

Contribution of allochthonous resources to breeding in a high-arctic avian predator

Jean-Rémi Julien · Pierre Legagneux ·
Gilles Gauthier · R. I. Guy Morrison ·
Jean-François Therrien · Joël Bêty

Received: 15 May 2013 / Revised: 5 September 2013 / Accepted: 6 November 2013 / Published online: 22 November 2013
© Springer-Verlag Berlin Heidelberg 2013

Abstract Allochthonous input of resources (i.e., originating from a place other than where they are found) can have a significant impact on food availability for consumers. We assessed the impact of an allochthonous source of food (the sewage outfall stream of a military base) on an avian predator breeding in a low-productivity, high-arctic site (Alert, 83°N, 62°W, Ellesmere Island), the long-tailed skua (*Stercorarius longicaudus*). We collected blood samples throughout the breeding season during two contrasting years of lemming abundance to characterize diet composition of skuas and evaluated the contribution of the anthropogenic and lemming food sources using stable isotopes (carbon ^{13}C and nitrogen ^{15}N). The isotopic signature of skuas changed seasonally because they switch

from a marine to a terrestrial diet when they come ashore to breed but also differed between the 2 years of the study. Anthropogenic food source accounted for 33 % of the summer diet but this proportion varied between years, from 41 % (5–95 ‰: 13–59 %) in a year of low lemming abundance to 16 % (5–95 ‰: 10–21 %) in a high year. Skua nest density recorded in years of low lemming abundance at Alert (0.15 nests/km²) was higher than at any other comparable arctic sites (0–0.02 nests/km²). Overall, the use of an anthropogenic food sources apparently subsidizes skua reproduction at this site, which could affect the food web of this low-productivity ecosystem.

Keywords Anthropogenic food source · Diet composition · Long-tailed skua · Lemming abundance · *Stercorarius longicaudus* · Stable isotopes

Electronic supplementary material The online version of this article (doi:10.1007/s00300-013-1423-4) contains supplementary material, which is available to authorized users.

J.-R. Julien · G. Gauthier · J.-F. Therrien
Département de biologie and Centre d'études nordiques,
Pavillon Vachon, Université Laval Québec, 1045 avenue de la
Médecine, Québec City, QC G1V 0A6, Canada

P. Legagneux (✉) · J. Bêty
Département de biologie and Centre d'études nordiques,
Université du Québec à Rimouski, 300 Allée des Ursulines,
Rimouski, QC G5L 3A1, Canada
e-mail: legagneux@gmail.com

R. I. G. Morrison
Canadian Wildlife Service, National Wildlife Research Centre,
Carleton University, 1125 Colonel By Drive (Raven Road),
Ottawa, ON K1A 0H3, Canada

Present Address:

J.-F. Therrien
Hawk Mountain Sanctuary, 410 Summer Valley Road,
Orwigsburg, PA 17961, USA

Introduction

The functioning of an ecosystem cannot be understood in isolation (Polis et al. 1997; Jefferies 2000). Allochthonous inputs have the potential to affect food webs strongly (Leroux and Loreau 2008), and ecologists are increasingly recognizing the effects that cross-ecosystem transport of energy and food resources can have on plant and animal populations (Polis and Hurd 1996; Polis et al. 1997; Huxel and McCann 1998; Jefferies 2000; Gauthier et al. 2011). An allochthonous resource becomes a subsidy when it increases the productivity of a consumer population (Polis et al. 1997). Allochthonous subsidies are particularly common between marine and terrestrial ecosystems (Polis and Hurd 1996; Polis et al. 1997). Many ecosystems are also recipients of anthropogenic (human origin) subsidies

such as food refuse or agricultural fertilizer (Jefferies et al. 2004; Weiser and Powell 2010). Food inputs from human activity (e.g., industrial fisheries, refuse dumps, urban waste) have been shown to sustain population increases of several opportunistic seabird species in recent decades (Pons and Migot 1995; Oro et al. 2004). Consequently, a full understanding of the population dynamic of a species often requires the inclusion of both autochthonous and allochthonous resource inputs.

Human activities in the Arctic have intensified during the last decades and are expected to grow exponentially in the future (Johnsen et al. 2010). Because primary productivity of ecosystems decreases and food webs become simplified as we move north (Oksanen and Oksanen 2000), arctic ecosystems should be especially sensitive to resource subsidies of anthropogenic origin (Gauthier et al. 2011). We addressed this question by examining the impact of a large and sustained food subsidy of human origin (sewage outfall containing macerated food waste) on an arctic avian predator, the long-tailed skua (*Stercorarius longicaudus*; hereafter skua) breeding in the vicinity of the military base/weather station at Alert (Ellesmere Island, Canada), the northernmost, permanently inhabited settlement on earth. Although skuas are sometimes considered generalist predators, lemmings represent a considerable proportion of their summer food sources (Anderson 1976; De Korte and Wattel 1988; Gilg et al. 2006). Lemmings are characterized by strong, cyclic fluctuations in abundance over much of the tundra (Ims and Fuglei 2005), including at Alert (Morrison, pers. obs.).

Our aims were to (1) measure inter- and intra-annual variations in the isotopic signature and diet composition of long-tailed skuas at a high-arctic site exposed to an anthropogenic food source using carbon and nitrogen stable isotopes (^{13}C and ^{15}N) (Inger and Bearhop 2008) and (2) evaluate the consequences of such an input on reproduction. Because skuas are seabirds that come ashore only during the breeding season, we first expected to detect a change in their isotopic signature indicative of a switch in diet from marine to terrestrial food sources early in the summer. Secondly, we predicted that sewage food scraps from the military base should represent a large part of the skua's diet composition at Alert but that this contribution should increase in years with low lemming abundance. Fluctuations in lemming abundance are known to influence skua reproduction (Maher 1970; Andersson 1976; De Korte and Wattel 1988; Gilg et al. 2006; Therrien et al. 2014). If anthropogenic resources subsidize breeding skuas, a reduced effect of annual variations in lemming abundance on their reproduction would be expected compared to other sites.

Materials and methods

Study site

Our study site was located at Alert (82°30'N, 62°20'W) on the northeast coast of Ellesmere Island, Nunavut, Canada (Figure S1 in Electronic Supplementary Material: ESM). The 65 km² study area is mainly composed of rugged terrain surrounded by hills and small valleys with rivers and lakes. The local terrain is barren, consisting of frost-shattered rock, gravel, and bare clay, with sparse vegetation cover (generally <15 %; MacDonald 1953). Because of its very high latitude, the local food web is impoverished and has very few prey and predator species compared to other arctic food webs (Gilg et al. 2003, 2006; Gauthier et al. 2011). Collared lemming (*Dicrostonyx groenlandicus*) is the only small rodent species present at the site. The Alert military base and weather station operate year round. The sewage of the base has been continuously discharged at the site for the past 50 years; in the early 1990s, the station switched from disposing food waste on a garbage dump to macerating it and discharging it with the sewage. Several species of birds are observed feeding regularly at the sewage outfall (Morrison, pers. obs.).

Field methods

Nest survey

Nests were found through both systematic and opportunistic searches in areas having the highest potential for nesting though search effort (in terms of number of people and time spent in the field) varied annually over the period 1998–2009. The strong territorial behavior (alarm calls and attacks) exhibited by nesting skuas facilitated nest detection. We recorded the position of each nest with a GPS unit as well as the numbers of eggs and their size (length and width). In order to compare years of high and low lemming abundance, we used data collected at Alert in 2003 and 2008, 2 years where the search effort for nesting skuas was comparable (the same surface area of 65 km² was surveyed each year) but lemming abundance varied considerably (see below). Mean laying date at Alert was 20 June (mean annual range 15–25 June) and mean hatching date was 14 July (mean annual range 9–19 July). We calculated egg volume (V ; cm³) using the standard formula ($V = K \times L \times W^2$; K = shape constant, L = length, W = width) with the shape constant ($K_v = 0.497$) for *Larus* spp. eggs (Hoyt 1979).

We also extracted from the literature skua nesting density recorded at other arctic sites in years of high and low lemming abundance, two sites in North America (Maher

1970; Therrien et al. 2014), one in Greenland (Gilg et al. 2006) and one in northern Europe (Andersson 1976).

Lemming abundance

Lemming abundance was evaluated annually since 1998 in a qualitative way by using three different classes of density: high, medium, and low according to daily sightings while conducting other research activities in the field. Considering the very large amplitude of variations in population density between years of high and low lemming abundance in most tundra ecosystems, this index should be sufficient to detect these extreme situations (e.g., Lecomte et al. 2008). The year 2003 was an exceptional year of high lemming abundance (Morrison, pers. obs.), which was further confirmed by the presence of snowy owls (*Bubo scandiacus*) that year, a rare species at Alert but whose presence and reproduction is closely tied to local peaks in lemming abundance across the tundra (Gauthier et al. 2004). In contrast, summer 2008 was one of the lowest lemming years observed throughout the study period (Morrison, pers. obs.). In that year, lemming abundance was also estimated using snap-traps. We used 150 traps placed along 3 transect lines in damp habitat and 3 lines in dry habitat and operated for 3 consecutive days from 23 to 29 July, for a total of 900 trap-nights. Trapping stations were 15 m apart along transects and consisted of 3 traps baited with peanut butter set within a 2 m radius of each station. Overall, only one collared lemming was caught leading to an index of abundance of 0.11 lemmings/100 trap-nights, which is similar to values recorded in years of low abundance on Bylot Island in the Canadian Arctic (Gruyer et al. 2008).

Collection of blood samples

Adult skuas were captured with rocket nets at the sewage outfall stream, from their arrival in early June through the summer in both 2003 and 2008. We also used a small “pull net” to capture incubating birds on their nest. The capture effort was greater in 2008 ($N = 35$ individuals with 8 recaptures, including 10 incubating birds) compared to 2003 ($N = 17$ individuals with no recaptures, including 7 incubating birds). Immediately after capture, a blood sample was collected from the brachial vein (about 300 μ l) in heparinized micro-hematocrit capillary tubes. Birds were then individually banded before release. Blood samples were centrifuged at 13,200g for 15 min. Red blood cells (hereafter RBC) and plasma were separated and stored frozen at -20°C until laboratory analyses. RBC were available for all birds captured/recaptured ($N = 61$) and plasma for 54 birds.

Sampling of food sources

During summer 2008, we collected samples of both inshore marine and terrestrial prey that are potentially consumed by skuas for stable isotope analysis (Table S1 in the ESM). Potential prey were determined on what was previously known regarding their summer diet in the high arctic (reviewed in Wiley and Lee 1998). Marine arthropods (amphipods) were collected by hand from tidal pools and small fishes were captured with minnow traps ($n = 3$). Terrestrial arthropods were selected at random from specimens collected in pitfall traps set throughout the summer in the course of another study aimed at assessing their seasonal variation in abundance (Bolduc et al. 2013). Samples ($n = 5$) were obtained from the most abundant groups: Diptera (Chironomidae, Muscidae, Calliphoridae and Tipulidae), Lepidoptera (Geometridae), and Hymenoptera (Ichneumonidae). To increase the sample size for lemming isotopic signatures, we gathered all lemming samples available throughout the years from Alert. Because the signature of the single lemming sample collected in 2003 ($\delta^{13}\text{C} = -25.3\text{‰}$ and $\delta^{15}\text{N} = 3.1\text{‰}$) was within the range of values of 2007 and 2008 samples ($-25.9/-27.1\text{‰}$ for $\delta^{13}\text{C}$ and $-0.7/3.9\text{‰}$ for $\delta^{15}\text{N}$ in 2007–2008, $n = 3$), we pooled all those samples. The potential food items present in the sewage outfall were highly heterogeneous and could be easily selected by skuas. To obtain representative samples of what was actually eaten by the birds, we used material from spontaneous regurgitations during handling of birds following their capture at the outfall stream. Only intact, undigested material (mostly rice and pasta) was retained ($n = 8$). Other studies have shown that regurgitation material is representative of what is eaten by seabirds and can be used for isotopic analyses (Votier et al. 2003, 2010). All samples were placed separately in plastic bags and stored frozen at -20°C except for arthropods that were preserved in 70 % ethanol. Ethanol is not likely to affect subsequent isotopic analyses (Hobson et al. 1997; Therrien et al. 2011).

Laboratory analyses

Stable isotopes

All samples were freeze-dried. Because it is generally recommended to extract lipids from tissues with a high concentration in lipids (like muscles), we extracted lipids from prey samples by boiling them for 20 min in a chloroform:methanol (2:1) solution with a Soxhlet apparatus. Since lipid content of blood is usually low and hence does not affect carbon and nitrogen isotopic ratios (Bearhop et al. 2000), we did not extract lipids from blood samples. Samples were then milled and weighed into tin cups

(approximately 0.22 mg) and sent to the *Stable Isotopes in Nature Laboratory*, University of New-Brunswick, Fredericton, NB, Canada, for analyses of carbon and nitrogen isotopic ratios. Samples were flash combusted at 1,100 °C using a Costech 4010 Elemental Analyzer and the resulting gases delivered via continuous flow into a DELTA^{plus} isotope ratio mass spectrometer. Stable isotope ratios are expressed as δ values relative to international standards and are measured in parts per thousand (‰; Bond and Hobson 2012). We evaluated the overall measurement precision by randomly duplicating a subset of our samples: this includes both precision error inherent to the mass spectrometer and within-sample variations due to lack of homogeneity of powdered samples. Sample replicates never had 1 SD > 0.17 ‰ for $\delta^{13}\text{C}$ and >0.06 ‰ for $\delta^{15}\text{N}$. Accuracy was estimated with measurements of a commercially available standard (Nicotinamide, Elemental Microanalysis Ltd.; Target ratios: $\delta^{13}\text{C} = -34.2$ ‰ and $\delta^{15}\text{N} = -1.8$ ‰): mean $\delta^{13}\text{C} = -34.2 \pm 0.1$ ‰ SD and mean $\delta^{15}\text{N} = -1.8 \pm 0.1$ ‰ SD ($n = 14$).

Stable isotope composition of different tissues reflects assimilated diet over different temporal scales based on the turnover rate specific to each tissue, which depends on its metabolic activity (Hobson and Clark 1992b). Accordingly, analyzing stable isotope concentration separately in plasma and RBC provides dietary information that integrates approximately 1 and 4 weeks, respectively (Hobson and Clark 1993; Inger et al. 2006). Metabolic activity is often selective for specific isotopes, leading to differences between the signature of a consumer tissue and its food sources (Hobson and Clark 1992a). It is thus necessary to correct for the isotopic discrimination specific for the tissue used when assessing diet with stable isotope analyses. We used average discrimination factors determined by Bearhop et al. (2002) for the blood of the Great Skua (*Catharacta skua*), a close relative of the long-tailed skua, feeding on meat and fish in which lipids had been removed. Discrimination values used were 1.7 ‰ for ^{13}C and 3.5 ‰ for ^{15}N .

Bird sexing

DNA was extracted from freeze-dried RBC using the procedure described in Aljanabi and Martinez (1997) and sex was genetically assessed for all individuals using the method described in Fridolfsson and Ellegren (1999).

Statistical analyses

We used linear mixed effect models to analyze the sources of variation in the blood stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) with the nlme package (Pinheiro et al. 2006) from software R, version 2.8.0 (R Development Core Team

2008). Dependent variables (either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$) were log-transformed to meet assumptions of normality. The fixed effects were date (in day of the year standardized as follows: $x_{\text{stand}} = (x_i - \bar{x})/\sigma$), year (with contrasting lemming abundances), sex, and blood component (RBC and plasma). Given that multiple blood samples were sometimes available per individual, we considered individuals as a random effect in the analyses, which resulted in giving the same weight to each individual and avoided pseudo-replication (Pinheiro and Bates 2000). The mean time elapsed between resampling of the same individuals was 17.3 days (range 9–30 days, $n = 8$).

We evaluated fixed effects through model selection using the Akaike's Information Criterion with the small sample size bias correction (AICc). We used parameter estimates averaged across all models (AICcmodavg package in R) to account for uncertainty in model selection (Burnham and Anderson 2002). The most complex model included all possible two-way interactions that were biologically interpretable.

We estimated the contribution of food sources to the diet with the Bayesian multi-source stable isotope mixing model of the SIAR package (Parnell et al. 2010). This approach allows for incorporating errors in the sources and samples. When working with n isotopes in systems containing more than $n + 1$ sources, Bayesian models offer several advantages over non-Bayesian approaches (see Tarroux et al. 2010). We used the "siarsolomcmc4" function that runs a Markov Chain Monte Carlo on stable isotope data of each individual to determine its dietary habits. We did not incorporate prior information. Small errors in discrimination factors due, for instance, to a mixed diet have the potential to bias mixing model output (Bond and Diamond 2011). To assess the robustness of our diet proportion estimates to these potential biases, we performed a sensitivity analysis for each year using extreme discrimination values for $\delta^{15}\text{N}$ (2.8 and 4.2 ‰) and $\delta^{13}\text{C}$ (1.1 and 2.3 ‰) given in Bearhop et al. (2002). We ran 4 models to simulate all the combinations of extreme discrimination values and compared the range of diet proportion estimates obtained from these models to those obtained using average discrimination values.

Birds captured at the sewage outfall stream are likely a mixture of breeding and non-breeding birds, with potentially some transient individuals in the latter group. A capture–recapture analyses based on 10 years of banding data at this site indeed showed that up to 18 % of newly marked birds could be transients (Julien et al. 2013). We thus estimated separately the diet composition of birds captured at the sewage outfall from those captured on their nest. We reconstructed diet composition using plasma because the higher turnover rate of this component compared to RBC reduces the residual marine input signal due

to feeding at sea prior to arrival to the breeding site in spring (see “Results” section). We excluded marine prey from potential food sources of birds captured at the nest (i.e., breeders) but not for those captured at the sewage outfall because breeding birds had moved to the terrestrial environment for several weeks at the time of capture and nesting skuas are unlikely to feed in the marine environment at that time (see ESM for supporting evidence).

We tested for an effect of year (that differed in term of lemming abundance) on clutch size and egg volume. For clutch size, we used logistical regression coded as 1 for nests with two eggs and 0 for nests with one egg (no other clutch sizes were recorded). For egg volume, we used linear mixed models with nest identity as a random factor to account for potential pseudo-replication.

Results

Variations in isotopic signatures

The isotopic signature of marine prey, terrestrial arthropods, lemmings, and anthropogenic food significantly differed from each other (MANOVA, pairwise comparisons: all $F_{1,10} > 11.50$, all $P < 0.003$, all Wilks $\lambda < 0.28$). Marine prey were considerably enriched in both ^{15}N and ^{13}C compared to all terrestrial prey (Fig. 1; Table S1 in the ESM). The $\delta^{13}\text{C}$ signature of arthropods and lemmings were relatively similar although arthropods were slightly enriched in ^{15}N . Finally, food regurgitated at the sewage outfall (hereafter referred to as anthropogenic source) was intermediate in ^{13}C between marine and other terrestrial prey but similar to arthropods in ^{15}N values. We thus used these food items as independent sources in isotopic models.

We found that skua $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values varied according to the blood component, date, and year, as well as sex for C (Table 1). The plasma was more impoverished in ^{13}C , and to a lesser extent in ^{15}N , than the RBC (Table 2; Fig. 2); thus, its isotopic ratio was more shifted toward terrestrial food sources than the RBC (Fig. 1). Furthermore, there was a strong seasonal decline in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from the beginning of June until mid-July in both blood components and years (Table 2; Fig. 2). Although birds captured in the first 2 weeks of July were on their nest, these data points fitted well with the seasonal trend already apparent in birds captured in June at the sewage outfall (Fig. 2). We nonetheless repeated the analyses excluding birds captured on their nests and found similar results (see Table S2 in the ESM). The interaction between date and blood component for $\delta^{13}\text{C}$ was due to weaker seasonal decline in RBC values compared to plasma (Table 2; Fig. 2). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were lower in 2003 (high lemming abundance year), compared to 2008 (low lemming

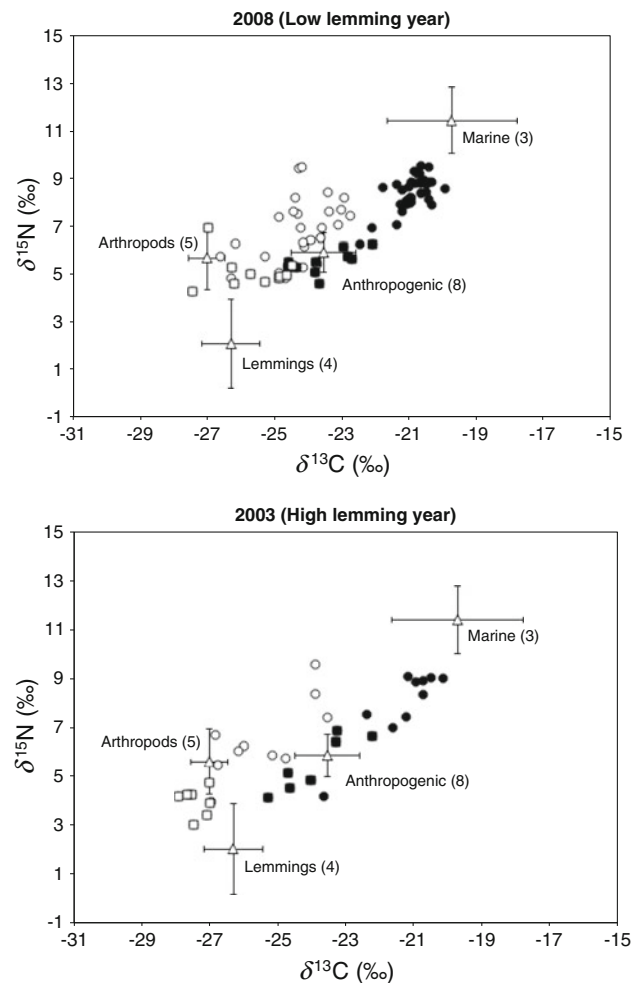


Fig. 1 Isotopic signature ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values) of food sources (white triangles; mean \pm standard deviation) and plasma (white symbols) and red blood cells (RBC; black symbols) of individual long-tailed skuas caught at Alert (Ellesmere Island) in years of high (2003) and low (2008) lemming abundance. Squares represent birds caught on their nests and circles those caught at the sewage outfall stream. Blood values were adjusted for discrimination factor (see “Materials and methods” section for details). Numbers indicate sample size for food sources (most food sources were collected in 2008, see “Materials and methods” section)

abundance) but there was an interaction between blood component and year ($\delta^{13}\text{C}$ only; Tables 1, 2). This interaction indicates that the decrease in $\delta^{13}\text{C}$ values between 2003 and 2008 was greater in plasma than in RBC (Table 2; Fig. 2). The interaction between year and date for $\delta^{13}\text{C}$ reflects a steeper seasonal decline in 2003 compared to 2008 (Table 2; Fig. 2). Finally, the interaction between sex and blood component indicates that males had slightly lower $\delta^{13}\text{C}$ values in plasma than in RBC compared to females.

Food proportions in diet

Anthropogenic food sources contributed between 20 and 25 % of the diet of skuas captured at the sewage outfall, a

Table 1 Model selection of the effects of year (high vs low lemming abundance), date, blood component (plasma vs red blood cells, RBC), sex and biologically relevant two-way interactions on the $\delta^{13}\text{C}$ (a) and $\delta^{15}\text{N}$ (b) values of long-tailed skua blood (n observations = 115; 61 RBC and 54 plasma from 52 different individuals used as a random factor)

Model	N_p	Δ_{AICc}	ω_i
a) $\delta^{13}\text{C}$			
1. Year*date + year*blood + date*blood + sex*blood	11	0.0	0.4
2. Year*date + year*blood + year*sex + date*blood + sex*blood	12	1.2	0.2
3. Year*date + year*blood + date*blood + sex*date + sex*blood	12	1.8	0.2
4. Year*date + year*blood + year*sex + date*blood + sex*date + sex*blood	13	2.9	0.1
5. Year*blood + date*blood + sex*blood	10	2.9	0.1
6. Year*date + year*blood + date*blood	9	4.7	0.0
7. Year*blood + year*blood*sex + date*blood	12	5.6	0.0
8. Year*date + year*blood + date*blood + sex	10	5.6	0.0
9. Year*blood + date*blood	8	7.7	0.0
10. Null model	3	238.6	0.0
b) $\delta^{15}\text{N}$			
1. Year + date + blood	6	0.0	0.2
2. Year*date + blood	7	0.3	0.2
3. Year + date + blood + sex	7	1.5	0.1
4. Year*blood + date	7	1.7	0.1
5. Year + date*blood	7	1.9	0.1
6. Year*date + date*blood	8	2.1	0.1
7. Year*blood + date*blood	8	3.6	0.0
8. Year*date + year*blood + date*blood	9	3.9	0.0
9. Year*blood + date*blood + sex	9	5.2	0.0
10. Year*date + year*blood + sex	10	5.5	0.0
11. Year*blood + year*sex + date*blood	10	6.1	0.0
12. Null model	3	149.9	0.0

The time period in the analysis extends from 30 May to 11 July. In the presence of an interaction between two factors, each individual factor was also retained in the model. N_p = number of parameters, Δ_{AICc} = difference in AICc between the current and preferred model, ω_i = AICc weight in favor of the model

value almost as large as lemmings (25–30 %; Fig. 3a). The contribution of these two food sources differed little between years of high and low lemming abundance. The contribution of the marine environment to the diet was around 20 % but varied greatly among individuals. These estimates were robust and not strongly affected by the isotopic discrimination values that we used. Indeed, the sensitivity analysis based on extreme discrimination values gave similar results compared to those obtained when average values were used (Table 3).

For birds captured at the nest in July, we also found a substantial contribution of anthropogenic food sources to their diet but that proportion differed markedly between the high (2003) and low (2008) lemming year (Fig. 3b). The proportion of anthropogenic sources was much higher (41 %; range 15–59 %) in the year when lemmings were scarce than when lemmings were abundant (16 %; 10–21 %), whereas lemming proportion in the diet followed exactly the opposite trend (42 %; 35–51 % during

the year of high lemming abundance vs. 24 %; 5–41 % during the low year). The variance in the proportion of all food sources was also higher in the low than in the high lemming year. These results were not sensitive to the assumption that nesting skuas were not using the marine environment. Indeed, the trends remained the same when marine sources were included even though the contribution of anthropogenic food sources decreased slightly (Figure S2, ESM).

Breeding activity

The clutch size at Alert tended to be higher during the year of high lemming abundance (1.92 ± 0.05 eggs [SE], $n = 26$ nests) than during the low year (1.70 ± 0.10 , $n = 10$ nests; Δ_{AICc} with null model was 0.63). Egg volume was also slightly greater during the year of high lemming abundance ($38.1 \pm 0.7 \text{ cm}^3$, $n = 50$ eggs) compared to the low year ($35.1 \pm 0.6 \text{ cm}^3$, $n = 17$; Δ_{AICc} with

Table 2 Parameter estimates (slopes with SE and 95 % confidence intervals) averaged across all models in Table 1 of the effects of blood components (1 = red blood cells (RBC); 0 = plasma), year (1 = low lemming—2008; 0 = high lemming—2003), sex (1 = M, 0 = F) and date (in standardized day of the year) on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values

$\delta^{13}\text{C}$	Beta	SE	95 % CI	
(Intercept)	−25.98	0.23	−26.42	−25.53
Year	1.66	0.25	1.18	2.25
Date	−0.83	0.10	−1.04	−0.63
Blood	3.53	0.27	3.00	4.05
Sex	−0.48	0.27	−1.02	0.05
Year*date	0.38	0.17	0.05	0.70
Year*blood	−0.84	0.27	−1.37	−0.31
Date*blood	−0.32	0.12	−0.56	−0.08
Sex*blood	0.71	0.25	0.21	1.21
Random effects				
Individual standard deviation	0.37			
Residual standard deviation	0.64			
$\delta^{15}\text{N}$	Beta	SE		
(Intercept)	5.53	0.19	5.15	5.90
Year	0.86	0.22	0.43	1.29
Date	−1.26	0.10	−1.45	−1.07
Blood	1.35	0.19	0.98	1.71
Sex	−0.13	0.23	−0.58	0.31
Year*date	0.26	0.19	−0.11	0.62
Year*blood	−0.2	0.31	−0.81	0.4
Date*blood	1.35	0.19	0.98	1.71
Random effects				
Individual standard deviation	0.40			
Residual standard deviation	0.75			

null model was 1.83). Similar results hold when clutch size was taking into account in the model. Finally, nest density was 2.6 times higher in the year of high lemming abundance (2003: 0.40 nest/km², $n = 26$ nests) than during the year of low abundance (2008: 0.15 nest/km², $n = 10$ nests; Figure S1 in the ESM).

At all other known sites where breeding density of skuas was recorded, nesting skuas were either totally absent or present at very low density (<0.02 nests/km²) in years of low lemming abundance but nested at densities ranging from 0.63 to 0.92 nest/km² in high lemming years (Fig. 4). Thus, difference in skua nesting density between years of high and low lemming abundance was >30-fold at all these sites.

Discussion

Based on repeated measures of isotopic ratios during 2 years of contrasting lemming abundance, we found

evidence that long-tailed skuas breeding at Alert use and benefit from allochthonous resources of human origin. Indeed, we found support for most of our initial predictions. Anthropogenic food resources from the sewage outfall stream of the military base contributed to the diet of skuas, and this contribution increased in nesting birds when lemmings were scarce. This alternative food source apparently dampened the effect of lemming population fluctuations on the annual breeding density of skuas at Alert compared to other Arctic sites.

Inter- and intra-year variations in diet

The strong seasonal decline in blood isotopic ratios occurred because skuas switch from a marine (enriched in both ¹³C and ¹⁵N; Fig. 1) to a predominantly terrestrial diet when they come ashore to breed. Moreover, the higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of RBC compared to plasma show that the signature in RBC was lagging behind plasma in adjusting to this recent diet switch because RBCs have a lower turnover rate than the plasma (Hobson and Clark 1993; Inger et al. 2006). Overall, individuals captured at the sewage outfall showed a significant but highly variable contribution of the marine environment to their diet. These birds represent a more heterogeneous sample than those captured on the nest because they are a mixture of transient and resident individuals (Julien et al. 2013) and potentially include breeders and non-breeders. We also captured them over a longer time period at the sewage outfall (~1 month) than on the nest (~10 days), with individuals captured earlier presumably showing a higher contribution of the marine environment to their diet due to a more recent habitat shift than those captured later on.

Although our study involved only two contrasting years of lemming abundance, we showed that the anthropogenic contribution to the skua's diet was of considerable importance and more than doubled in nesting birds during a year of very low lemming abundance. Moreover, $\delta^{13}\text{C}$ of plasma showed a steeper seasonal decline in 2003 (the high lemming year) than in 2008, presumably because lemmings, which have a low isotopic signature, made a greater contribution to the diet in that year as the breeding season progressed. The fact that we detected little increase in the contribution of lemmings to the diet of skuas captured at the sewage outfall in the high lemming year compared to nesting birds may be due to the timing of their capture. Indeed, birds were captured at the sewage outfall early in the season, mostly before the onset of laying. As movements of pre-laying birds are not constrained by the need to incubate and protect their nest, they may exploit a more diverse prey base than nesting birds.

The high variance (i.e., inter-individual variation) in the relative contribution of different food sources during the

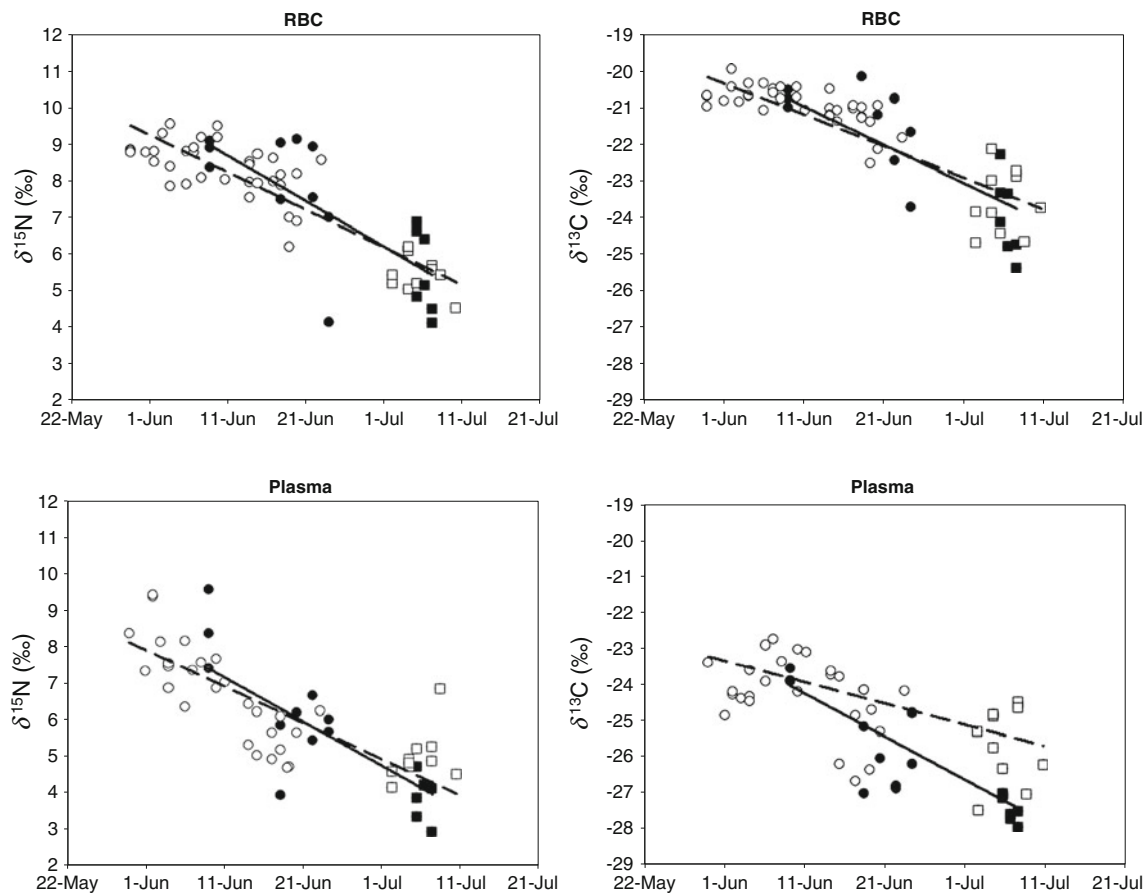


Fig. 2 Seasonal change in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values for red blood cells (RBC) and plasma of long-tailed skuas caught at Alert in years of high (2003, *black symbols and solid line*) and low (2008, *white symbols, dashed line*) lemming abundance. *Squares* represent birds caught on their nests and *circles* those caught at the sewage outfall. Blood values were adjusted for discrimination factors (see “[Materials](#)

and methods” section for details). Date was back-transformed (from standardized days) to produce this figure. This transformation induced a slight change in slopes, explaining the non-parallel slopes between years for the $\delta^{15}\text{N}$ where only additive effects were retained (Table 1b)

year of low lemming abundance could be explained by differences in individual foraging strategies when the preferred prey is scarce. For example, in years when low lemming abundance reduces the number of breeding skuas, some individuals might prefer feeding on arthropods around their nest rather than leaving the territory to forage farther away, while others could prefer taking advantage of the high availability of anthropogenic food away from their territory.

Blood $\delta^{13}\text{C}$ values appeared to differ between sexes in birds caught at the sewage outfall early in the season, but not in breeding birds. This could be explained by different arrival dates of the sexes or by different foraging behavior shortly after arrival on the tundra. In Greenland, De Korte and Wattel (1988) reported that the two sexes used different foraging strategies during the breeding season, which could explain differences in diet composition.

Even though our data supported our initial predictions, we recognize that they are based on only 2 years of data with contrasting lemming abundance. However, we choose

these 2 years a priori because of (1) a large difference in lemming abundance, (2) similar capture and nest searching efforts, and (3) availability of large number of blood samples. Thus, there was no bias in the selection of those 2 years with respect to the results that we present. Moreover, while we found no evidence that lemming isotopic signatures differed between years, sample size was small and most samples were collected in 2008. Although annual differences in isotopic signatures of prey could be a potential source of bias in our study, sampling of lemming isotopic signatures across several years on Bylot Island (73°08'N, 79°59'W) showed little annual variation (Gauthier et al. unpub. data). Future studies should thus aim to verify the patterns found in this study using larger sample sizes over more years.

Allochthonous resources and breeding productivity

Skua reproduction is dependent on food (especially lemmings) availability. Indeed, a strong relationship between

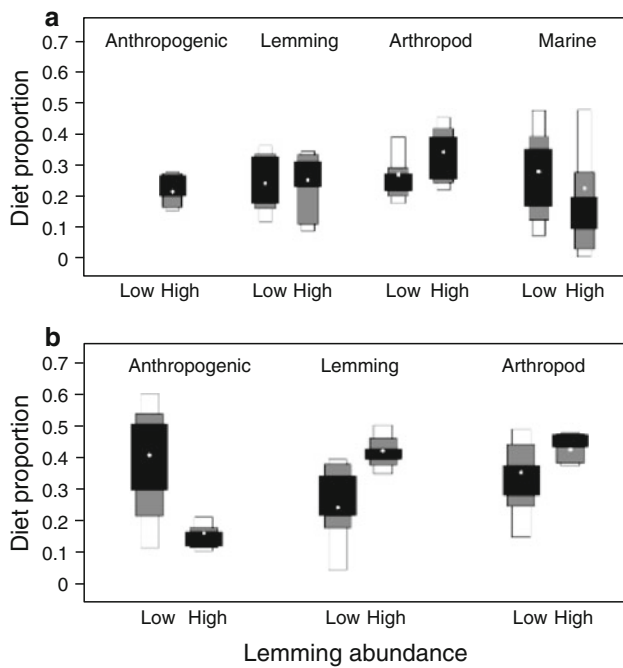


Fig. 3 Diet reconstruction using SIAR mixing models based on plasma isotopic signatures of long-tailed skuas at Alert in years of high (2003) and low (2008) lemming abundance. In upper part, **a** birds caught at the sewage outfall stream (30 May to 23 June; 2003 $n = 10$ and 2008 $n = 27$). In lower part, **b** birds caught at their nests (3–11 July 2003 $n = 7$ and 2008 $n = 10$; marine subsidies were excluded from this specific analysis, see “Materials and methods” section for details). Median (white dot), 50, 75, and 95 % credible intervals (dark gray, light gray, and white boxes, respectively) of the probability distributions of food proportions in diet are presented

the annual lemming abundance and the number of breeding pairs was shown at several Arctic sites (Maher 1970; Andersson 1976, 1981; Gilg et al. 2006). Skua nest density was relatively low at Alert compared to other sites in a high lemming year. This is probably because Alert is the northernmost site, and thus, ecosystem productivity is presumably lowest at such latitude. It is, however, remarkable to note that skua nest density was higher at

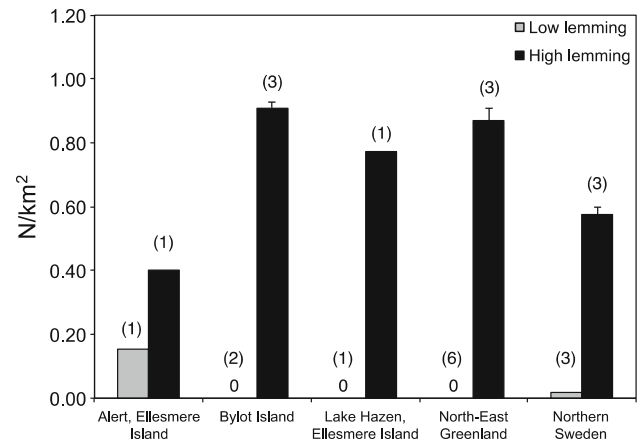


Fig. 4 Comparison of long-tailed skua nest density (N/km^2) recorded at Alert (present study), Bylot Island (73°08'N, 79°59'W; Therrien et al. 2014), Lake Hazen on Ellesmere Island (81°50'N, 70°25'W; Maher 1970), northeast Greenland (72°30'N 24°00'W; Gilg et al. 2006) and northern Sweden (68°27'N, 20°20'E; Andersson 1976) during years of high (black) and low lemming abundance (gray). “0” = no nesting activity found. Numbers in parentheses indicate the number of years of data at each site and error bars are standard errors based on yearly values

Alert than at all other sites in a low lemming year, with several sites reporting a total absence of nesting activity in those years. Clutch size and egg size have also been reported to vary in relation to food availability (Andersson 1976, 1981). In contrast to these studies, clutch and egg size varied only slightly between 2 years of contrasting lemming abundance at Alert. Because Alert is a site where birds consistently had access to an allochthonous food source for breeding likely explains the maintenance of reproduction in years when lemmings are scarce unlike at other sites. These results suggest that allochthonous resources of human origin can subsidize the local population of an avian predator breeding in a harsh arctic environment and dampen natural fluctuations in food abundance due to cyclic lemming populations.

Table 3 Diet reconstruction using SIAR mixing models based on plasma isotopic signatures of long-tailed skuas caught at the sewage outfall according to different values of discrimination

Discriminant factor	Lemming year		Sources			
	C (‰)	N (‰)	Anthropogenic	Lemmings	Arthropods	Marine
2.3	4.2	High	0.18	0.35	0.34	0.13
		Low	0.24	0.26	0.26	0.23
1.1	2.8	High	0.23	0.25	0.30	0.22
		Low	0.26	0.19	0.20	0.36
2.3	2.8	High	0.18	0.26	0.39	0.18
		Low	0.23	0.29	0.27	0.31
1.1	4.2	High	0.23	0.33	0.26	0.17
		Low	0.27	0.26	0.18	0.19
1.7	3.2	High	0.21	0.30	0.32	0.17
		Low	0.25	0.22	0.23	0.30

We simulate all the combinations of extreme discrimination values for $\delta^{15}N$ (2.8 and 4.2 ‰) and $\delta^{13}C$ (1.1 and 2.3 ‰) given in Bearhop et al. (2002). Average values (1.7 ‰ for $\delta^{15}N$ and 3.2 ‰ for $\delta^{13}C$) are equivalent to Fig. 3a

Implications of allochthonous subsidies

Consumption of food of human origin can sometimes negatively affect breeding success and reproductive output in seabirds (Pierotti and Annett 1991; Annett and Pierotti 1999; Grémillet et al. 2008). However, in many situations, the use of anthropogenic food sources, like human garbage, can have a positive effect on population size of opportunistic predators, including gulls and skuas (Pons and Migot 1995; Contesse et al. 2004; Weiser and Powell 2010).

The consequences of allochthonous subsidies can be dramatic and have cascading effects on other species in the food web. For instance, Weiser and Powell (2010) showed a positive relationship between the occurrence of garbage in the diet of Glaucous Gull (*Larus hyperboreus*) and their fledging rate and sub-adult survival in northern Alaska. They suggested that this could increase local gull populations, which in turn could affect their natural prey species, including several species of shorebirds and waterfowl of conservation concern in Alaska. The same pattern may occur at our study site. Indeed, if anthropogenic food sources contribute to maintain a larger and more stable long-tailed skua population locally, this could lead to increased predation on other species present in the area, such as the Red Knot (*Calidris canutus*), a declining species considered of Special Concern by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2011) and recently listed under Canada's Species at Risk Act. Indeed, given the high daily consumption rates measured for breeding long-tailed skua (Gilg et al. 2006; Therrien et al. 2014), even a slight increase in breeding density could strongly affect alternate prey species such as shorebirds. On the other hand, the availability of the anthropogenic source could divert skuas from seeking alternate prey in years of low lemming abundance, thereby providing survival benefits for shorebirds in the area. A full examination of these trophic links will require further studies at the food web level.

The functional significance of top predators in a food web depends on the main forces driving ecosystems. If food webs are bottom-up controlled, change in abundance of top predators will have little impact on the food web but greater impacts are expected if they exert a strong top-down control on lower trophic levels (Lecomte et al. 2009). There is increasing evidence that predators play a role in controlling Arctic food webs (Gilg et al. 2003; Gauthier et al. 2004; Legagneux et al. 2012; McKinnon et al. 2013). It has been suggested that allochthonous resources may enhance the functional role of predators in the tundra ecosystem due to its low productivity and biodiversity and relatively simple structure (Gauthier et al. 2011), which may be the case at Alert. Allochthonous food subsidies could allow predators to reach higher densities than those

predicted based solely on the primary productivity of the autochthonous system, which could in turn have indirect and cascading effects on other trophic levels. Therefore, a full understanding of the food web dynamic requires taking into consideration both autochthonous and allochthonous sources (Jefferies 2000; Leroux and Loreau 2008).

Acknowledgments We thank the Canadian Armed Forces and Environment Canada for permission to work at Alert and the staff of the Canadian Forces Station for their very professional and extensive support. We thank F. Vézina, J. Carrier, M. Cloutier, and C. Morrison for field assistance, A. Tarroux for technical assistance with SIAR, and F. Rousseau for help with statistical analyses. We are very grateful to B. Walter for his excellent nest searching during summer 2003. We are greatly indebted to G. Yannic for kindly sexing the birds. We also thank M.-C. Cadieux and all members of Gauthier's laboratory at Laval for fruitful discussions and comments on this project, as well as P. Flint for his comments on our original manuscript. Financial support was provided by the International Polar Year program of the Government of Canada, the Natural Science and Engineering Research Council of Canada, the National Wildlife Research Centre of Environment Canada, the Centre d'Études Nordiques, and the Université du Québec à Rimouski.

References

- Aljanabi SM, Martinez I (1997) Universal and rapid salt-extraction of high quality genomic DNA for PCR-based techniques. *Nucleic Acids Res* 25:4692–4693
- Andersson M (1976) Population ecology of the long-tailed skua (*Stercorarius longicaudus* Vieill.). *J Anim Ecol*:537–559
- Andersson M (1981) Reproductive tactics of the long-tailed skua (*Stercorarius longicaudus*). *Oikos* 37:287–294
- Annett C, Pierotti R (1999) Long-term reproductive output in Western Gulls: consequences of alternate tactics in diet choice. *Ecology* 80:288–297
- Bearhop S, Teece MA, Waldron S, Furness RW (2000) Influence of lipid and uric acid on d C-13 and d N-15 values of avian blood: implications for trophic studies. *Auk* 117:504–507
- Bearhop S, Waldron S, Votier SC, Furness RW (2002) Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. *Phys Biochem Zool* 75:451–458
- Bolduc E, Casajus N, Legagneux P, McKinnon L, Gilchrist HG, Leung M, Morrison R, Reid D, Smith PA, Buddle CM, Bêty J (2013) Terrestrial arthropod abundance and phenology in the Canadian Arctic: modelling resource availability for Arctic-nesting insectivorous birds. *Can Entomol* 145:155–170
- Bond AL, Diamond AW (2011) Recent Bayesian stable-isotope mixing models are highly sensitive to variation in discrimination factors. *Ecol Appl* 21:1017–1023
- Bond AL, Hobson KA (2012) Reporting stable-isotope ratios in ecology: recommended terminology, guidelines and best practices. *Waterbirds* 35:324–331
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York
- Contesse P, Hegglin D, Gloor S, Bontadina F, Deplazes P (2004) The diet of urban foxes (*Vulpes vulpes*) and the availability of anthropogenic food in the city of Zurich, Switzerland. *Mamm Biol* 69:81–95

- COSEWIC (2011) Canadian wildlife species at risk. Government of Canada. <http://www.cosewic.gc.ca/>. Accessed 5 Sep 2013
- De Korte J, Wattel J (1988) Food and breeding success of the long-tailed skua at Scoresby Sund, Northeast Greenland. *Ardea* 76:27–41
- Fridolfsson A, Ellegren H (1999) A simple and universal method for molecular sexing of non-ratite birds. *J Avian Biol* 30:116–121
- Gauthier G, Bêty J, Giroux JF, Rochefort L (2004) Trophic interactions in a high arctic snow goose colony. *Int Comp Biol* 44:119–129
- Gauthier G, Berteaux D, Bêty J, Tarroux A, Therrien J-F, McKinnon L, Legagneux P, Cadieux MC (2011) The arctic tundra food web in a changing climate and the role of exchanges between ecosystems. *Ecoscience* 18:223–235
- Gilg O, Hanski I, Sittler B (2003) Cyclic dynamics in a simple vertebrate predator-prey community. *Science* 302:866–868
- Gilg O, Sittler B, Sabard B, Hurstel A, Sane R, Delattre P, Hanski L (2006) Functional and numerical responses of four lemming predators in high arctic Greenland. *Oikos* 113:193–216
- Grémillet D, Pichegru L, Kuntz G, Woakes AG, Wilkinson S, Crawford RJM, Ryan PG (2008) A junk-food hypothesis for gannets feeding on fishery waste. *Proc R Soc B* 275:1149–1156
- Gruyer N, Gauthier G, Berteaux D (2008) Cyclic dynamics of sympatric lemming populations on Bylot Island, Nunavut, Canada. *Can J Zool* 86:910–917
- Hobson KA, Clark RG (1992a) Assessing avian diets using stable isotopes. 2. Factors influencing diet-tissue fractionation. *Condor* 94:189–197
- Hobson KA, Clark RG (1992b) Assessing avian diets using stable isotopes. 1. Turnover of C-13 in tissues. *Condor* 94:181–188
- Hobson KA, Clark RG (1993) Turnover of ^{13}C in cellular and plasma fractions of blood: implications for nondestructive sampling in avian dietary studies. *Auk* 110:638–641
- Hobson KA, Gibbs HL, Gloutney ML (1997) Preservation of blood and tissue samples for stable-carbon and stable-nitrogen isotope analysis. *Can J Zool* 75:1720–1723
- Hoyt DF (1979) Practical methods of estimating volume and fresh weight of bird eggs. *Auk* 96:73–77
- Huxel GR, McCann K (1998) Food web stability: the influence of trophic flows across habitats. *Am Nat* 152:460–469
- Ims RA, Fuglei E (2005) Trophic interaction cycles in tundra ecosystems and the impact of climate change. *Bioscience* 55:311–322
- Inger R, Bearhop S (2008) Applications of stable isotope analyses to avian ecology. *Ibis* 150:447–461
- Inger R, Ruxton GD, Newton J, Colhoun K, Robinson JA, Jackson AL, Bearhop S (2006) Temporal and intrapopulation variation in prey choice of wintering geese determined by stable isotope analysis. *J Anim Ecol* 75:1190–1200
- Jefferies RL (2000) Allochthonous inputs: integrating population changes and food-web dynamics. *TREE* 15:19–22
- Jefferies RL, Rockwell RF, Abraham KE (2004) Agricultural food subsidies, migratory connectivity and large-scale disturbance in arctic coastal systems: a case study. *Int Comp Biol* 44:130–139
- Johnsen KI, Alfthan B, Hislop L, Skaalvik JF (2010) Protecting Arctic biodiversity. United Nations Environment Programme, GRID-Arendal, Norway
- Julien JR, Gauthier G, Morrison RIG, Bêty J (2013) Survival rate of the long-tailed jaeger (*Stercorarius longicaudus*) at Alert, Ellesmere Island, Nunavut. *Condor* 115:543–550
- Lecomte N, Careau V, Gauthier G, Giroux JF (2008) Predator behaviour and predation risk in the heterogeneous Arctic environment. *J Anim Ecol* 77:439–447
- Lecomte N, Ehrlich D, Ims RA, Yoccoz NG (2009) Toward understanding the effect of top predators on ecosystems. *Biol Rep* 1:26
- Legagneux P, Gauthier G, Berteaux D, Bêty J, Cadieux MC, Bilodeau F, Bolduc E, McKinnon L, Tarroux A, Therrien JF, Morissette L, Krebs CJ (2012) Disentangling trophic relationships in a high arctic tundra ecosystem through food web modeling. *Ecology* 93:1707–1716
- Leroux SJ, Loreau M (2008) Subsidy hypothesis and strength of trophic cascades across ecosystems. *Ecol Lett* 11:1147–1156
- MacDonald SD (1953) Report on biological investigations at Alert. N.W.T. Natl Mus Can Bull 128:241–256
- Maher WJ (1970) Ecology of long-tailed jaeger at Lake-Hazen, Ellesmere-Island. *Arctic* 23:112–129
- McKinnon L, Berteaux D, Gauthier G, Bêty J (2013) Predator-mediated interactions between preferred, alternative and incidental prey in the arctic tundra. *Oikos* 122:1042–1048
- Oksanen L, Oksanen T (2000) The logic and realism of the hypothesis of exploitation ecosystems. *Am Nat* 155:703–723
- Oro D, Cam E, Pradel R, Martinez-Abraín A (2004) Influence of food availability on demography and local population dynamics in a long-lived seabird. *Proc R Soc B* 271:387–396
- Parnell AC, Inger R, Bearhop S, Jackson AL (2010) Source partitioning using stable isotopes: coping with too much variation. *PLoS ONE* 5:e9672
- Pierotti R, Annett CA (1991) Diet choice in the herring gull—constraints imposed by reproductive and ecological factors. *Ecology* 72:319–328
- Pinheiro JC, Bates DM (2000) Mixed effects models in S and S-Plus. Springer, New York
- Pinheiro JC, Bates DM, Debroy S, Deepayan S (2006) nlme: linear and nonlinear mixed effects model. R package version 3.1-77. <http://www.R-project.org>. Accessed 5 Sep 2013
- Polis GA, Hurd SD (1996) Linking marine and terrestrial food webs: Allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *Am Nat* 147:396–423
- Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Ann Rev Ecol Syst* 28:289–316
- Pons JM, Migot P (1995) Life-history strategy of the herring gull—changes in survival and fecundity in a population subjected to various feeding conditions. *J Anim Ecol* 64:592–599
- R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Tarroux A, Ehrlich D, Lecomte N, Jardine TD, Bêty J, Berteaux D (2010) Sensitivity of stable isotope mixing models to variation in isotopic ratios: evaluating consequences of lipid extraction. *Methods Ecol Evol* 1:231–241
- Therrien JF, Fitzgerald G, Gauthier G, Bêty J (2011) Diet-tissue discrimination factors of carbon and nitrogen stable isotopes in blood of Snowy Owl (*Bubo scandiacus*). *Can J Zool* 89(343):347
- Therrien JF, Gauthier G, Korpimäki E, Bêty J (2014) Predation pressure by avian predators suggests summer limitation of small mammal populations in the Canadian Arctic. *Ecology* (in press)
- Votier SC, Bearhop S, MacCormick A, Ratcliffe N, Furness RW (2003) Assessing the diet of great skuas, *Catharacta skua*, using five different techniques. *Polar Biol* 26:20–26
- Votier SC, Bearhop S, Witt MJ, Inger R, Thompson D, Newton J (2010) Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. *J Appl Ecol* 47:487–497
- Weiser EL, Powell AN (2010) Does garbage in the diet improve reproductive output of Glaucous Gulls? *Condor* 112:530–538
- Wiley RH, Lee DS (1998) Long-tailed jaeger (*Stercorarius longicaudus*). In: Poole A, Gill F (eds) The birds of North America, No. 365. The Academy of Natural Sciences, Philadelphia, pp 1–24