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Benefiting from a migratory prey: spatio-temporal patterns in allochthonous subsidization of an arctic predator

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Summary

1. Flows of nutrients and energy across ecosystem boundaries have the potential to subsidize consumer populations and modify the dynamics of food webs, but how spatio-temporal variations in autochthonous and allochthonous resources affect consumers' subsidization remains largely unexplored.

2. We studied spatio-temporal patterns in the allochthonous subsidization of a predator living in a relatively simple ecosystem. We worked on Bylot Island (Nunavut, Canada), where arctic foxes (*Vulpes lagopus* L.) feed preferentially on lemmings (*Lemmus trimucronatus* and *Dicrostonyx groenlandicus* Traill), and alternatively on colonial greater snow geese (*Anser caerulescens atlanticus* L.). Geese migrate annually from their wintering grounds (where they feed on farmlands and marshes) to the Canadian Arctic, thus generating a strong flow of nutrients and energy across ecosystem boundaries.

3. We examined the influence of spatial variations in availability of geese on the diet of fox cubs (2003–2005) and on fox reproductive output (1996–2005) during different phases of the lemming cycle.

4. Using stable isotope analysis and a simple statistical routine developed to analyse the outputs of a multisource mixing model (SIAR), we showed that the contribution of geese to the diet of arctic fox cubs decreased with distance from the goose colony.

5. The probability that a den was used for reproduction by foxes decreased with distance from the subsidized goose colony and increased with lemming abundance. When lemmings were highly abundant, the effect of distance from the colony disappeared. The goose colony thus generated a spatial patterning of reproduction probability of foxes, while the lemming cycle generated a strong temporal variation of reproduction probability of foxes.

6. This study shows how the input of energy owing to the large-scale migration of prey affects the functional and reproductive responses of an opportunistic consumer, and how this input is spatially and temporally modulated through the foraging behaviour of the consumer. Thus, perspectives of both landscape and foraging ecology are needed to fully resolve the effects of subsidies on animal demographic processes and population dynamics.

Key-words: *Anser caerulescens*, predator–prey interaction, SIAR mixing model, subsidies, *Vulpes lagopus*

Introduction

Although it is convenient to describe ecosystems as discrete entities differing in species composition, food chain length, or patterns of nutrient cycling, flows of nutrients and energy across ecosystem boundaries are ubiquitous and generate spatial coupling of ecosystems (Polis & Hurd 1996; Polis, Anderson & Holt 1997; Loreau & Holt 2004). Therefore, demographic processes underlying the dynamics of animal populations from a given ecosystem cannot be understood in isolation (Polis, Anderson & Holt 1997; Polis, Power &

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Huxel 2004). For example, a population belonging to a given ecosystem can be subsidized by allochthonous resources that have direct effects on its dynamics and indirect, cascading effects on its local prey or predators (Summerhayes & Elton 1923; Polis, Anderson & Holt 1997; Polis, Power & Huxel 2004). Subsidies can thus shape dynamics of populations through effects on demographic processes and consequently affect consumer–resources interactions and eventually the functioning of food webs (Polis & Hurd 1996).

The concept of allochthonous subsidy nicely complements the food chain models that have dominated food web ecology for decades (Van de Koppel *et al.* 2005). One of these models, the exploitation ecosystem hypothesis, predicts how the primary productivity of an ecosystem should influence the length of its food chain, and whether plant–herbivore or predator–prey interactions should drive the system (Oksanen *et al.* 1981; Oksanen & Oksanen 2000; Gauthier *et al.* 2004). Despite the fruitful debates stimulated by this model in food web theory (bottom-up and top-down forces: Power 1992; trophic cascades: Polis *et al.* 2000), it has failed to predict the trophic structure of many food webs (Polis & Strong 1996; Wegener & Odasz-Albrigtsen 1998; Krebs *et al.* 2003; Gauthier *et al.* 2004) because it did not take into account allochthonous subsidization (Oksanen & Oksanen 2000; Gauthier *et al.* 2011). There is thus a clear need for ecologists to better understand the nature and consequences of allochthonous subsidization. Although theoretical and empirical studies measuring effects of allochthonous resources on populations are rapidly accumulating, it is still unclear at what scale the energy input impacts consumers of the recipient ecosystem, a situation driven by the gap between landscape ecology and studies on trophic interactions (Callaway & Hastings 2002; Stapp & Polis 2003; Matthews & Mazumder 2006; Massol *et al.* 2011).

We used a simple tundra ecosystem exposed to the input of a subsidized resource to quantify, in a spatially explicit way, the effects of such resources on a local consumer whose diet and reproduction are shaped by fluctuating local resources (Angerbjörn, Tannerfeldt & Erlinge 1999; Roth 2002). On Bylot Island (Nunavut, Canada), arctic foxes (*Vulpes lagopus* L.) mainly feed during summer on cyclic brown and collared lemmings (*Lemmus trimucronatus* and *Dicrostonyx groenlandicus* Traill), their primary prey, and greater snow geese (*Anser caerulescens atlanticus* L.; geese hereafter), their secondary prey (Bêty *et al.* 2001, 2002). Geese are migratory birds and spend the winter in temperate areas, where they are subsidized by resources provided by farmlands, especially cornfields (Gauthier *et al.* 2005; Fig. 1a). Hence, every spring, geese bring to the tundra nutrients from farmlands and temperate marshes, thereby connecting temperate and Arctic ecosystems (Jefferies, Rockwell & Abraham 2004). This link between ecosystems differing in productivity could allow arctic foxes to reach abundance levels not predicted from the sole primary productivity of the tundra (Oksanen & Oksanen 2000; Gauthier *et al.* 2004, 2011).

This study system is particularly suited for answering the critical question of how space modulates the strength of response of a local consumer to subsidized resources. Indeed, geese breed colonially and are thus located in a restricted portion of the study area, whereas foxes breed in dens distributed across the entire study area (Fig. 1b) where their diet and reproductive output can be monitored. We predicted that the use of a prey subsidized by allochthonous resources (geese) by a local consumer (foxes) is maximal where the prey is most abundant (near the goose colony), but gradually fades with increasing distance from the colony, and is temporally variable in response to the lemming cycles. We made the same prediction regarding the reproductive output of the local consumer. We verified those predictions using a combination of long-term field monitoring (geese, lemmings, foxes), short-term isotopic measurements, isotope mixing modelling (SIAR; Parnell *et al.* 2010) and a statistical routine used to analyse the outputs of this mixing model.

Materials and methods

STUDY AREA

We worked from 1996–2005 on the south plain of Bylot Island (Fig. 1b), Sirmilik National Park of Canada (72°53′N, 78°54′W). Our 425 km^2 study area mostly consists of moist upland plateau (mesic tundra) intersected by lowland valleys filled with wetlands (Massé, Rochefort & Gauthier 2001). About 20 000 pairs of greater snow geese nest on the study area (Reed, Hughes & Boyd 2002). Density of other migrating birds is small compared to geese (Lepage, Nettleship & Reed 1998). Two lemming species coexist on Bylot. Brown and collared lemmings prefer wetland habitats and mesic tundra, respectively (Rodgers & Lewis 1986). Other herbivores such as the rock ptarmigan (*Lagopus mutus*) and the arctic hare (*Lepus arcticus*) are found at low density on the island (Gauthier *et al.* 2004). The arctic fox is the main terrestrial predator of the food web (Gauthier *et al.* 2004), and its summer diet is essentially composed of geese (mostly eaten as eggs and goslings) and lemmings. Evidence that lemmings and geese are the two major prey of foxes comes from faecal analyses, prey remains on dens and behavioural observations (Bêty *et al.* 2002; D. Berteaux, unpublished). Spatial distribution of arctic fox dens on the study area is not influenced by food resources, but rather by geomorphology and microclimate (Szor, Berteaux & Gauthier 2008).

STUDY DESIGN

We quantified the spatial dynamics of allochthonous subsidization in two steps. First, we estimated the contribution of geese to the summer diet of arctic fox cubs along an axis of increasing distance from the edge of the goose colony (0–36 km; hereafter called distance from the colony, see Fig. 1b) during 3 years of contrasted small rodent abundance (0, 0·22 and 0·83 lemmings caught per 100 trap-nights in 2003, 2004 and 2005, respectively; Fig. 1c; Gruyer, Gauthier & Berteaux 2008). Because of the low number of breeding dens during a low lemming year such as 2003 (see Results), we sampled only one den in 2003 and report data only for descriptive purposes. We estimated the contribution of geese to the summer diet of arctic fox cubs with stable isotope analyses of cubs' blood samples. Isotopic quantification of the diet of a consumer is possible when food sources are isotopically distinct (Phillips, Newsome & Gregg 2005). We anticipated differences in carbon isotopic signatures between lemmings and geese because they absorb nutrients from different food webs (Kelly 2000).

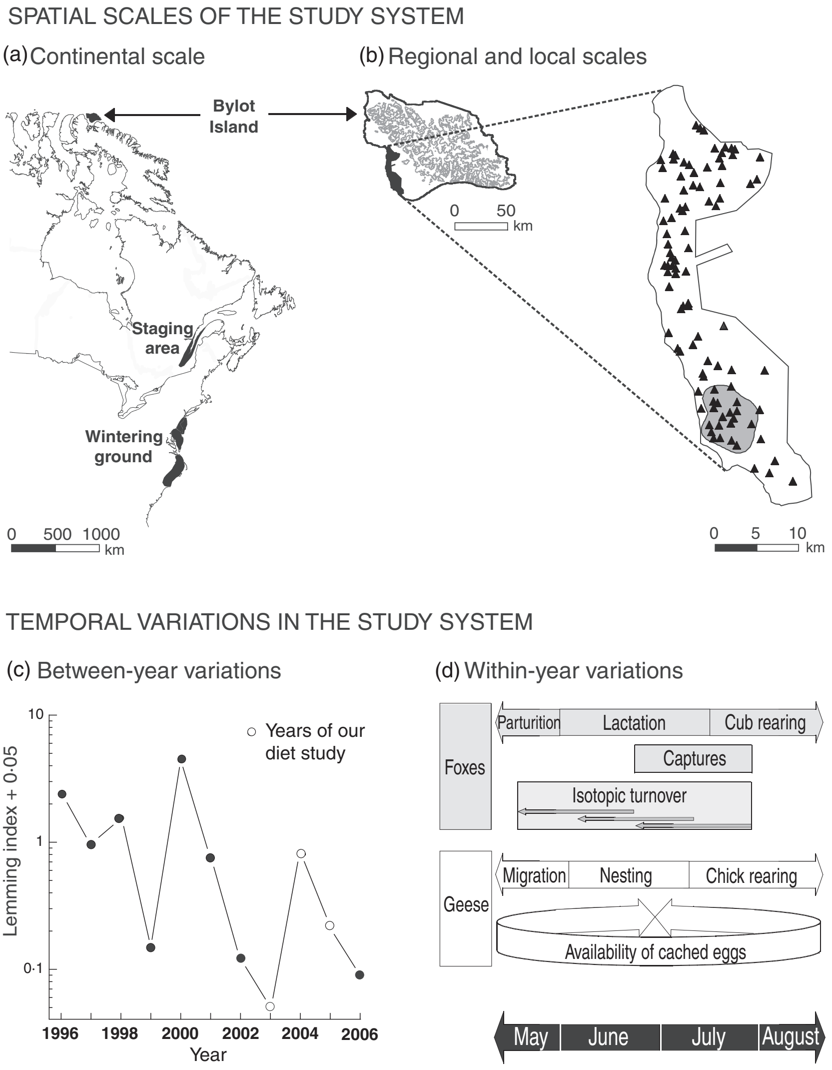

Fig. 1. Spatial scales of the study system and its temporal variations. (a) Continental scale: main areas used by migrating greater snow geese during their annual life cycle, from their temperate wintering ground and staging area to their arctic breeding ground on Bylot Island, Canada. (b) Regional and local scales: Bylot Island and the study area, showing the goose colony (grey patch) and the distribution of arctic fox dens (black triangles). (c) Temporal (between-year) variations in lemming abundance showing phases of the lemming cycle on Bylot Island from 1996–2006. (d) Temporal (within-year) variations in the reproductive stages of arctic fox and greater snow goose, with a representation of the period of cub captures, the isotopic half-life of blood cells relative to the period of capture (arrows indicate the half-life period of 40 days preceding the capture of three hypothetical individuals; Lecomte *et al.* 2011) and the availability of goose eggs for foxes.

Lemmings feed exclusively on arctic C_3 plants, whereas geese feed on both arctic C_3 plants (on breeding ground) and temperate C_3 and C_4 plants (on wintering and staging areas; Fig. 1a; Gauthier, Bêty & Hobson 2003). Second, we examined the reproductive output of arctic foxes (probability of a den being used for reproduction and litter size on breeding dens) over a 10-year period (1996–2005) along the same axis of increasing distance from the colony.

ARCTIC FOX MONITORING

From 1996–2005, we monitored arctic fox dens to identify active breeding dens and estimate litter sizes. From 1996–2002, we searched for fox dens in the study area, and we found new dens every year (the size of the surveyed area increased during the study; Bêty *et al.* 2002). In 2003, we conducted an extensive and systematic den survey in the 425 km^2 study area (Szor, Berteaux & Gauthier 2008). We are confident that we found most, if not all, dens because arctic fox dens are generally easy to detect, as repeated use tends to result in lush vegetation on dens (Audet, Robbins & Larivière 2002). Every known den was visited at least once per summer to assess the presence of cubs through visual observation and thus determine whether the den was used by reproducing foxes. From 2003–2005, we monitored diet of cubs from the beginning of the rearing season around mid-May (Macpherson 1969; Audet, Robbins & Larivière 2002) until den departure around early August. To describe diet, we used the isotopic signatures of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) of whole blood, which represents the nutrients assimilated over a period of about 2 months before the collection (Lecomte *et al.* 2011). We trapped cubs on their den with collapsible live traps (Model 205, Tomahawk Live Trap Company, Tomahawk, WI, USA) on 11 August 2003, from 19 June to 28 July 2004 and from 28 June to 27 July 2005. We collected blood from the cephalic vein of 55 cubs trapped on 15 breeding dens (one den in 2003, eight in 2004 and six in 2005; 1–10 cubs per den) and then stored in ethanol 70%. We sampled cubs from 64% of breeding dens on the study area during those years.

PREY MONITORING

We monitored geese by extensively searching nests of marked geese during nesting periods (see Lecomte, Gauthier & Giroux 2008), and by mapping the average extent of the goose colony from 1996–2005 (Fig. 1b) using a cross-validated fixed 95% kernel (Seaman & Powell 1996) of the position of marked goose nests (ArcView GISTM 3·2a, Animal movement extension; Hooge, Eichenlaub & Solomon 1999). Average nesting density of geese in the colony ranged from 1–11 nests/ha between 1996 and 2005, with no particular increasing or decreasing trend observed over this period. We monitored lemmings in two ways: we calculated one index to estimate temporal variations, while the other estimated spatial variations. First, we calculated an annual index of lemming abundance (hereafter: the lemming temporal index) from snap-trap censuses performed each July from 1996–2005. This index is expressed as the number of lemmings caught per 100 trap-nights and is based on ≥1000 trap-nights per year (Gruyer, Gauthier & Berteaux 2008). Second, we assessed spatial variation in lemming availability by estimating spatial heterogeneity in lemming habitat use over the study area. Using counts of burrows and faeces performed in 2005, we estimated the lemmings' relative use of ten habitat types (see Appendix S2 for details). These counts mostly reflect a multi-annual average summer use of each habitat type because faeces and burrows persist for multiple years (Szor, Berteaux & Gauthier 2008). We then generated a lemming spatial index by combining the relative use by lemmings of each habitat type to the availability of these same habitats in a 2 km radius around each den (2 km is the average radius of a fox summer home range in our study area; A. Tarroux and D. Berteaux, unpublished radiotracking data). The lemming spatial index varied between 0·2 and 0·5, with lower values indicating lower lemming habitat quality around dens. Variations of this index over the study are available in Szor, Berteaux & Gauthier (2008). Finally, during the summers of 2004–2005, we opportunistically collected throughout the study area muscle from fresh carcasses of lemmings and geese (adults and goslings), and egg content of freshly broken eggs (only one sample per nest) for stable isotope analyses.

STABLE ISOTOPE ANALYSES

We used stable isotopes to estimate the contribution to fox diet of the two main prey types (lemmings and geese) for which we had non-isotopic evidence of consumption during the summer. We first measured the δ^{13}C and δ^{15}N of fox whole blood and prey tissues (see Appendix S1 for laboratory methods). Then, using a manova, we determined whether the signatures of different prey items were clustered enough to pool their signatures (Appendix S1). We pooled signatures from the two lemming species, but those of goose items (adults, eggs and goslings) were not clustered enough to be pooled (Fig. 2). We used the SIAR package (Parnell *et al.* 2010) with the R 2·12 platform (R Development Core Team 2011) to estimate the contribution of each prey to fox diet. This flexible framework of mixing models accounts for variability in prey signatures and uncertainty in isotopic discrimination.

We corrected fox signatures for isotopic discrimination (i.e. difference between diet and tissues) using the estimates developed for blood cells of yearling arctic foxes fed a terrestrial diet (Appendix S1; Lecomte *et al.* 2011). To examine the relative use by foxes of autochthonous resources vs. those subsidized by allochthonous sources, we subsequently combined the contributions of the different prey into two groups, that is, lemmings and goose items (*a posteriori* aggregation; Phillips, Newsome & Gregg 2005).

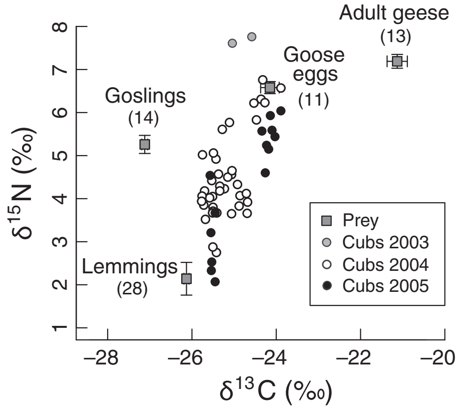

Fig. 2. Carbon and nitrogen isotopic signatures (δ^{13}C and δ^{15}N, corrected for discrimination) of arctic fox cubs and prey in 2003–2005 on Bylot Island, Canada. Squares represent the average signatures (±SE) of the four prey types, whereas circles represent the signatures of individual cubs.

DATA ANALYSES

Diet

We tested whether the contribution of goose to the diet of arctic fox cubs decreased with distance from the colony (1st prediction), by relating isotopic diet reconstruction (response variable) to three fixed predictors: distance from den to the colony, lemming temporal index as a categorical variable (2004 higher value contrasted to 2005 lower value) and date of cub capture. Date of capture accounted for the potential effects of lactation on cubs' isotopic signatures (Fig. 1d and Appendix S1) because capture date was correlated to cub age (Pearson correlation: $r = 0·7$, $P = 0·003$) and thus to milk contribution to diet. Variations in date of capture may also reflect variations in relative contributions of lemmings and geese to cub diet because goose reproduction phenology influences fox foraging behaviour (Fig. 1d; Careau *et al.* 2008b). As sibling fox cubs from the same den were not independent samples, we used data from every cub in the analysis, but specified den identity as a random variable in the mixed models.

We generated the response variable (proportion of goose in diet for each cub) by using the probability distribution provided by SIAR. All solutions in this distribution are possible, and only using the mean is a common mistake, as foreseen by Phillips & Gregg (2003). To test whether the contribution of goose to cubs diet decreased with distance from the colony, we ran a three-step statistical routine (*sampling, model selection and averaging*) as follows. First, we *sampled* 700 000 solutions (or iterations) generated by the Markov chain Monte Carlo of SIAR by excluding the first 200 000 solutions (burn-in), retaining one for every 10 solutions generated (thinning) and finally excluding solutions outside the 5–95th percentile interval to obtain a final set of 45 000 solutions. We then built six linear models, each containing one or two fixed predictors (distance den-colony, lemming temporal index, date of capture; see Appendix S3 for the list of models) and den identity as a random variable. For each of the 45 000 SIAR solutions sampled, we *selected* the model that minimized the Akaike Information Criterion corrected for small sample size (AICc; Burnham & Anderson 2002). We then calculated the number of times each model was selected as the best and divided this value by 45 000 to obtain a frequency of selection (π) for each model. The best-fit models are those with the highest frequency of selection (Burnham & Anderson 2002). We then *averaged* parameter estimates and their 95% confidence intervals over the 45 000 iterations for a given best-fit model, and we finally used *model averaging* to obtain parameter estimates and their 95% confidence intervals averaged over best-fit models (Burnham & Anderson 2002). We ran the routine using a script (available upon request) written in R (R Development Core Team 2011).

Reproduction

We tested the second prediction that fox reproductive output decreases with distance from the goose colony by using AICc to select the generalized linear mixed models (GLMMs) that best fit variations in the indexes of reproductive output (probability of a den being used for reproduction and litter size on breeding dens). We modelled the probability of a den being used for reproduction using the presence or absence of reproduction on a den as a binary distributed response in a mixed logistic regression, and we modelled litter size on breeding dens as a Poisson distributed count response. For each index of reproductive output, we compared 13 biologically plausible models built with the following fixed predictors: distance den-colony, lemming temporal index, lemming spatial index and interactions between the lemming temporal index and other predictors (see Appendix S3 for the list of models). We included den identity as a random variable because we repeated observations of the same dens across years. Autocorrelograms (function acf in R) indicated no temporal autocorrelation between data from consecutive years within a given den. We assessed goodness-of-fit of models using the Pearson χ^2 test. We considered models with the smallest AICc value and those with ΔAICc < 2 as having substantial empirical support (Burnham & Anderson 2002). In case of uncertainty in model selection, we used multi-model inference to calculate parameter estimates and their 95% confidence intervals. We performed statistical analyses with the R 2·12 platform (R Development Core Team 2011) and SAS (SAS Institute 2006).

Results

DIET OF ARCTIC FOX CUBS

The percentage of geese in the diet of cubs averaged 97% in 2003 (0 lemming caught per 100 trap-nights) and ranged from 21 to 96% and from 18 to 79% in 2004 and 2005, respectively (0·22 and 0·83 lemming caught per 100 trap-nights; Fig. 3). Distance from the colony and date of capture best explained these variations (best-fit model: distance from the colony + date of capture; Appendix S3). According to this model, the contribution of geese to the diet of cubs decreased by 14% per 10 km away from the goose colony (CI 95% [2, 27], n = 53 cubs on 14 dens; Fig. 3). However, the effect of date of capture on cubs' diet was minimal as 95% CI of parameter estimates overlapped zero (slope = 5% per week, CI 95% [−14, 37], n = 53 cubs on 14 dens). The lemming temporal index did not affect cubs' diet (this variable was not retained in the best-fit models, Appendix S3), indicating that the diet of cubs was similar during 2 years with different lemming abundance.

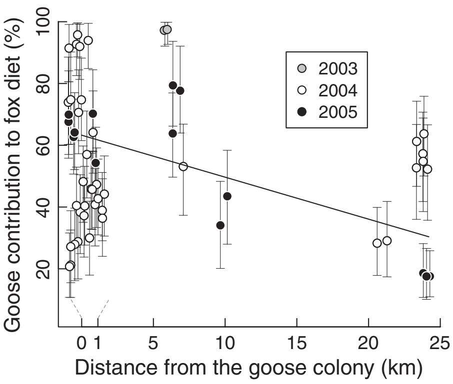

Fig. 3. Influence of the distance between arctic fox dens and the goose colony on the contribution of geese to the diet of arctic fox cubs studied on Bylot Island (Canada) during low abundance of lemmings (2003, only shown for descriptive purposes), high abundance of lemmings (2004) and declining abundance of lemmings (2005). Circles correspond to the average goose contribution to cubs' diet, and error bars represent the 5–95th percentiles of the distribution of contributions (estimated with SIAR). The predicted curve is drawn from the estimates of parameters obtained with the best-fitting model (see Results). Some points are offset with respect to distance from the goose colony to display the full sample size; the offset being more pronounced up to 1 km from the goose colony (because of the high number of cubs sampled in this area), the funnel-shaped dashed lines thus indicate the range of values within this interval.

REPRODUCTIVE OUTPUT OF ARCTIC FOXES

From 1996–2005, the probability of a den being used for reproduction averaged 10% and ranged from 0 to 100%. This wide variation was best explained by two models including the following variables: distance from the colony, lemming temporal index, lemming spatial index and interaction between lemming temporal index and distance from the colony (Appendix S3). According to multi-model averaging, a 71% decrease in the probability of a den being used for reproduction was predicted per 10 km away from the goose colony (CI 95% [66%, 75%], n = 530 observations on 97 dens; Fig. 4a). This 71% decrease applies at low values of the lemming temporal index (*i.e.* 0·1 lemmings caught per 100 trap-nights) and is reduced by a factor of 32% for every additional lemming caught per 100 trap-nights (CI 95% [7%, 62%], n = 530 observations on 97 dens), because the interaction term between distance from the colony and lemming temporal index influenced the probability of a den being used for reproduction. When two lemmings are caught per 100 trap-nights, the probability of a den being used for reproduction decreases by 51% per 10 km away from the goose colony (CI 95% [37%, 62%]), and when > 3 lemmings are caught per 100 trap-nights, the probability of a den being used for reproduction no longer decreases with the distance from the goose colony (−35%, CI 95% [−59%, 2%], n = 530 observations on 97 dens; Fig. 4a). At low values of the lemming temporal index (< 0·15 lemmings caught per 100 trap-nights), no reproduction occurred further than 8 km from the goose colony, but at higher values of the lemming temporal index,

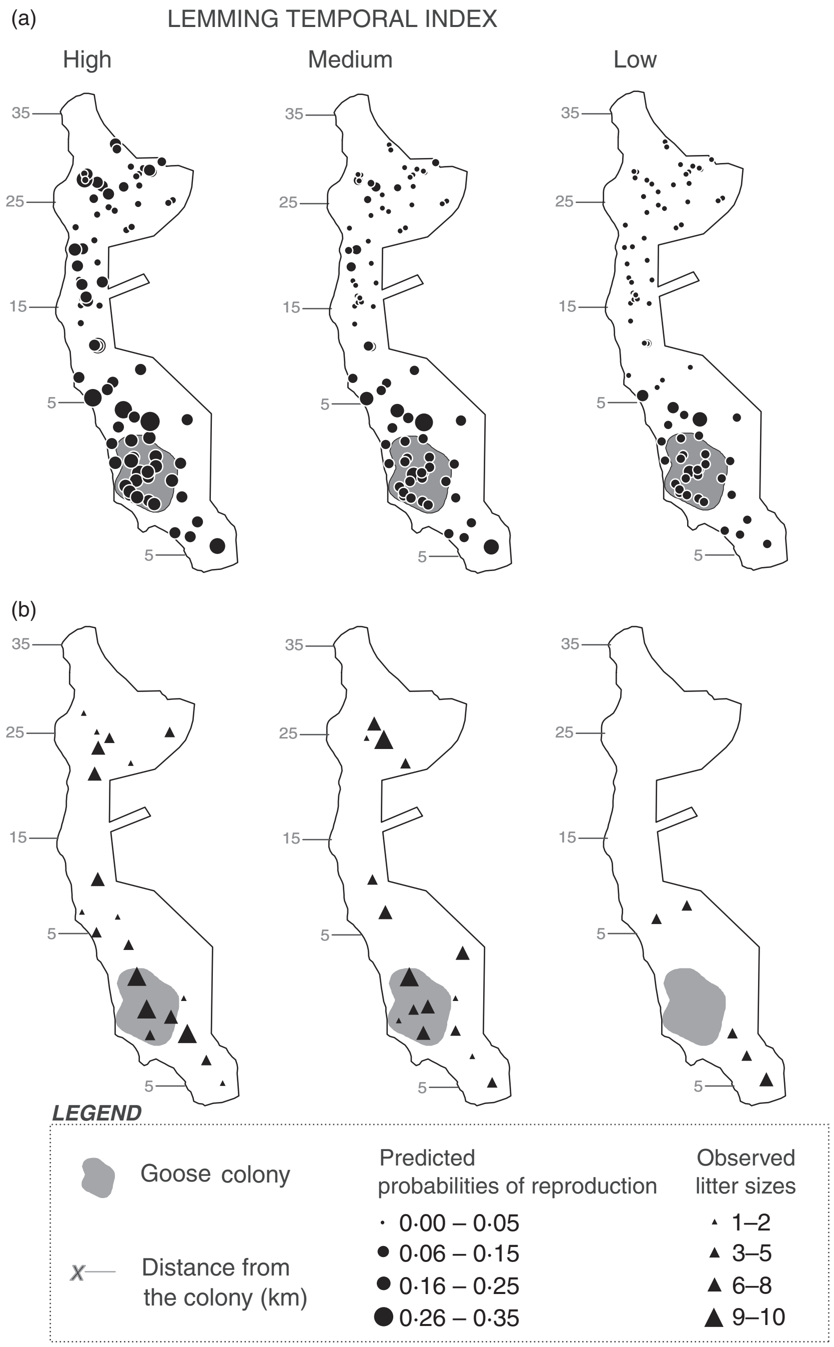

Fig. 4. Spatio-temporal patterns in arctic fox reproductive output at different values of the lemming temporal index on Bylot Island, Canada, for the period 1996–2005. (a) Circles indicate den locations. Their sizes represent probabilities of a den being used for reproduction at high, medium and low values of the lemming temporal index (4, 2 and 0 lemmings caught per 100 trap-nights, respectively), as predicted with the best-fitting model (Table S2.3A). (b) Triangles indicate den locations. Their sizes represent observed litter sizes averaged for each den over years of high, medium and low values of the lemming temporal index. Years were classified according to the following intervals of the lemming temporal index: > 2–4 (high), > 0·15–2 (medium) and 0–1·15 (low) lemmings caught per 100 trap-nights.

breeding occurred throughout the study area (Fig. 4b). At 30 km and 15 km from the goose colony, the probability of a den being used for reproduction increased by 129% and 53%, respectively, for every additional lemming caught per 100 trap-nights (30 km: CI 95% [68%, 215%], 15 km: CI 95% [18%, 97%], Fig. 4a). Closer to 6 km from the goose colony, the probability of a den being used for reproduction no longer increased with additional lemmings caught per 100 trap-nights (19%, CI 95% [−1%, 44%], Fig. 4a). The effect of the lemming spatial index was minimal as 95% CI of its parameter estimate overlapped zero (slope = −0·06, CI 95% [−0·16, 0·05], n = 530 observations on 97 dens).

Litter size on breeding dens varied from 1 to 10 cubs (4·5 ± 0·3 [SE], Fig. 4b). Although the model including only the lemming spatial index had a ΔAICc < 2 (Table S3.2B, Appendix S3), the effect of the lemming spatial index on the litter size was minimal as 95% CI of parameter estimates overlapped zero (slope = 8%, CI 95% [−14, 37]).

Discussion

We showed that both the contribution of geese to the diet of arctic fox cubs and the probability of a den being used for reproduction by foxes decreased with distance from the goose colony. This spatial pattern was superimposed on a strong temporal variation in fox reproduction, originating from the lemming cycle. The patterns we describe are robust because we are confident that we inventoried most, if not all, fox dens over a wide area (425 km^2) and sampled 64% of breeding dens for isotopic analysis of cub diet. In addition, the spatial and temporal patterns in goose and lemming availability were monitored over the same large spatial scale, while patterns in fox reproduction were monitored over a 10-year period.

The main contributions of this study fall into three categories: (i) the spatial patterns modulating the allochthonous subsidization of an arctic terrestrial predator; (ii) the interaction between these spatial patterns and the temporal variations in the availability of local resources; and (iii) a robust technical routine for isotopic tracking of resources, using outputs from models of isotopic diet reconstruction.

EFFECTS OF SUBSIDIES: THE SPATIAL COMPONENT

Despite more than 10 years of theoretical and empirical investigations, tracking the ecological effects of subsidies through space has proved challenging, especially once subsidies have entered an ecosystem (Callaway & Hastings 2002; Stapp & Polis 2003; Matthews & Mazumder 2006; Anderson, Wait & Stapp 2008). In general, recipient populations show direct numerical response (through aggregation and reproduction; Polis, Anderson & Holt 1997; Yang *et al.* 2010), but how this response varies through space is still unclear. In our study system, the restricted distribution of the source (geese) and the site-constrained foraging behaviour of the consumer (foxes) spatially modulate the input of subsidized prey within the food web (Fagan, Lutscher & Schneider 2007). Foxes are constrained by the location of their breeding dens, and those denning outside the colony probably increased the diffusion of energy originating from geese across the tundra by foraging within the colony and provisioning their litter away from it. Goose nests can occasionally be found at very low density outside the colony (Bêty *et al.* 2002), and it cannot be excluded that foxes prey on these nests because predation rate increased at low goose density in our study area (Bêty *et al.* 2001). This might explain that some cubs had up to 60% of goose tissues in their diet at more than 20 km from the colony (Fig. 3). In spite of that, our isotopic analyses clearly show that goose contribution decreased with distance from the colony, as does the availability of this major alternative food source in a low productive ecosystem.

An allochthonous resource is defined as a subsidy when it increases the productivity of a consumer population (Polis, Anderson & Holt 1997). Everything else being equal, spatial patterns in the productivity of the subsidized population should then parallel spatial patterns in the consumption of the subsidy. From an Arctic perspective, geese are not strictly an allochthonous resource because they feed in the tundra for 3 months of the year (Gauthier *et al.* 2004, 2011). However, the viability of their life cycle and their current population size are heavily dependent on resources from their wintering and staging grounds (Jefferies, Rockwell & Abraham 2004; Gauthier *et al.* 2005), which in turn may provide a subsidy to arctic predators. On Bylot Island, the consumption of geese by foxes and the probability that a fox den was used for reproduction both decreased with distance from the goose colony, and these effects were dampened as lemming abundance increased. This suggests that geese, a resource located in a restricted portion of the study area during the nesting period, could support fox populations by supporting their reproduction.

The demonstration of a spatially explicit reproductive response to a subsidized prey is important to better understand allochthonous subsidization. Yet how does this reproductive response affect population dynamics of the predator? This requires data on juvenile and adult dispersal and mortality, which may all decrease when food is abundant in summer territories (Tannerfeldt, Angerbjörn & Arvidson 1994; Goltsman *et al.* 2005; Samelius, Alisauskas & Larivière 2011). Arctic foxes prolong pulses of bird eggs through their caching behaviour (Samelius *et al.* 2007; Careau *et al.* 2008b) and can eat cached eggs during winter (Fay & Stephenson 1989; Prestrud 1992; Careau *et al.* 2008a) and up to the following spring (Stickney 1991; Samelius *et al.* 2007; Fig. 1d). This could enhance their winter survival (Careau *et al.* 2008a), although impacts on recruitment and adult population size still need to be rigorously quantified. Current knowledge thus suggests that goose-driven patterns in fox reproductive response observed in our study could scale-up to a spatially modulated numerical response, with long-lasting effects of subsidized prey on predator population dynamics. Although more empirical support is needed, this hypothetical scaling-up of reproductive response to numerical response fits predictions from a projection matrix model (Henden *et al.* 2009), showing that outside lemming crashes, management actions that improve reproductive output through increased resource availability have the largest effect on arctic fox growth rate. As highlighted by Henden *et al.* (2009), the influence of reproductive parameters on the capacity for growth in arctic fox populations is also supported by the wide variation in reproductive output within the species (Tannerfeldt & Angerbjörn 1998; Gauthier *et al.* 2004), compared to a much less variable survival (Meijer *et al.* 2008).

EFFECTS OF SUBSIDIES AND LOCAL RESOURCES: THE SPATIAL AND THE TEMPORAL COMPONENTS

There is a clear need for empirical information about the respective influences of subsidies and local resources on subsidized consumers (but see Anderson, Wait & Stapp 2008). We showed that spatial variations in the availability of a subsidized prey can also shape the dynamics of reproduction in temporally patterned populations, whose productivity is mainly influenced by the availability of their preferential cyclical prey (Angerbjörn, Tannerfeldt & Erlinge 1999; Elmhagen *et al.* 2000).

In addition to showing that dens were more likely to be used for reproduction when lemmings were more abundant, we also found that the availability of geese shaped the dynamics of fox reproduction. The spatial extent of goose subsidization was clearly revealed by the absence of reproduction further than 8 km from the colony when abundance of lemmings was very low (Fig. 4b), but the negative effect of distance from the colony disappeared when lemmings were highly abundant (> 3 lemmings caught per 100 trap-nights). However, the predicted threshold of three lemmings per 100 trap-nights, above which distance from the colony had no more negative effect on fox reproduction, was reached only once in 10 years (Fig. 1c). This suggests that nesting geese, a resource located in a restricted portion of the study area, could support fox populations by augmenting their reproduction, although this effect was lower when lemmings were abundant. This dampened effect of goose availability when lemmings were abundant could result from the observation that cubs raised within the colony seemed to depend less on geese during high lemming years, as shown by the wide variability in the proportion of goose in the diet of cubs close to the colony in 2004 (Fig. 3). The mechanism generating this variability likely originates in the variable feeding strategies of adult foxes or cubs. We thus conclude that geese are a crucial resource for fox reproduction that may contribute to maintain this predator population above the level predicted solely by the primary productivity of the tundra ecosystem (Oksanen *et al.* 1981; Polis & Strong 1996; Gauthier *et al.* 2004, 2011).

The absence of reproduction further than 8 km from the colony when lemming abundance was very low (Fig. 4b) raised interesting insights linking foraging behaviour and demographic processes. Indeed, such limitation in the spatial extent of subsidies' benefits could result from the travelling costs associated with the provisioning of cubs. During lemming crashes, previous studies observed a prey-switching behaviour between the preferential local prey and the alternative prey in this study system (Bêty *et al.* 2002; Careau *et al.* 2008b; Lecomte *et al.* 2008). For example, during a crash, 100% of attacks by arctic foxes in the colony were directed toward goose nests compared to 50% of attacks during a decline (Bêty *et al.* 2002); such observations can be put in the context of our isotopic study, with the two cubs sampled in the low lemming year showing 97% goose in diet, while goose contribution to fox cubs' diet was 54% on average during years of declining and high abundance of lemmings. Our study suggests that such prey-switching behaviour might have been the mechanism for maintaining reproduction during crashes of local resources, yet at a reduced spatial scale corresponding to the area where subsidized resources were available. This tandem of temporal and spatial scales acting on the predator reproductive response is a novel perspective on how prey-switching behaviour can scale-up to demographic processes in predator populations (Lecomte *et al.* 2008).

The probability of a den being used for reproduction was influenced by the availability of both local and external resources, but litter size was not. Food resources generated by the goose colony probably induced an aggregative response of reproducing foxes, thus affecting the probability that a den located around the colony was used for reproduction. Why these food resources did not affect litter size is less clear, given that previous studies showed that availability of rodents and other food resources did affect litter size in arctic fox (Angerbjörn *et al.* 1991; Tannerfeldt & Angerbjörn 1998; Strand *et al.* 2000). One hypothesis is that the availability of winter and spring resources, such as seal carrion and seal pups, interacted with the availability of lemmings. In another arctic fox population of the Canadian Arctic, marine food sources became more important to arctic foxes in winters with low lemming populations (Roth 2002), and variation in marine productivity affected arctic fox abundance (Roth 2003). The effects of allochthonous resources on the dynamics of this predator may thus have multiple facets.

The patterns we describe are robust, but as our study is not experimental, we cannot exclude the possibility that spatio-temporal gradients in reproductive responses were not solely because of the differences in availability of lemmings and geese. However, the strength of the observed gradients coupled with the well-established effects of resource availability on arctic fox life history (Angerbjörn *et al.* 1991; Tannerfeldt, Angerbjörn & Arvidson 1994; Eide, Jepsen & Prestrud 2004; Gauthier *et al.* 2004) suggests that alternative spatial biases should have a minimal effect on our results.

The patterns we describe may apply to other arctic fox populations exploiting allochthonous resources (Roth 2003; Eide *et al.* 2005; Samelius *et al.* 2007). More generally, our results highlight that spatio-temporal interactions between autochthonous prey and those subsidized by allochthonous sources, and between preferred and alternative prey, can profoundly shape the responses of consumers to resources (Callaway & Hastings 2002; Sabo & Power 2002). Understanding such complex interactions would benefit from further theoretical modelling that could generate testable predictions about the dynamics of subsidized populations under different scenarios of prey dynamics and origins.

STATISTICAL FRAMEWORK FOR STABLE ISOTOPE ANALYSES

Coupling isotopic diet reconstruction, environmental variables and consumer dynamics is critical to disentangle the process of allochthonous subsidization of animal populations. Yet, doing so quantitatively in a robust manner is still highly challenging and very rarely done. The main technical challenge to the robust inclusion of isotopically derived diet estimates in statistical analyses is that diet estimates obtained from isotopic mixing models (e.g. IsoSource, Phillips & Gregg 2003; SIAR, Parnell *et al.* 2010) are a range of possible solutions. Using only the mean of possible solutions in statistical analyses is a common mistake, as foreseen by Phillips & Gregg (2003). The statistical routine introduced in this paper allows the use of all possible solutions and relies on simple steps (resampling, model selection, model averaging) already known to animal ecologists. The routine can be used for several, popular mixing models, such as IsoSource (Phillips & Gregg 2003) and SIAR (Parnell *et al.* 2010). This is an important step to widen the scope of isotopically derived estimates of diet, which can now be used in a robust statistical framework to quantify the interplay between use of food resources and various individual and environmental variables.

Conclusion

We demonstrated that a transfer of energy at the continental scale (goose migration) modulates consumer dynamics along spatio-temporal gradients and has therefore the potential to modify interactions between consumers and resources and eventually the functioning of food webs. Indeed, such spatio-temporal patterns in reproduction could allow subsidized consumers to reach abundance levels not predicted solely by the primary productivity of the autochthonous ecosystem (Oksanen *et al.* 1981; Polis & Strong 1996; Gauthier *et al.* 2004, 2011). Resolving the effects of subsidies on food web dynamics and interactions between consumers and resources should thus incorporate perspectives of demographic processes underlying population dynamics along spatio-temporal gradients, but also take into account connections between distant food webs (Loreau & Holt 2004; Massol *et al.* 2011).

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Supporting information

Additional supporting information may be found in the online version of this article:

Appendix S1. Technical additions to the Methods section ‘Stable isotope analyses’.

Appendix S2. Detailed description of the methods used to generate the lemming spatial index.

Appendix S3. Detailed results of the model selections.

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