order to estimate the quantity of material, and concentrations of PO_4^{3-} , NO_3^{-} , and NH_4^+ deposited on land through bird excreta, 30 plastic tarpaulins (tarps, each 1 m²) were placed on the ground on Middle Sister Island 20-27 May 2010. Prior to field placement, all tarps were weighed to the nearest 0.10 g. Following density categories described in Rush et al. (2011): Low cormorant nest density $(\leq 3 \text{ nests per 10 m radius } [1 \text{ to 96 nests ha}^{-1}])$, Medium density (4–8 nests per 10 m radius [97 to 255 nests ha⁻¹]), and High density sites (>8 nests per 10 m radius [>255 nests ha^{-1}]); 10 sampling sites were delineated to reflect each nest density category. Tarps were staked to the ground at the center of each 10 m radius plot and left in place for one week. After one week tarps, with deposited material, were collected, placed in separate plastic bags, and removed from the island. Samples were stored at -20 °C. All tarps were weighed to the nearest 0.10 g with the mass of deposited materials calculated to reflect g/m². In preparation for nutrient analysis, tarps were soaked for one hour using 18.9 L of tap water. The resulting solution was immediately subsampled and filtered through Whatman GF/C filters (1.2 µm pore size; Whatman, Maidstone, U.K.). A 0.5 L sample was collected from each extract and analyzed for PO_4^{3-} . NO_3^- , and NH_4^+ . Concomitant with extract sampling, like samples of tap water were obtained to be used as blanks run in tandem with our tarp samples for nutrient concentrations.

Nutrients

All laboratory nutrient analyses were conducted at the University of Georgia's Institute of Ecology Analytical Chemistry Laboratory. All standard methods for preparation, analysis, and calculation can be found on their website (http://www.swpa.uga.edu/). Nitrate-N and total N were measured using EPA standard method 353.2 (colorimetric, automated, cadmium reduction), ammonia N using EPA standard method 350.1 (colorimetric, automated phenate), and PO_4^{3-} using EPA standard method 365.1 (colorimetric, automated, ascorbic acid) (USEPA, 1983). Prior to analysis, a solution of persulfate, boric acid, and sodium hydroxide was added to 500 mL of each sample for oxidization and digestion. Samples were then filtered through a 0.45 µm filter and processed on an Alpkem RFA300 continuous flow colorimetric analyzer.

Statistical analysis

Sources of variation in the mass and chemical characteristics of litterfall collected from among the different nest density categories were compared using a Bayesian framework implemented in the R2WinBUGS package in R (R Development Core Team, 2011; Sturtz et al., 2005). We elected to use a Bayesian approach as this type of analysis can prove advantageous when sample sizes are small or the data are not asymptotic (Kéry, 2010). The R2WinBUGS package interfaces with the software package WINBUGS (Fryback et al., 2001) providing model parameters and credible intervals for the observed data. Uninformative priors (normal distributions with zero mean and a standard deviation of 100) were used for all model parameters. For each model, we ran three parallel Markov chain Monte Carlo (MCMC) chains for 50,000 iterations. The first 30,000 burn-in iterations were discarded and chains were thinned to obtain a sample of 10,000 values for each parameter from the joint posterior probability distribution. We examined the Gelman-Rubin statistic (Rhat; Gelman et al., 2004) for each parameter for evidence of lack of convergence. We deemed the convergence of all models was acceptable with Rhat of <1.01 for all variables (Gelman and Hill, 2007).

Custom contrasts were used for comparisons among nest density groups. For each contrast, we considered deposition mass or nutrient concentration as differing among nest density categories if the 95% credibility interval of the contrast did not include zero.

Nest density and environmental characteristics

Drawing inference from our collection sites on Middle Sister Island, we evaluated the potential nutrient loading by double-crested cormorants on a nearby island in western Lake Erie, Middle Island. As on Middle Sister Island, cormorants on Middle Island nest in trees from about late March through early September (T. Dobbie, pers. comm.). Complete island counts of all nesting cormorants have been completed on west Lake Erie islands since 1979 (Weseloh et al., 2002). However, unlike Middle Sister Island, active monitoring of cormorant nest activities has been carried out at specific locations and study plots on Middle Island in 2001 (Hebert et al., 2005) and annually since 2004 (Boutin et al., 2011). In 2004, 12 north-south transects were established across the island with permanent census stations established every 50 m along each transect. Nest counts are carried out annually at each census location using a plotless point centered guarter method, where all nests falling inside a 10 m circle are counted and identified to species (census methods further described in McGrath and Murphy, 2012).

Using nest density information collected for Middle Island in June 2010, we extrapolated our week-long study results from Middle Sister Island. Here, we assume (conservatively) that the greatest densities occur at the time of nest census, typically mid to late-June. Our deposition study on Middle Sister Island was carried out before the height of nesting season and likely represents a conservative estimate of deposition at the height of the breeding season.

For each census location, using the criterion used to categorize nest densities on Middle Sister Island, we assigned each census location into one of three nest densities: Low, Medium or High. Sites with zero nests within the census area were considered to receive no direct deposition and were not included in our cumulative assessments. Using measurements obtained from Middle Sister Island, and nest counts from Middle Island we estimated mean daily deposition rates for the surveyed areas on Middle Island (mg/m² day⁻¹).

Results

No precipitation occurred during the one week period that tarps were left on Middle Sister Island. The mass of materials deposited on tarps during the one-week sampling differed significantly among nest density groupings and followed in the order of nesting density with lowest mass collected in Low density sites $(55.13 \pm 35.26 \text{ g/m}^2)$, followed by Medium (118.78 \pm 38.66 g/m²), and High density $(225.05 \pm 60.00 \text{ g/m}^2)$, (Table 1). Base concentration of PO₄³⁻, NO₃⁻ and NH₄⁺ measured in water used to extract materials were relatively minor (PO₄³⁻: 0.001 \pm 0.001 mg/L; NO₃⁻: 0.21 \pm 0.05 mg/L; NH₄⁺: 2.17 ± 1.25 mg/L). After adjusting for the water-borne concentrations, total phosphate, nitrate and ammonium concentrations differed significantly among some, but not all cormorant nest densities (Table 1). Phosphate concentrations were lowest in the solutions developed from the Low density collections (23.03 \pm 10.36 mg/L) but did not differ between Medium and High density collections (Table 1). Like PO_4^{3-} , NO_3^- and NH_4^+ concentrations were lowest at Low nest density sites but did not differ among Medium and High densities (Table 1).

On Middle Island during June 2010, 292 double-crested cormorant nests were counted within the 52 (10 m radius) survey sites. Nest densities ranged from 1 to 27 nests per 10 m radius with 35% (18/52) of the 52 survey sites with no nest present, 19% (10/52) of survey sites had Low density (1–3 nests/10 m radius), 15% (8/52) were Medium density

306

Table 1

For each measurement, values represent mean \pm SD. Upper-case letters following values reflect significant differences (non-overlapping 95% credible intervals) and *n* gives sample size from tarpaulin collections. Nutrient values adjusted for concentrations measured in water used to extract materials. Daily dry deposition estimated using weekly wet deposition values and not statistically compared.

Nest density	n	Weekly wet deposition				
		Deposition (g/m ²)	PO4 ³⁻ (mg/L)	NO ₃ ⁻ (mg/L)	NH4 ⁺ (mg/L)	
Low ^a Medium ^b High ^c	10 10 10	$\begin{array}{r} 55.13 \pm 35.26^{\text{A}} \\ 118.78 \pm 38.66^{\text{B}} \\ 225.05 \pm 60.00^{\text{C}} \end{array}$	$\begin{array}{r} 23.03 \pm 10.36^{\text{A}} \\ 48.36 \pm 14.53^{\text{B}} \\ 53.38 \pm 6.11^{\text{B}} \end{array}$	$\begin{array}{l} 2.02 \pm 1.01^{A} \\ 3.87 \pm 1.35^{B} \\ 2.99 \pm 2.22^{AB} \end{array}$	$\begin{array}{l} 209.58 \pm 85.81^{\text{A}} \\ 304.80 \pm 87.91^{\text{B}} \\ 369.06 \pm 186.45^{\text{B}} \end{array}$	
Nest density		Estimated mean daily dry d	ated mean daily dry deposition			
		PO_4^{3-} (mg/m ² day ⁻¹)	$\frac{NO_3^-}{(mg/m^2 day^{-1})}$		${ m NH_4^+} \over ({ m mg}/{ m m}^2~{ m day}^{-1})$	
Low Medium High		62.18 130.57 144.13	5.45 10.45 8.07		565.87 822.96 996.46	

^a Low cormorant nest density (1 to 96 nests ha⁻¹).

^b Medium cormorant nest density (97 to 255 nests ha⁻¹).

^c High cormorant nest density (>255 nests ha⁻¹).

(>3 ≤ 8 nests/10 m radius) and 31% (16/52) of survey sites were High nest density (>8 nests/10 m radius). Like Middle Sister Island, other tree-nesting colonial waterbird species were present (great blue heron (*Ardea herodias*, L.), great egret (*Ardea alba*, L.) and black-crowned night-heron (*Nycticorax nycticorax*, L.)) but only the nests of great blue heron were present within the census areas, with nest numbers relatively minor compared with those of cormorants (16 versus 292). Extrapolating nutrient deposition estimates from Middle Sister Island to the 2010 breeding season for Middle Island yields the following daily mean estimated deposition for each square meter of census area: 4.78 mg PO₄³⁻ m² day⁻¹, 0.32 mg NO₃⁻ m² day⁻¹ and 33.93 mg NH₄⁺ m² day⁻¹.

Discussion

The density of cormorant nests can influence both the quantity and chemical characteristics of litterfall beneath nest sites. Whereas the mass of litterfall differed among nest densities, concentrations of PO_4^{3-} , NO_3^{-} and NH_4^{+} exhibited less variation among nest densities (Table 1). Potential sources of variability in litterfall may include the clumped distribution of nests on supporting islands, whereas nest densities of >255 ha⁻¹ may occur within a limited area focusing litterfall within a small spatial scale. Statistical differences in PO_4^{3-} , NO_3^- and NH_4^+ concentrations relative to nest density category suggests little difference in litterfall and nutrient subsidies above Medium nest densities (97 to 255 nests ha^{-1}). This could provide a nest density target for management actions aimed at maintaining or reducing allochthonous contributions to these islands, as reduction of nest densities from High to Medium may not alleviate nutrient input pressure to the ecosystem. The Middle Island management plan (Parks Canada, 2008) aims to maintain a density of 30-60 cormorant nests ha^{-1} , or 1–2 nests per 10 m radius. This nest density range falls within our Low nest density category $(1-96 \text{ nests ha}^{-1})$. In 2010, 54% of survey sites on Middle Island were characterized by Low nest densities of <97 nests ha⁻¹. Although suggesting that approximately half the island received allochthonous contributions on the lower end of our estimates, the limited temporal and spatial scope of our collections indicate the possibility that our measurements underestimate deposition, with greater quantity deposited throughout the breeding season.

Sources of variation in the quantity and composition of deposition can be influenced by the behavior of the contributing species. As ground and tree nesters, cormorants can physically damage trees by breaking branches and removing vegetation (Hobara et al., 2001), which fall to the ground. Although we did not quantify physical damage, previous research has linked changes in vegetation and loss of canopy cover with an increase in cormorant nest density (Boutin et al., 2011; Hebert et al., 2005). Changes in nest density and the distribution of additional contributory species can also influence the quantity and composition of deposition. Although relevant information is currently lacking for most waterbird species, inference can be drawn from other colony-nesting bird species where some information is available. For instance, the mean daily deposition measured at Low density nest sites on Middle Sister Island (62.2 mg PO_4^{3-} m² day⁻ 5.5 mg NO_3^- m² day⁻¹, 538.9 mg NH4⁺ m² day⁻¹) exceed quantities obtained for a ground-nesting seabird, the fairy prion (*Pachyptila turtur*, Kuhl), (5.28 mg P m² day⁻¹, 1.35 mg NO₃⁻¹ m² day⁻¹, and 10.31 mg $NH4^+$ m² day⁻¹; Mulder and Keall, 2001) but fall within the range reported for other burrow-nesting seabirds (58-90 mg P m² day⁻¹, 350–1378 mg N m² day⁻¹; Furness, 1991). In contrast, the extrapolated estimates for Middle Island are below measurements given by Mulder and Keall (2001). However, changes in soil chemistry and habitat communities have been identified even at these lower levels of nutrient input (Mulder and Keall, 2001).

The size of waterbird colonies within Lake Erie can also vary substantially among years, either naturally or through management (Weseloh et al., 2002). For instance, from 2007, the year before cormorant management was initiated on Middle Island, to 2010, the number of survey sites in the Low nest density category changed from 37% to 54%. During the same time period, the percentage of survey sites in the Medium and High nest density categories decreased from 63% to 46%.

Despite the observed changes in cormorant nest densities, the persistence of nutrient pools can have long-term impacts on the affected ecosystems (Boutin et al., 2011; Mulder and Keall, 2001). For instance, soils characterized by high nutrient concentrations often favor plant species capable of achieving high rates of resource acquisition over short time periods (Vidal et al., 2000). Locations with high nest densities are often associated with depauperate plant communities, characterized by lower diversity and more invasive species (Hogg et al., 1989), a situation true for Middle Island (Boutin et al., 2011). Decomposition of organic material may also be protracted in areas characterized by high soil N concentrations (Osono et al., 2006). For instance, nitrogen deposition at similar or lower concentrations than those identified in our study, have been linked to slower turnover of organic matter in forest environments (Berg and Matzner, 1997; Osono et al., 2006). The buildup of organic materials under nest sites can reduce nutrient mobilization, seed germination and recruitment of species historically present in the seedbank (Boutin et al., 2011; Osono et al., 2006). Leaching of nutrients that are not chemically or biologically sequestered

can also result in community changes extending beyond the recipient island (Breuning-Madsen et al., 2008). To this end, the unique conditions of each island and surrounding communities must be considered when predicting the ecological effects of nutrient export (Rush et al., 2011).

Established effects of waterbirds on soil, plant and higher communities suggest many effects of nutrient subsidies may be unpredictable. Because these feedbacks may not be consistent over space or time, research addressing the physical and biological properties of Lake Erie islands as well as the materials deposited on them, will aid the conservation of these communities. Results drawn from this study can be used to establish guidelines, including options available for cormorant management.

Acknowledgments

We thank M. Cook for his assistance with sample analysis. V. Minelga (Point Pelee National Park) provided information on Middle Island nest densities and K. Leclair developed the map. This research was funded by Parks Canada and the Canada Research Chair program. We are indebted to J. Olin and JGLR reviewers for comments provided on an earlier draft of this manuscript.

References

Barber, S.A., 1984. Soil Nutrient Availability. Wiley, New York, NY.

- Berg, B., Matzner, E., 1997. Effect of N deposition on decomposition of plant litter and soil organic matter in forest systems. Environ. Rev. 5, 1–25.
- Bird, M.I., Tait, E., Wurster, C.M., Furness, R.W., 2008. Stable carbon and nitrogen isotope analysis of avian uric acid. Rapid Commun. Mass Spectrom. 22, 3393–3400.
- Boutin, C., Dobbie, T., Carpenter, D., Hebert, C.E., 2011. Effects of double-crested cormorants (*Phalacrocorax auritus* Less.) on island vegetation, seedbank, and soil chemistry: evaluating island restoration potential. Restor. Ecol. 19, 720–727.
- Breuning-Madsen, H., Ehlers, C.B., Borggaard, O.K., 2008. The impact of perennial cormorant colonies on soil phosphorus status. Geoderma 148, 51–54.
- Ellis, J.C., Fariña, J.M., Witman, J.D., 2006. Nutrient transfer from sea to land: the case of gulls and cormorants in the Gulf of Maine. J. Anim. Ecol. 75, 565–574.
- Fryback, D.G., Stout, N.K., Rosenberg, M.A., 2001. An elementary introduction to Bayesian computing using WinBUGS. Int. J. Technol. Assess. 17, 93–113.
- Furness, R.W., 1991. The occurrence of burrow-nesting among birds and its influence on soil fertility and stability. In: Meadows, P.S., Meadows, A. (Eds.), The Environmental Impact of Burrowing Animals and Animal Burrows. Oxford University Press, Oxford, pp. 53–65.
- Gelman, A., Hill, J., 2007. Data Analysis Using Regression and Multilevel/Hierarchical Models. Cambridge University Press, Cambridge, UK.
- Gelman, A., Carlin, J.B., Stern, H.S., Rubin, D.B., 2004. Bayesian Data Analysis, 2nd edition. Chapman and Hall/CRC, Boca Raton, FL.
- Hebert, C.E., Duffe, J., Weseloh, D.V.C., Senese, E.M.T., Haffner, G.D., 2005. Unique island habitats may be threatened by double-crested cormorants. J. Wildl. Manage. 69, 68–76.
- Hobara, S., Ösono, T., Koba, K., Tokuchi, N., Fujiwara, S., Kameda, K., 2001. Forest floor quality and N transformations in a temperate forest affected by avian-derived N deposition. Water Air Soil Pollut. 130, 679–684.
- Hobara, S., Koba, K., Osono, T., Tokuchi, N., Ishida, A., Kameda, K., 2005. Nitrogen and phosphorus enrichment and balance in forests colonized by cormorants: implications of the influence of soil adsorption. Plant Soil 268, 89–101.

- Hogg, E.H., Morton, J.K., Venn, J.M., 1989. Biogeography of island floras in the Great Lakes. 1. Species richness and composition in relation to gull nesting activities. Can. I. Bot. 67, 961–969.
- Kamstra, J.M., Ooldham, M.J., Woodliffe, P.A., 1995. A life science inventory and evaluation of six natural areas in the Erie islands, Essex County, Ontario: Fish Point Provincial Nature Reserve, Lighthouse Point Provincial Nature Reserve, Stone Road Complex, Middle Point, East Sister Island Provincial Nature Reserve and Middle Island. Aylmer District, Ontario Ministry of Natural Resources, Aylmer, ON.
- Kéry, M., 2010. Introduction to WinBUGS for ecologists: a Bayesian approach to regression, ANOVA, mixed models and related analyses. Academic Press, New York, NY, Value and Value and Value analyses. Academic Press, New York, NY, Value and Va
- Kolb, G.S., Jerling, L., Essenberg, C., Palmborg, C., Hambäck, P.A., 2012. The impact of nesting cormorants on plant and arthropod diversity. Ecography 35, 726–740.
- Lindeboom, H.J., 1984. The nitrogen pathway in a penguin rookery. Ecology 65, 269–277. McGrath, D.M., Murphy, S.D., 2012. Double-crested cormorant (*Phalacrocorax auritus*) nesting effects on understory composition and diversity on island ecosystems in Lake Erie. Environ. Manage. 50, 304–314.
- Mizota, C., 2009. Temporal variations in the concentration and isotopic signature of ammonium- and nitrate-nitrogen in soils under a breeding colony of blacktailed gulls (*Larus crassirostris*) on Kabushima Island, northeastern Japan. Appl. Geochem. 24, 328–332.
- Mulder, C.P.H., Keall, S.N., 2001. Burrowing seabirds and reptiles: impacts on seeds, seedlings and soils in an island forest in New Zealand. Oecologia 127, 350–360.
- Osono, T., Hobara, S., Fujiwaraa, S., Kobab, K., Kamedac, K., 2002. Abundance, diversity, and species composition of fungal communities in a temperate forest affected by excreta of the great cormorant *Phalacrocorax carbo*. Soil Biol. Biochem. 34, 1537–1547.
- Osono, T., Hobara, S., Kobac, K., Kamedad, K., Takeda, H., 2006. Immobilization of avian excreta-derived nutrients and reduced lignin decomposition in needle and twig litter in a temperate coniferous forest. Soil Biol. Biochem. 38, 517–525.
- Parks Canada, 2008. The Middle Island Conservation Plan. Point Pelee National Park of Canada. http://www.pc.gc.ca/eng/pn-np/on/pelee/plan/plan8.aspx.
- R Development Core Team, 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rippey, E., Rippey, J.J., Dunlop, J.N., 2002. Increasing numbers of pied cormorants breeding on the islands off Perth, Western Australia and consequences for the vegetation. Corella 26, 61–64.
- Rush, S.A., Verkoeyen, S., Dobbie, T., Dobbyn, S., Hebert, C.E., Gagnon, J., Fisk, A.T., 2011. Influence of increasing populations of double-crested cormorants on soil nutrient characteristics of nesting islands in western Lake Erie. J. Great Lakes Res. 37, 305–309.
- Sanchez-Pinero, F., Polis, G.A., 2000. Bottom-up dynamics of allochthonous input: direct and indirect effects of seabirds on islands. Ecology 81, 3117–3132.
- Schmidt, S., Dennison, W.C., Moss, G.J., Stewart, G.R., 2004. Nitrogen ecophysiology of Heron Island, a subtropical coral cay of the Great Barrier Reef, Australia. Funct. Plant Biol. 31, 517–528.
- Smith, V.R., 1967. Chemical composition of precipitation at Marion Island (sub-Arctic). Atmos. Environ. 21, 1159–1165.
- Smith, J.S., Johnson, C.R., 1995. Nutrient inputs from seabirds and humans on a populated coral cay. Mar. Ecol. Prog. Ser. 124, 189–200.
- Sturtz, S., Ligges, U., Gelman, A., 2005. R2WinBUGS: a package for running WinBUGS from R. J. Stat. Softw. 12, 1–16.
- USDA (U.S. Department of Agriculture), 2006. Final Environmental Assessment: Reducing Double-Crested Cormorant Damage in Ohio. USDA, APHIS, WS, Columbus, Ohio, USA (http://www.fws.gov/midwest/MidwestBird/documents/OhioDCCOfinalEA.pdf. [Last accessed October 2012]).
- USEPA (U.S. Environmental Protection Agency), 1983. Methods for Chemical Analysis of Water and Wastes, EPA-600/4 4-79-020. USEPA, Cincinnati, Ohio, USA.
- Vidal, E., Médail, F., Tatoni, T., Bonnet, V., 2000. Seabirds drive plant species turnover on small Mediterranean islands at the expense of native taxa. Oecologia 122, 427–434.
- Weseloh, D.V.C., Pekarik, C., Havelka, T., Barrett, G., Reid, J., 2002. Population trends and colony location of double-crested cormorants in the Canadian Great Lakes and immediately adjacent areas, 1990–2000: a manager's guide. J. Great Lakes Res. 28, 125–144.
- Wires, L.R., Cuthbert, F.J., 2010. Characteristics of double-crested cormorant colonies in the U.S. Great Lakes island landscape. J. Great Lakes Res. 36, 232–241.