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A review of seasonal declines in clutch size of waterfowl (Anatidae) in the northern and southern hemispheres

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The size of the clutch declines with the date of laying of the first egg in many, but not all waterfowl (Anatidae). This paper reviews the published data on rates of decline in clutch size of waterfowl during the breeding season to: (i) determine whether the decline rates were related to the length of the breeding season at the nesting site, and/or to whether the birds were nesting in captivity or in the wild and; (ii) to propose tests of the reasons that have been suggested previously to account for these seasonal declines in clutch size. Rates of decline were greater at higher latitudes (50°) (where breeding seasons are relatively short) than at middle latitudes (30° – 49°) (where breeding seasons are longer). The majority of waterfowl that exhibited no or low rates of decline nested at middle latitudes, or in captivity. These findings are consistent with the three main factors (seasonally declining nutrient reserves, physiological effects of diminishing daylength, seasonally diminishing chances of survival) that have been proposed as causes of intra-seasonal declines in clutch size of waterfowl. Feeding studies, relocation studies, and experiments in which light regimes are manipulated, are required to distinguish between these three possible causes of falling clutch size with laying date in waterfowl.

1. Introduction

Clutch size (number of eggs laid per female) declines with date of laying in many waterfowl (Anatidae; Klomp 1970, Toft et al. 1984, Hamann & Cooke 1989, Bluhm 1988). Much attention has been directed at investigating the causes of this phenomenon. Excluding renesting and female age, the main reasons postulated for seasonal reductions in clutch sizes of waterfowl are: (i) seasonally decreasing levels of nutrients (fat and/or protein) stored by the female (Reynolds 1972, Hamann & Cooke 1989); (ii) reducing gonadal activity caused by increasing daylength during the breeding season (Bluhm 1988) and; (iii) a diminishing chance of survival in offspring from later-laid eggs, and/or in females that lay and rear young later in the season (Toft et al. 1984, Duncan 1987). These first and third reasons are not mutually exclusive, as the first may drive the third (Drent & Daan 1980, Toft et al. 1984).

Intra-seasonal declines in clutch size are not universal in waterfowl, for example, they appear to be uncommon in southern hemisphere waterfowl (Hemsley 1973, Braithwaite 1977, Norman & McKinney 1987, Briggs 1990, Marchant & Higgins 1990, Armstrong & Siegfried 1991). Nor are seasonal rates of decline in clutch size con-

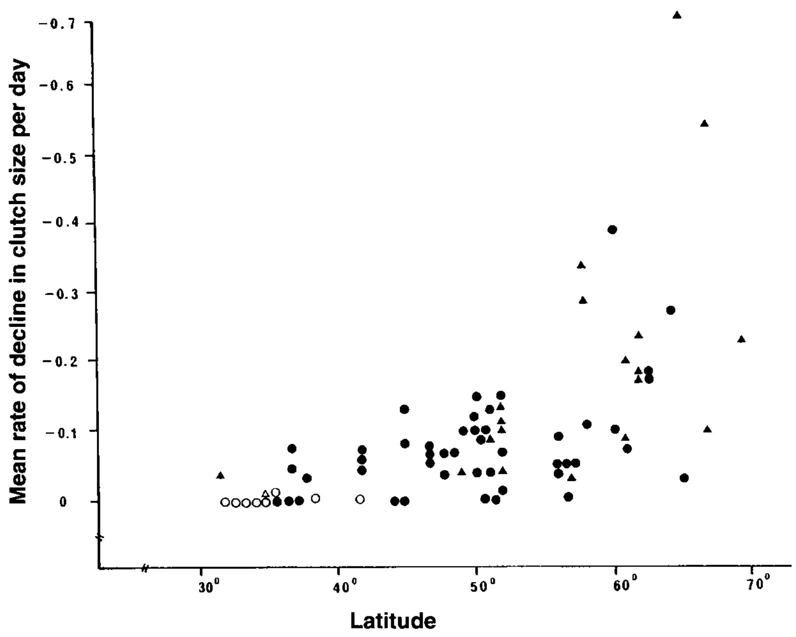

Fig. 1. Relationship between nesting latitude and intra-seasonal rate of decline in clutch size of wild-nesting waterfowl (reduction in number of eggs laid per clutch with each day that laying is delayed). Insignificant or zero rates of decline (both entered as zero) in wild-nesting waterfowl are also shown. ▲ = northern hemisphere swans and geese; ● = northern hemisphere ducks; △ = southern hemisphere swans; ○ = southern hemisphere ducks.

stant between species, breeding locations, or studies (see Appendices 1–3). The purposes of this paper are: (i) to review intra-seasonal rates of decline in clutch size of waterfowl; (ii) to determine whether these declines show associations with the length of the breeding season (indexed by latitude), or with nesting in the wild or as captives and; (iii) to propose tests of the previously suggested reasons for the declining clutch size in waterfowl with laying date.

2. Methods

Rates of seasonal decline in clutch size (reduction in the number of eggs laid per clutch with the date the first egg is laid), or raw data on clutch sizes and the dates that laying started, were obtained from the available literature (Appendices 1, 2, 3). Rates of seasonal clutch decline in species (sub-species where available) of waterfowl were taken from the source publication if given, calculated from the raw data, or estimated from at least three mean clutch sizes and their respective mean laying dates published by the original author. Data from known renests, parasitised nests, and from birds breeding for the first time were excluded from the study. The slope of a seasonal decline in clutch size was regarded as significant if the level of significance ($P < 0.05$) of r or F was given, could be calculated, or if a seasonal reduction in the number of eggs laid per clutch was very clearly demonstrated by the graph of clutch size against time. Non-significant (r, F or χ^2, $P > 0.05$) and no declines in clutch size with laying date were stated as such in the original papers. Only linear rates of decline were considered in this paper because of the large variation in the type and amount of information available from the source literature.

Rates of decline in the same species or sub-species which were reported in the one paper, nested at the same site, and which did not differ between years, were entered as one rate of decline in the analyses. Data for the same species or sub-species which were reported in the same paper, but whose rates of decline differed (significantly different slopes, $P < 0.05$) between years, were entered separately in the analyses. Decline rates of different species or individual sub-species were always analysed separately, as were all rates of decline obtained from different papers. Data from species without sub-specific details were analysed separately from their particular sub-species. The latitude of the nesting location from the original paper was used as the index of the length of the breeding season (see Wyndham 1986). Species and sub-species were sorted into two groups for analysis; those that nested 50°N (no southern records), and those that nested < 50°N or S. Fifty degrees of latitude was chosen because it was close to the median nesting latitude for the records of wild ducks. Parametric statistical tests follow Zar (1984); non-parametric tests follow Ryan et al. (1985).

3. Results

In one or more studies 71% of the duck taxa (species and sub-species; n = 31) exhibited a significant linear decline in clutch size with laying date; and 29% did not (Appendices 1, 2). Clutch size declined inconsistently in three taxa of ducks, and in one species clutch size increased and then decreased (Appendices 1, 2). In 81% of the taxa of swans and geese studied (species and sub-species; n = 16) clutches declined sometimes or always, and there were no seasonal declines in clutch size in 19% of taxa (Appendices 1, 3). Clutch size declined inconsistently, and also seasonally increased and decreased, in one species of swan (Appendices 1, 3). Of the ducks whose clutches did not diminish in size with laying date (all records; n = 14) 21% nested in captivity (Appendix 1). This contrasts with the 8% incidence of captive nesting among ducks whose clutches did decline seasonally (all records; n = 37) (Appendix 2). None of the geese and swans whose clutches declined with laying date (all records; n = 22) nested in captivity (Appendix 3). There was one record of captive breeding among the swans and geese whose clutches did not decline in size with time (all records; n = 5) (Appendix 1).

Of the free-living ducks whose clutches declined seasonally (all wild-breeding records; n = 34) 41% nested below 50°N or S (Fig. 1, Appendix 2). By contrast, 73% of the free-living ducks whose clutches did not decline seasonally (all wild-breeding records; n = 11) nested at a lower latitude than 50°N or S (Fig. 1, Appendix 1). Both species of free-living swan and goose whose clutches were not reduced in size with laying date (all wild-breeding records; n = 4) nested below 50°N or S (Fig. 1, Appendix 1). Among the free-living swans and geese whose clutches declined with increased delay in laying date (all wild-breeding records; n = 22), 14% bred below 50°N or S (Fig. 1, Appendix 3).

Wild ducks which laid smaller clutches as the breeding season progressed generally nested at higher latitudes than ducks which did not (Table 1; ANOVA, F = 10.3, df = 1, 43, P < 0.01). However, this difference lost significance when

Table 1. Mean rates of seasonal decline in clutch size (reduction in number of eggs laid per clutch with each day that laying is delayed) ± SD, and mean nesting latitude (to nearest degree) ± SD, of all ducks, swans and geese for which records are available. NH, northern hemisphere breeding; SH, southern hemisphere breeding, CH, combined northern and southern hemisphere breeding data. Data from Appendices 1, 2 and 3. n = total number of records.

Category	Rate of decline	Nesting latitude	n
Seasonal decline in clutch size			
Wild birds			
Ducks			
NH	–0.09±0.07	51±7	33
SH	–0.01	35	1
CH	–0.08±0.07	50±8	34
Swans			
SH	–0.06±0.04	48±8	4
Geese			
NH	–0.21±0.18	59±9	18
Captive birds			
Ducks			
NH	–0.07±0.03	47±5	3
No seasonal decline in clutch size			
Wild birds			
Ducks			
NH	–	45±8	7
SH	–	36±2	4
CH	–	41±8	11
Swans			
CH	–	39±4	2
Geese			
NH	–	44	1
Captive birds			
Ducks			
NH	–	50±8	3
Geese			
NH	–	52	1

the comparison was limited to the northern hemisphere (Table 1) (ANOVA, F = 3.8, df = 1, 38, 0.10 > P > 0.05). The number of records of swans and geese was too low for similar statistical comparison. However, wild swans and geese whose clutches declined seasonally also nested at higher latitudes, on average, than the swan and goose whose clutch sizes did not decline with time (Table 1).

Within-season rates of decline in clutch sizes of ducks, swans and geese were generally more rapid at higher latitudes than at middle latitudes (Fig. 1). Wild ducks that nested at or above 50°N (no southern records) had significantly faster rates of decline in clutch size with date of first laying (mean = –0.09, SD = 0.09, n = 23), than wild ducks that nested below 50°N or S (mean = –0.04, SD = 0.04, n = 22; Mann-Whitney test, W (see Ryan et al. 1985) = 640, P = 0.012; Appendices 1, 2). This difference lost significance when southern hemisphere ducks were removed from the analysis (Mann-Whitney test, W = 541, P = 0.058; Appendices 1, 2). Rates of decline in clutch size of wild swans and geese that nested at or above 50°N (no southern records) (mean = –0.21, SD = 0.17, n = 19) were considerably greater than the rates of decline in clutch size of wild swans and geese that nested below 50°N or S (mean = –0.01, SD = 0.02, n = 7) (Appendices 1, 3). The rates of decline in clutch size of ducks, swans and geese with laying date became more variable at higher nesting latitudes (Fig. 1).

Clutch size did not decline with laying date in five of the seven southern hemisphere species of waterfowl for which data are available (Appendices 1, 2, 3). In one other austral species, clutch size declined inconsistently (Appendices 1, 3).

4. Discussion

Most of the waterfowl that did not show seasonal declines in their clutch size nested at middle latitudes (30°–49°) where breeding seasons are relatively long, or in captivity where food is provided, and hence levels are likely to be more constant than in the wild. Furthermore, rates of decline with laying date were generally more rapid at higher latitudes, where breeding seasons are shorter, than at middle latitudes where breeding seasons are longer. These results are consistent with the hypothesis that seasonal declines in clutch size are caused by decreasing survival rates of late layers and their broods (Toft et al. 1984, Duncan 1987). Survival of late-hatched broods would be expected to diminish as breeding latitude increased, that is, as season length decreased. More rapid rates of decline in clutch size at higher latitudes are consistent also with the hypothesis that seasonal declines in clutch size are caused by gonadal suppression as a result of increasing daylength during the breeding season (Bluhm 1988).

The results do not refute the hypothesis that seasonally declining clutch sizes are caused by falls in the amount of stored nutrient reserves available to the breeding female (Reynolds 1972, Hamann & Cooke 1989). Waterfowl nesting at higher latitudes lose body reserves more rapidly during laying than do waterfowl nesting at lower latitudes (Mainguy & Thomas 1985).

Several factors will influence rates of decline at given latitudes, and between taxa of waterfowl. Examples of such factors are specific durations of incubation and fledging (see Hepp et al. 1989), the ability of species and individuals to renest (Klomp 1970), the microclimate of the breeding habitat (for example, maritime areas having warmer climates and longer growing seasons than inland areas at the same latitude), movement patterns (migratory species need to retain post-breeding body reserves for flying), when and where individuals acquire nutrients for breeding, the gonadal responses of species and sub-species to changes in daylength (Murton & Kear 1976), and annual variations in temperature and rainfall in wintering, staging and nesting habitats. In combination or singly, these modifying factors could cause the rather large variations in rates of decline in clutch size at the same latitude, especially in Arctic areas.

It is not clear whether the lack of seasonal decline in the clutch size of southern hemisphere waterfowl studied to date is related to their low nesting latitudes (regardless of hemisphere), or to their southern rather than northern breeding location. This problem could be resolved by studying waterfowl breeding at relatively high latitudes in the southern hemisphere. If ducks nesting in the Falkland Islands (52°S), South Georgia (55°S), southern Argentina or Chile (50°–55°S), or on Macquarie Island (55°S) were to show rates of seasonal decline in their clutch size similar to those of waterfowl nesting at equivalent climates in the northern hemisphere then breeding hemisphere would not affect rate of decline in clutch size with laying date. No published data are available yet on clutch sizes in relation to laying date in waterfowl breeding at high latitudes in the southern hemisphere. This would be a productive area for future research.

Breeding populations that have recently been established at latitudes outside their natural range, experimental relocations, changes in light regime (see Meijer et al. 1990), and feeding experiments could be used to investigate the mechanisms that control intra-seasonal declines or increases in clutch size of waterfowl. Reduction or loss of seasonal decline in clutch size when increased food is supplied to the breeding female would show that variation in clutch size with laying date, while it may be ultimately evolved, is controlled by an external proximate factor, namely nutrition. A greater or reduced rate of within-season decline in clutch size with a shift to a higher or lower latitude, or with an experimental change in light and dark regime, would show that daylength proximately controls decline rates (see Bluhm 1988). Hormones, without daylength cues, may also influence clutch size in waterfowl, as in European Kestrels *Falco tinnunculus* (Meijer et al. 1990).

The same rate of seasonal decline in the clutch size of birds from the same population when supplied with increased food, breeding under a different light regime, or nesting at a different latitude, would suggest that variations in clutch size with laying date may be controlled by ultimate factors only. That is, seasonal declines in clutch size of waterfowl are likely to be caused by evolved responses to the chance of survival of parents and/or young from laying a particular size of clutch at a certain time of the season (see Toft et al. 1984, Duncan 1987). Proximate and ultimate factors could operate together in complex ways to influence relationships between clutch size and laying date in waterfowl, as in other avian species (see Meijer et al. 1990).

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Selostus: **Vesilintujen pesyekoon pieneneminen munintakauden kuluessa**

Monet vesilinnut (Anatidae) munivat sitä pienempiä pesyeitä kuta myöhemmin ne alkavat muninnan. Kirjoituksessa tarkastellaan julkaistuja tietoja pesyekoon pienenemisnopeudesta. Artikkelin takoituksena on selvittää liittyykö havaittu pesyekoon pienenemisnopeus pesimiskauden pituuteen tai siihen, onko lajeja tutkittu luonnossa vai tarhaoloissa.

Pesyekoon pieneneminen munintakauden kuluessa oli nopeampaa pohjoisessa tai etelässä (50°), missä pesintäkaudet ovat melko lyhyitä, kuin keskileveyksillä (30° – 49°), missä pesintäkaudet ovat melko pitkiä. Valtaosa lajeista, joiden pesyekoko ei muuttunut ollenkaan tai muuttui vain vähän muninta-ajankohdan suhteen pesi keskileveyksillä tai tarhoissa.

Tulokset ovat yhdenmukaiset kolmen aikaisemman ilmiön selittämiseksi esitetyn hypoteesin kanssa (vararavintovarastojen väheneminen, päivän pituuden muuttuminen sekä emojen ja pesyeiden selviytymistodennäköisyyden pieneneminen). Hypoteesien testaamiseksi tarvitaan kokeita joissa linnuilla annetaan lisäravintoa, niitä siirretään eri alueille tai niiden ympäristön valojaksoa muutetaan.

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Appendix 1. Waterfowl whose clutch sizes do not decline significantly (r, F or χ^2-value, $P > 0.05$) seasonally. All data are from free-living birds unless otherwise indicated. Known parasitised nests and renests are excluded. [A] From source reference, to nearest degree; [B] Birds nesting in captivity; [C] Dry weight of clutch contents.

Species	Direction of slope	Nesting latitude[A]	Source
Ducks			
Aix sponsa	No trend, n = 146	37°N	Clawson et al.1979
Chenonetta jubata	No trend, n = 42	35°S	Briggs 1990
Anas strepera	Non-significant decline, n = 49	37°N	Amat 1982
Anas platyrhynchos	No trend[B], n = 20	42°N	Eldridge & Krapu 1988
Anas platyrhynchos	No trend[B], n = 36	58°N	Pehrsson 1991
Anas gibberifrons	No trend, n = 28	35°S	Marchant & Higgins 1990
Anas castanea	Increase (F-test, P = 0.02) then decrease (P = 0.01), n = 221	38°S	Norman & McKinney 1987
Anas clypeata	Non-significant decline[B], n = 28	51°N	McKinney 1967
Anas clypeata	No trend, n = 13	51°N	Poston 1969
Anas smithii	No trend, n = 73	34°S	Armstrong & Siegfried 1991
Somateria mollissima sedentaria	No trend, n = 110	57°N	Freeman 1970
Somateria mollisima dresseri	Non-significant decline, n = 178	44°N	Paynter 1951
Netta rufina	No trend, n = 48	37°N	Amat 1982
Oxyura jamaicensis	Non-significant decline, n = 51	51°N	Siegfried 1976
Swans and geese			
Cygnus atratus	Increase (F-test,P < 0.001) then decrease, n = 199	35°S	Braithwaite 1977
Cygnus atratus	No trend, n = 107	35°S	Braithwaite 1977
Cygnus atratus	No trend, n = 9770	42°S	Hemsley 1973
Branta canadensis maxima	Non-significant decline[C], n = 41	44°N	Mainguy & Thomas 1985
Branta leucopsis	Non-significant increase[B], n = 6	52°N	West et al. 1986

Appendix 2. Ducks whose clutch sizes decline seasonally. All data are from free-living birds unless otherwise indicated. Known parasitised nests and renests are excluded. Significance tests are signifances of r (all P < 0.05) unless otherwise indicated. [A] Mean reduction in clutch size per day; [B] From source reference, to nearest degree; [C] Estimated linear relationship from data available, significance could not be calculated; [D] Birds nesting in captivity; n.a. = not available.

Species	Slope[A]	Significance	Nesting latitude[B]	Source
Aix sponsa	–0.05[C]	n.a., n = 85	42°N	Grice & Rogers 1965
Aix sponsa	–0.07	t-test, n = 20	42°N	Haramis & Thompson 1985
Aix sponsa	–0.08	n.a., n = 56	45°N	Morse & Wight 1969
Aix galericulata	–0.13	r = –0.62, n = 19	51°N	Davies & Baggott 1989
Anas penelope	–0.05[C]	n.a., n = 100	56°N	Newton & Campbell 1975
Anas strepera	–0.06	r = –0.52, n = 157	48°N	Lokemoen et al. 1990
Anas strepera	–0.09[C]	n.a., n = 322	51°N	Hines & Mitchell 1983
Anas strepera	–0.05[C]	n.a., n = 102	56°N	Newton & Campbell 1975
Anas platyrhynchos	–0.04	F-test, n = 189	37°N	Amat 1982
Anas platyrhynchos	–0.06[D]	n.a., n = 241	42°N	Krapu 1981
Anas platyrhynchos	–0.07	r = –0.52, n = 64	47°N	Krapu & Doty 1979
Anas platyrhynchos	–0.05	r = –0.64, n = 87	47°N	Krapu et al. 1983
Anas platyrhynchos	–0.06	F-test, n = 76	47°N	Cowardin et al. 1985
Anas platyrhynchos	–0.03	r = –0.49, n = 128	48°N	Lokemoen et al. 1990
Anas platyrhynchos	–0.10[D]	r = –0.46, n = 52	50°N	Batt & Prince 1979
Anas platyrhynchos	–0.01[C]	n.a., n = 114	52°N	Hill 1984
Anas platyrhynchos	–0.04[C]	n.a., n = 1274	56°N	Newton & Campbell 1975
Anas rubripes	–0.03	r = –0.01, n = 36	38°N	Stotts 1956
Anas acuta	–0.10[C]	n.a., n = 290	50°N	Duncan 1987
Anas acuta	–0.04[D]	r = –0.46, n = 41	50°N	Duncan 1987
Anas discors	–0.06	r=–0.57, n = 62	48°N	Lokemoen et al. 1990
Anas discors	–0.10[C]	t-test, n = 136	50°N	Dane 1966
Anas superciliosa	–0.01	r = –0.42, n = 57	35°S	Marchant & Higgins 1990
Aythya affinis	–0.04	F-test, n = 129	51°N	Afton 1984
Aythya ferina	–0.07	F-test, n = 166	37°N	Amat 1982
Aythya fuligula	–0.09[C]	n.a., n = 1436	56°N	Newton & Campbell 1975
Aythya valisneria	–0.07	F-test, n = 129	52°N	Sugden 1978
Somateria mollissima mollissima	–0.05[C]	n.a., n = 856	57°N	Milne 1974
Somateria mollissima borealis	–0.27[C]	r = –0.99, n = 15	64°N	Cooch 1965
Somateria fischeri	–0.07[C]	n.a., n = 70	61°N	Dau 1976
Histrionicus histrionicus	–0.03	t-test, n = 77	65°N	Bengston 1972
Melanitta fusca	–0.39[C]	n.a., n = 104	60°N	Koskimies 1957
Bucephala albeola	–0.12[C]	n.a., n = 75	50°N	Erskine 1971
Bucephala albeola	–0.15	r = –0.62, n = 35	52°N	Gauthier 1989
Bucephala clangula	–0.11[C]	n.a., n = 51	58°N	Eriksson 1979
Mergus cucullatus	–0.13[C]	n.a., n = 30	45°N	Morse et al. 1969
Mergus merganser	–0.10	r = –0.48, n = 193	60°N	Eriksson & Niittyla 1985

Appendix 3. Swans and geese whose clutch sizes decline seasonally. All data are from free-living birds. Known parasitised nests and renests are excluded. n = no. clutches measured. Significance tests are significances of r (all $P < 0.05$) unless otherwise indicated. [A] Mean reduction in clutch size per day; [B] From source reference, to nearest degree; [C] Estimated linear relationship from data available, significance could not be calculated; n.a. = not available.

Species	Slope[A]	Significance	Nesting latitude[B]	Source
Cygnus olor	–0.09	r = –0.35, n = 134	51°N	Perrins & Ogilvie 1981
Cygnus olor	–0.10	r = –0.78, n = 120	52°N	Reynolds 1972
Cygnus olor	–0.04[C]	n.a., n = 42	52°N	Birkhead et al. 1983
Cygnus atratus	–0.01[C]	n.a., n = 88	35°S	Braithwaite 1977
Anser albifrons frontalis	–0.20	F-test, n = 64	61°N	Ely & Raveling 1984
Anser anser	–0.03	n.a., n =234	57°N	Newton & Kerbes 1974
Chen canagica	–0.18	n.a., n = 426	62°N	Eisenhauer & Kirkpatrick 1977
Chen canagica	–0.24	r = –0.62, n = 393	62°N	Rohwer & Eisenhauer 1989
Anser caerulescens atlanticus	–0.23	n.a., n = 21	69°N	Boyd 1989
Anser caerulescens caerulescens	–0.71[C]	n.a., n.a.	65°N	Kerbes 1969 in Newton 1977
Anser caerulescens caerulescens	–0.34	F-test, n = 89	58°N	Finney & Cooke 1978
Anser caerulescens caerulescens	–0.29	F-test, n = 30	58°N	Hamann & Cooke 1989
Anser rossii	–0.54[C]	n.a., n = 98	67°N	Ryder 1967
Anser rossii	–0.10[C]	n.a., n = 460	67°N	Ryder 1972
Branta canadensis	–0.04[C]	n.a., n = 56	49°N	Vermeer & Davies 1978
Branta canadensis	–0.03[C]	n.a., n = 273	32°N	Combs et al. 1984
Branta canadensis interior	–0.14[C]	n.a., n = 117	52°N	Raveling & Lumsden 1977
Branta canadensis interior	–0.11[C]	n.a., n = 96	52°N	Raveling & Lumsden 1977
Branta canadensis hutchinsii	–0.09	r = –0.41, n = 176	61°N	MacInnes & Dunn 1988
Branta canadensis minima	–0.18	r = –0.52, n= 89	62°N	Rohwer & Eisenhauer 1989
Branta bernicula nigricans	–0.17	r = –0.56, n = 106	62°N	Rohwer & Eisenhauer 1989
Branta bernicula hrota	–0.13[C]	n.a., n = 164	65°N	Barry 1962