

Response of nesting savannah sparrows to 25 years of habitat change in a snow goose colony¹

Robert F. ROCKWELL² & Christopher R. WITTE, American Museum of Natural History, New York,

New York 10024, U.S.A., e-mail: rfr@amnh.org

Robert L. JEFFERIES, Department of Botany, University of Toronto, Toronto, Ontario M5S 3B2, Canada.

Patrick J. WEATHERHEAD, Program in Ecology and Evolutionary Biology, University of Illinois,

Urbana, Illinois 61801, U.S.A.

Abstract: Duplication of a study conducted 25 years earlier reveals that the number of savannah sparrows nesting adjacent to the coastal salt marshes of La Pérouse Bay in northern Manitoba, Canada, has declined by 77%. This decline coincides with a 63% reduction in vegetation cover in the bird's preferred grassland-shrub habitat. The habitat degradation resulted from processes associated with destructive foraging by the increasing mid-continent population of lesser snow geese during their breeding season. Growth of this snow goose population has been initiated and sustained by a series of anthropogenic factors operating primarily on the snow goose wintering grounds, far south of these Arctic coastal habitats. Thus, the indirect human impact on nesting by savannah sparrows is the result of a complex chain of ecological events operating on connected habitats across a large geographical expanse. Mitigation of such effects and an assessment of the impacts in general must take into account such complexities.

Keywords: savannah sparrow, snow goose, habitat degradation, collateral damage, anthropogenic effects, connected habitats, Hudson Bay.

Résumé : Après avoir répété une étude menée il y a 25 ans, nous avons découvert que les effectifs de Bruant des prés qui niche près des marais côtiers salés de la baie La Pérouse dans le nord du Manitoba, au Canada, ont baissé de 77 %. Ce déclin coïncide avec une réduction de 63 % du couvert végétal de l'habitat de prédilection de l'oiseau, soit la prairie arbustive. La détérioration de l'habitat peut être associée au broutement de la végétation par les petites oies des neiges pendant la période de reproduction. Le broutement des oies s'est en effet intensifié au cours des dernières années, conséquence d'une augmentation du nombre d'individus. La croissance de la population d'Oie des neiges a été amorcée et entretenue par une série de facteurs anthropiques, particulièrement dans les lieux d'hivernage des oies qui sont situés beaucoup plus au sud que les habitats côtiers de l'Arctique. En somme, l'impact indirect des humains sur la nidification des bruants des prés est le résultat d'une chaîne complexe d'événements écologiques qui ont agi sur des habitats interreliés et qui ont eu des répercussions sur une vaste région. L'atténuation de ces effets et l'évaluation des impacts devraient tenir compte d'une telle complexité.

Mots-clés : Bruant des prés, Oie des neiges, détérioration de l'habitat, dommages collatéraux, effets anthropiques, habitats interreliés, baie d'Hudson.

Nomenclature: Porsild & Cody, 1980; American Ornithologists' Union, 1998.

Introduction

Identifying negative human impacts on natural populations is often straightforward, particularly in cases where direct overexploitation of a population or its habitat causes a population decline (Goudie, 2000). Matters are less straightforward when the negative impacts are brought about through alterations of ecological relationships across connected habitats, particularly when the causes and effects are both ecologically and geographically separated (Young & Chapin, 1995; Bazely & Jefferies, 1997; Polis, Anderson & Holt, 1997). A further difficulty in documenting negative impacts on populations is the need for reliable data collected prior to a perceived decline. Here, we take advantage of data on a tundra-breeding population of savannah sparrows (*Passerculus sandwichensis*) collected 25 years ago to assess how intervening, anthropogenic-based increases in numbers of lesser snow geese (*Chen caerulescens caerules-*

cens), paired with their destructive foraging in the Hudson Bay lowlands, have affected the nesting biology of the savannah sparrows sharing that habitat.

The mid-continent population of lesser snow geese traditionally wintered in coastal marshes of the Gulf of Mexico (Bateman, Joanen & Stutzenbaker, 1988). Beginning in the early 1940's, and responding to protection from predators afforded by islands in flooded coastal rice fields, wintering geese began to roost on these agricultural islands (Lynch, O'Neil & Lay, 1947; Lynch, 1975). Exacerbated by coastal development, this quickly led to increasing use of adjacent inland agricultural lands, where the birds fed on waste grain and intact crops. This shift has continued, with lesser snow geese now wintering as far north as Iowa and Nebraska when weather permits (Abraham *et al.*, 1996; Jefferies, Henry & Abraham, 2003). This unintentional provisioning of food has contributed to a rapid and sustained increase in the mid-continent snow goose population. The increase has been exacerbated by other anthropogenic factors, including

¹Rec. 2002-05-13; acc. 2002-09-24.

²Author for correspondence.

the construction of migratory waterfowl refuges and a reduction (until very recently) in harvest by hunters (Abraham *et al.*, 1996; Jefferies, Henry & Abraham, 2003). While there is no indication that the increasing numbers of snow geese are seriously damaging their wintering habitats or those encountered in the United States and southern Canada during migration, the same is not true for their northern staging and nesting habitats.

Destructive snow goose foraging (grubbing), especially during spring staging and immediately before nesting, has resulted in significant habitat changes at several coastal sites in the Hudson Bay lowlands (Abraham *et al.*, 1996; Abraham & Jefferies, 1997; Jefferies, Henry & Abraham, 2003). One of the most extensively studied and well-documented sites is La Pérouse Bay, east of Churchill, Manitoba, Canada (Srivastava & Jefferies, 1996; Jefferies, 1997; Bazely & Jefferies, 1997; Jano, Jefferies & Rockwell, 1998; Handa, Harmsen & Jefferies, 2002; Jefferies & Rockwell, 2002). Vegetation in both the lower and upper sections of the coastal marshes has been badly damaged or destroyed and the habitat severely degraded, an effect that is exacerbated through physical processes initiated by vegetation removal (Hik, Jefferies & Sinclair, 1992). Loss of vegetation and exposure of sediments results in hypersaline conditions and changes in soil physical properties that are inimical to plant growth (Iacobelli & Jefferies, 1991; Srivastava & Jefferies, 1995; 1996). Intertidal and supratidal swards of grasses and sedges have been replaced by mudflats that are hypersaline in summer and which support only highly salt-tolerant annual species (*Salicornia borealis* and *Atriplex glabiscula*) (Jefferies *et al.*, 1995; Jefferies & Rockwell, 2002). Although forage availability in inter- and supratidal habitats has become more limiting in recent decades, the snow goose population has continued to grow as birds have exploited freshwater wetlands adjacent to the coast (Abraham & Jefferies, 1997; Cooch, Rockwell & Brault, 2001). This more inland habitat has now also become degraded, as has the transition zone, where supra-tidal graminoid-willow assemblages grade into communities richer in shrubs, especially willows (Kotanen & Jefferies, 1997; Jano, Jefferies & Rockwell, 1998; Handa, Harmsen & Jefferies, 2002).

Records from the late 1960s and early 1970s indicate that a now-degraded portion of this transition zone was formerly an intact shrub-grassland habitat and was used extensively for nesting and/or foraging by a number of species of passerines. These included blackpoll warblers (*Dendroica striata*), yellow warblers (*Dendroica petechia*), horned larks (*Eremophila alpestris*), savannah sparrows, American tree sparrows (*Spizella arborea*), white-crowned Sparrows (*Zonotrichia leucophrys*), common and hoary Redpolls (*Carduelis flammea* and *C. hornemanni*), and Lapland longspurs (*Calcarius lapponicus*) (Cooke *et al.*, 1975). An obvious question is has the degradation of this habitat negatively impacted any of the passerine species that use it? Addressing this question is important because if the habitat damage by the geese has harmed other breeding birds, and additional harm can be anticipated in the future, then this "collateral damage" becomes another factor to be considered when deciding how snow goose populations should be managed.

In 1976, before this area became degraded, Weatherhead (1979) initiated a behavioural study of savannah spar-

rows, and as part of his work, the nesting population was thoroughly inventoried and the vegetation cover was quantitatively assessed. We repeated the nesting inventories in 1999, 2000, and 2001 to evaluate potential impact and repeated the vegetation assessment in 1999. The latter was undertaken in part to quantify vegetation changes at finer scale than was possible with LANDSAT imagery (Jano, Jefferies & Rockwell, 1998). We report here that over the past 25 years both the nesting density of savannah sparrows and the vegetation cover have significantly declined in this willow-grassland habitat. We argue that the results indicate that even this generally abundant and resilient species has been impacted by snow goose-induced habitat changes that ultimately are driven by anthropogenic causes thousands of kilometres away.

Methods

The study was carried out immediately southeast of the Hudson Bay Project Research Station at La Pérouse Bay, 30 km east of Churchill, Manitoba, Canada. The study site (northwest corner: 58° 43.5' N, 93° 27.9' W) is an area of grass, sedge, and shrub and is described in Weatherhead (1979). A grid system was established in 1976 that consisted of north to south lanes (each 50 metres wide) and east to west rows (each 50 metres wide). Intersects were marked with wooden stakes. Using aerial photos, field notes, landmarks, and compass bearings, we were able to find many of the original wooden stakes and to re-establish the eastern sector of the grid system in 1999. We focused our efforts on this sector because it was the primary nesting habitat of savannah sparrows in the 1970s (Weatherhead, 1979) and because there was a low incidence of interference by polar bears (*Ursus maritimus*). In total, we used 28 of the original 50-m × 50-m grid cells, covering a combined area of 7 hectares. They were organized as 4 contiguous north to south lanes (referred to as I, J, K, L) intersected by 7 east-west rows. Row 1 was closest to the Mast River, a source of fresh water. We duplicated as far as possible the methods and procedures used in Weatherhead's (1979) original study.

Savannah sparrows nest on the ground, usually at the bases of shorter shrubs where there is ample grass used for nest construction and concealment (Weatherhead, 1979; Wheelwright & Rising, 1993). Because nests can be quite cryptic, we located them by thorough searches of the entire grid system every 4-5 days beginning in late May and extending until late July. Entry into the study area was prohibited at other times. Some nests were discovered by flushing females from nests. Nests were marked with flagging tape in 1976 and with short stakes from 1999 to 2001. They were also marked on grid maps, and precise GPS locations were recorded in the latter 3 years. Analysis of variance of the density of nests per grid cell and contingency analyses of the distributions of cells with and without nests were used to evaluate the data. We avoided inflation of overall α -error rates using Bonferroni adjustments to the p -values required for significance.

The diagonals of each grid cell were used as vegetation transects. They were traversed on foot, and the vegetation and habitat status at each pace was recorded. In 1976, habitat status was classified as one of the following: bare soil,

shallow pond, sedge-short grass, mixed grass-short willow, *Elymus* (*Leymus arenarius*), and willow species (further classified by height). In 1999, the habitat status was classified using a comparable, but more botanically explicit, procedure. We identified grasses, sedges, and willows and included several species that were apparently rare or absent in 1976. We also included an assessment of the status of shrubs, as dead (100% dead branches), dying (more than 1/3 dead branches), or living (less than 1/3 dead branches).

Our primary intent was to examine the overall change in vegetative cover available for nesting savannah sparrows. Owing to the rarity of some of the more intensively evaluated vegetation classes in 1999, it was necessary to collapse the habitat data into three classes (“barren”, “grass”, and “shrub”) that were synonymous with the original classes recognized in 1976. Then, the “barren” habitat consisted of the bare soil and pond classes, the “grass” class included the sedge-short grass and *Elymus* classes, and the “shrub” class included the mixed grass-short willow/shrub class and all willow classes. In 1999, the “barren” class included the bare soil and pond classes, as well as several classes not present in 1976 (or so exceptionally rare they were not recorded) but representing habitats not used by savannah sparrows for nesting. These included dry algal mats on bare soil, *Salicornia borealis*, *Senecio congestus*, *Atriplex glabriuscula*, mosses, and completely dead shrubs with no ground vegetative cover. In 1999, the “grass” class included grasses and sedges, and the “shrub” class consisted of all species of *Salix*, together with *Betula glandulosa* and *Myrica gale*, all of which had to be at least partially living.

Data from the 2 diagonals in each cell were pooled, and the frequencies of the 3 habitat classes were tallied. The frequency vector for each cell represents the number of paces of each habitat type encountered along the 2 diagonals. The frequency data were cross-classified by year, lane, and row. We evaluated changes in the relative distribution of the three habitat states over time and across the 2 spatial variables using log-linear models, an approach sometimes referred to as multidimensional contingency analysis (Bishop, Fienberg & Holland, 1975; Jefferies & Rockwell, 2002). The distribution of states was considered a response variable, while year, lane, and row were considered classification variables. Since our objective was to determine changes in the relative proportions of the three response variable states over time, we only considered models that included second and higher order terms involving habitat state, and only values associated with such terms are given in the Results. This constraint is consistent with the fixed nature of each transect over time (Fienberg, 1980; Everitt, 1992; Jefferies & Rockwell, 2002). The log-linear models used to determine dependency of state type on year, lane, and row were generated using the CATMOD procedure from SAS[®] 8.0. Effects were evaluated statistically using the Wald statistic, with significance of second and higher order terms confirmed with the use of a log-ratio chi-square statistic of the less saturated model (Stokes, Davis & Koch, 2000). Since the nature of hierarchical model analysis requires repeated evaluation of subsets of the data, we have reduced inflation of our overall α -error rate with a Bonferroni approach that requires $p < 0.05/28 \cong 0.0018$.

Results

In 1976, there were 24 savannah sparrow nests distributed among the 28 grid cells. Savannah sparrows were also studied on this site in 1977, and while nest searches were not exhaustive as in 1976, sparrow densities appeared comparable to 1976 (Weatherhead, unpubl. data.). In 1999, 2000 and 2001 the numbers of savannah sparrow nests were 6, 4, and 7, respectively. This 77% reduction in average nesting density is depicted in figure 1, where the data are summarized as nests per hectare. Both the analysis of variance and contingency analysis indicate that there are no significant differences among the 1999, 2000, and 2001 estimates and that all of those are significantly less than the estimate in 1976. (Overall ANOVA: $F = 11.45$; $df = 3, 108$ $p < 0.0001$ with pair-wise contrasts evaluated under a Bonferroni adjusted $p < 0.008$. Overall $G = 12.15$, $df = 3$, $p < 0.005$; subset 1999-2001 $G = 1.07$, $df = 2$, $p > 0.5$; heterogeneity $G = 11.08$, $df = 1$, $p < 0.001$.)

The relative frequencies of the 3 habitat types, summarized for the 7 rows and each of the 4 contiguous north to south lanes, are depicted for both 1976 and 1999 in figure 2. An overall log-linear model analysis of the data indicates that changes in the relative distribution of the 3 habitat types depend on unique combinations of year, lane, and row (Wald statistic = 112.57; $df = 36$; $p < 0.0001$). Further analyses of each cell indicate that there has been a significant change in each cell during the 23 years (range of Wald statistics: 30.02 to 92.71, each with $df = 2$ and $p < 0.0001$). Although the precise extent and pattern of the change differs spatially (consistent with the significant overall analysis), the general trend is clear. In all cells, the proportion of “barren” habitat has significantly increased by values ranging from 51% to 423%. This increased “barren” habitat has been consistently gained as a result of reductions in the shrub class (significant reductions ranging from 46% to 94%).

Beyond the reduction in the extent of the shrub habitat class, the remnant shrubs themselves differ from those surveyed in 1976 in that 89% of them are dying (more than 1/3 of their branches are dead). This effect is independent of location within the study area. In 1976, few of the shrubs

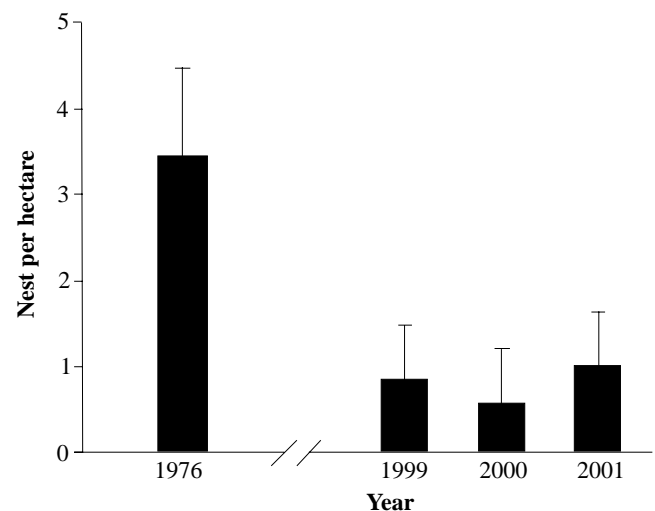


FIGURE 1. Nesting density of savannah sparrows at La Pérouse Bay (with 95% confidence limits).

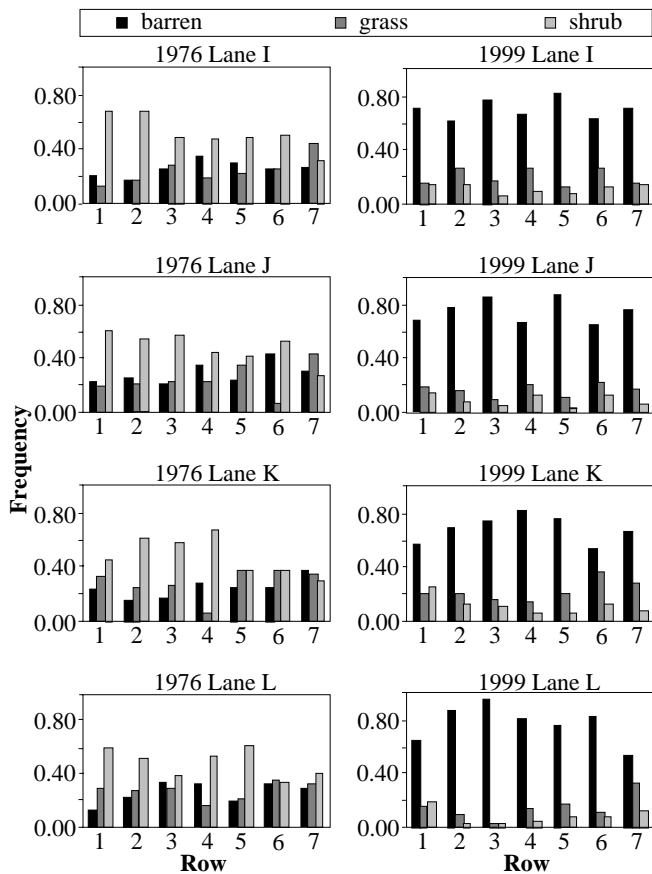


FIGURE 2. Changes in habitat composition over 23 years along 4 north to south transects at La Pérouse Bay.

defining this habitat type were dying. Shrub death is related to increased salinity (see below) and is part of a continuum leading from live shrubs directly to the “barren” habitat class, which includes completely dead shrubs lacking ground vegetative cover. As branches of shrubs die, they are often broken off near their bases by passing caribou (*Rangifer tarandus*) and polar bears or sheared by physical forces associated with ice, snow, storm tides, and spring flooding. The same is the case for the nearly complete central portions of dead shrubs that persist for a short time as “skeletons”. Ultimately, storm tides and spring floods remove broken and sheared remnants from the area.

Discussion

The nesting density of savannah sparrows in the study area has decreased significantly from 3.44 nests/hectare in 1976 to an average of 0.80 nests/hectare in 1999–2001. This 77% reduction corresponds to an annual geometric decline over the 25 years of approximately 6% ($\lambda = 0.943$). In the immediate Churchill area, National Breeding Bird Survey (BBS) data are only available for some of the years between 1976 and 2001. Our analysis of these data (retrieved from the BBS web site www.mp2-pwrc.usgs.gov/bbs/) indicates there was no significant change in the index of breeding savannah sparrows over that period ($F = 0.76$, $p = 0.41$). Our analysis of the BBS data for all of Manitoba for all years from 1976 to 2000 (obtained from the BBS web site www.cws-scf.ec.gc.ca/nwrc/bbs.htm) indicates that the

species index is increasing at an annual geometric rate of approximately 2.9% ($\lambda = 1.029$, $F = 197.83$, $p < 0.001$). Based on the available data, then, we conclude that the decline in nesting demonstrated for savannah sparrows at La Pérouse Bay is a localized effect rather than an epi-phenomenon of a more global species reduction.

The vegetation cover in the La Pérouse Bay study site has been reduced, on average, by 63% corresponding to an annual geometric decline over the 23 years of approximately 4% ($\lambda = 0.959$). This finer-level analysis is consistent with declines indicated by more broadly based remote sensing of vegetation (Jano, Jefferies & Rockwell, 1998). Our analyses also indicate that the majority of the vegetation change at the study site is loss of shrubs, a plant group that is less salt-tolerant than the coastal graminoid vegetation (Jefferies, Jensen & Abraham, 1979; Bazely & Jefferies, 1997; Handa, Harmsen & Jefferies, 2002). The observed pattern of loss of shrubs, including the substantial increase in dying shrubs, is consistent with salinization and desertification processes associated with the removal of ground-level vegetation near the bases of shrubs (Iacobelli & Jefferies, 1991; Srivastava & Jefferies, 1995; 1996; Bazely & Jefferies, 1997). Large numbers of nesting and staging snow geese were observed grubbing among willows in this area from 1984 through 1988 (Rockwell, unpubl. data) and are the most likely cause of loss of shrubs (Jefferies, 1988). Shrubs are a key structural component defining adequate nesting and foraging habitat for savannah sparrows in this region (Weatherhead, 1979), and their loss is the primary contributor to the decline in nesting by savannah sparrows.

Recent surveys of equally degraded habitat extending up to several kilometres beyond the study site have also shown that the nesting density of savannah sparrows is less than 1 nest/hectare (Rockwell, unpubl. data). Although we have no historic savannah sparrow nesting data for these more extensive former snow goose staging and nesting areas, the observations support the conclusion that savannah sparrow nesting has been negatively impacted by snow goose-induced habitat degradation at a broader scale across the La Pérouse Bay region. The geographic scale of this effect is currently under investigation.

Habitat degradation associated with the expanding mid-continent population of lesser snow geese has been well documented for salt marshes of the Hudson Bay lowlands. This study demonstrates at ground level that the degradation extends into more inland shrub habitat and that, as a consequence, local nesting by savannah sparrows has declined substantially. Although this is the only passerine species for which we have adequate historic data, we suggest that other species historically using this type of habitat, especially those that are less broadly adapted and resilient than savannah sparrows (e.g., tree sparrows), may also have declined locally. Our results provide an example of how human actions influencing a species in one geographic area can negatively impact another geographically distant species through a complex ecological chain of events across connected habitats. The assessment and mitigation of human environmental impacts should account for such complex ecological interactions and connectivity (Webster *et al.*, 2002). In this specific case, actions aimed at reducing or reversing the impact of the anthropogenic-based increases in the mid-continent population of lesser snow geese need

to consider impacts on passerine species occupying areas adjacent to traditional snow goose nesting habitat.

Acknowledgements

We thank the many field workers who have successfully avoided polar bears and searched for savannah sparrow nests at La Pérouse Bay. We particularly appreciate the efforts of J. Granick, S. Hansen, D. Larsen, P. Matulonis, and J. Walker. This research has been supported in part through funds provided by the Central and Mississippi Flyway Councils, U.S. Fish and Wildlife Service (Region 6), The City University of New York (PSC-CUNY Research Award Program), and Wapusk National Park. We appreciate the cooperation of Wapusk National Park and their Warden Services in supporting our efforts.

Literature cited

- Abraham, K. F., R. L. Jefferies, R. F. Rockwell & C. D. MacInnes, 1996. Why are there so many white geese in North America? Pages 79-92 in Proceedings of the 7th International Waterfowl Symposium, Ducks Unlimited, Memphis, Tennessee.
- Abraham, K. F. & R. L. Jefferies, 1997. High goose populations: Causes, impacts and implications. Pages 7-72 in B. Batt (ed.). Arctic Ecosystems in Peril: Report of the Arctic Goose Habitat Working Group. Arctic Goose Joint Venture, Canadian Wildlife Service, Ottawa and U.S. Fish and Wildlife Service, Washington, D.C.
- American Ornithologists' Union, 1998. Check-list of North American Birds, 7th edition. American Ornithologists' Union, Washington, D.C.
- Bateman, H. A., T. Joanen & C. D. Stutzenbaker, 1988. History and status of midcontinental snow geese in their Gulf Coast winter range. Pages 495-516 in M. W. Weller (ed.). Waterfowl in Winter. University of Minnesota Press, Minneapolis, Minnesota.
- Bazely, D. R. & R. L. Jefferies, 1997. Trophic interactions in arctic ecosystems and the occurrence of a terrestrial trophic cascade. Pages 183-208 in S. J. Woodin & M. Marquiss (ed.). Ecology of Arctic Environments. Blackwell, Oxford.
- Bishop, Y. M. M., S. E. Fienberg & P. W. Holland, 1975. Discrete Multivariate Analysis: Theory and Practice. MIT Press, Cambridge, Massachusetts.
- Cooch, E. G., R. F. Rockwell & S. Brault, 2001. Retrospective analysis of demographic responses to environmental change: A lesser snow goose example. Ecological Monographs, 71: 377-400.
- Cooke, F., Ross, R.K., Schmidt, R. K. & Pakulak, A. J., 1975. Birds of the tundra biome at Cape Churchill and La Pérouse Bay. Canadian Field-Naturalist, 89: 413-422.
- Everitt, B. S., 1992. The Analysis of Contingency Tables. Chapman & Hall, London.
- Fienberg, S. E., 1980. The Analysis of Cross-Classified Categorical Data. MIT Press, Cambridge, Massachusetts.
- Goudie, A., 2000. The Human Impact on the Natural Environment, 5th edition. MIT Press, Cambridge, Massachusetts.
- Handa, I. T., R. Harmsen & R. L. Jefferies, 2002. Patterns of vegetation and the recovery potential of degraded areas in a coastal marsh system of the Hudson Bay lowlands. Journal of Ecology, 90: 86-99.
- Hik, D. S., R. L. Jefferies & A. E. R. Sinclair, 1992. Foraging by geese, isostatic uplift and asymmetry in the development of salt-marsh plant communities. Journal of Ecology, 80: 395-406.
- Iacobelli, A. & R. L. Jefferies, 1991. Inverse salinity gradients in coastal marshes and the death of stands of *Salix*: The effects of grubbing by geese. Journal of Ecology, 79: 61-73.
- Jano, A. P., R. L. Jefferies & R. F. Rockwell, 1998. The detection of change by multitemporal analysis of LANDSAT data: The effects of goose foraging. Journal of Ecology, 86: 61-73.
- Jefferies, R. L., 1988. Pattern and process in arctic coastal vegetation in response to foraging by Lesser Snow Geese. Pages 281-300 in M. Werger, P. J.M. van der Aart, H. J. During & J. T. A. Verhoeven (ed.). Plant Form and Vegetation Structure. S.P.B. Academic Publishers, The Hague.
- Jefferies, R. L., 1997. Long-term damage to sub-arctic coastal ecosystems by geese: Ecological indicators and measures of ecosystem dysfunction. Pages 151-165 in R. M. M. Crawford (ed.). Disturbance and Recovery in Arctic Lands. Kluwer Academic Publishers, Dordrecht.
- Jefferies, R. L., F. L. Gadallah, D. S. Srivastava & D. J. Wilson, 1995. Desertification and trophic cascades in arctic coastal ecosystems: A potential climatic change scenario? Pages 201-206 in T. Callaghan (ed.). Global Change and Arctic Terrestrial Ecosystems. Proceedings from the NINA Symposium, Oppdahl.
- Jefferies, R. L., H. A. L. Henry & K. F. Abraham, 2003. Agricultural nutrient subsidies to migratory geese and change in Arctic coastal habitats. G. A. Polis & M. E. Power (ed.). Food Webs at the Landscape Level. University of Chicago Press, Chicago, Illinois: in press.
- Jefferies, R. L., A. Jensen & K. F. Abraham, 1979. Vegetational development and the effect of geese on vegetation at La Pérouse Bay, Manitoba. Canadian Journal of Botany, 57: 1439-1450.
- Jefferies, R. L. & R. F. Rockwell, 2002. Foraging geese, vegetation loss and soil degradation in an arctic salt marsh. Applied Vegetation Science, 5: 7-16.
- Kotaniemi, P. M. & R. L. Jefferies, 1997. Long term destruction of wetland vegetation by Lesser Snow Geese. Écoscience, 4: 1895-1898.
- Lynch, J. J., 1975. Winter ecology of snow geese on the Gulf Coast 1925-1975. Page 45 in Proceedings of the 37th Midwest Fish and Wildlife Conference, Toronto, Ontario.
- Lynch, J. J., T. O'Neil & D. W. Lay, 1947. Management significance of damage by geese and muskrats to Gulf coast marshes. Journal of Wildlife Management, 11: 50-77.
- Polis, G. A., W. B. Anderson & R. D. Holt, 1997. Towards an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics, 28:289-316.
- Porsild, A. E. & W. J. Cody, 1980. Vascular Plants of Continental Northwest Territories, Canada. National Museum of Canada, Ottawa, Ontario.
- Srivastava, D. S. & R. L. Jefferies, 1995. Mosaics of vegetation and soil salinity: A consequence of goose foraging in an arctic salt marsh. Canadian Journal of Botany, 74: 75-83.
- Srivastava, D. S. & R. L. Jefferies, 1996. A positive feedback: Herbivory, plant growth, salinity and the desertification of an arctic salt marsh. Journal of Ecology, 84: 31-42.
- Stokes, M. E., C. S. Davis & G. G. Koch, 2000. Categorical Data Analysis Using the SAS[®] System, 2nd edition. SAS Institute, Cary, North Carolina.
- Weatherhead, P. J., 1979. Ecological correlates of monogamy in tundra-breeding savannah sparrows. Auk, 96: 391-401.
- Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch & R. T. Holmes, 2002. Links between worlds: Unraveling migratory connectivity. Trends in Ecology and Evolution, 17: 76-83.
- Wheelwright, N. T. & J. D. Rising, 1993. Savannah sparrows. Pages 1-28 in A. Poole & F. Gill (ed.). The Birds of North America, No. 45. The Academy of Natural sciences, Philadelphia, Pennsylvania; The American Ornithologists' Union, Washington, D.C.
- Young, O. R. & F. S. Chapin, 1995. Anthropogenic impacts on biodiversity in the Arctic. Pages 183-196 in F. S. Chapin & C. Körner (ed.). Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences. Springer-Verlag, Berlin.