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Source: Wildlife Biology, 11(2) : 109-121

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/0909-6396(2005)11[109:DROAFA]2.0.CO;2

Dietary responses of arctic foxes *Alopex lagopus* to changing prey availability across an Arctic landscape

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Eide, N.E., Eid, P.M., Prestrud, P. & Swenson, J.E. 2005: Dietary responses of arctic foxes *Alopex lagopus* to changing prey availability across an Arctic landscape. - Wildl. Biol. 11: 109-121.

This study examines how the distribution and abundance of prey species influenced arctic fox *Alopex lagopus* diet on Svalbard during the summers of 1997, 1998 and 1999. The arctic fox together with the glaucous gull *Larus hyperboreus* are the only predators of this terrestrial ecosystem, and during summer the potential prey are confined to a few prey species such as various colonial seabirds, geese and Svalbard reindeer *Rangifer tarandus platyrhynchus*. There is great variation in distribution of prey over short distances, resulting in highly contrasting patterns in terms of both prey abundance and availability. Arctic fox diet was investigated by collecting scats (N = 818) at dens used for breeding. A cluster analysis based on similarities in the contents of scats revealed that arctic fox habitat could be divided into three distinct prey resource landscapes: two inland areas dominated by the prey species 'reindeer' and 'reindeer and geese', respectively, and one coastal resource area dominated by 'seabirds'. The occurrence of reindeer, geese and seabirds in the scats varied significantly among these resource landscapes. Svalbard reindeer, seabirds belonging to *Alcidae* and *Procellariidae* and geese belonging to *Anseridae* were the dominant prey species; volume percentages in the scats were 33, 33 and 15%, respectively. Svalbard rock ptarmigan *Lagopus mutus hyperboreus*, eggs, waders, snow buntings *Plectrophenax nivalis* and vegetation also occurred in minor proportions of the scats. The arctic fox showed a functional response to changes in prey availability. There was a positive correlation between the availability of these main prey species and their occurrence in the scats. Whenever available, arctic foxes preferred geese to seabirds and reindeer, and seabirds to reindeer. The arctic foxes in our study were opportunistic feeders, varying their food habits with prey availability.

Key words: arctic fox, diet, faecal analysis, functional response, predation, preference

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Received 23 January 2002, accepted 18 August 2004

Associate Editor: John D.C. Linnell

The distribution and abundance of prey affect the feeding ecology of generalist carnivores. Generalist predators like foxes can adapt to a wide range of prey species and environments, illustrated by the food habits of both the red fox *Vulpes vulpes* (Jedrzejewska & Jedrzejewski 1998) and the arctic fox *Alopex lagopus* (Prestrud 1992a, Frafjord 1993, Hersteinsson & Macdonald 1996, Angerbjörn et al. 1999). Although generalist predators have the ability to forage on a wide variety of prey, they are normally observed to utilise only a few species as their main prey (e.g. Goszczynski 1974). This restriction is often explained as a balance between two contrasting strategies: spending a long time searching for high-energy food or dedicating minimal time for common but less profitable prey species (MacArthur & Pianka 1966). A true optimal forager will be a generalist when resources are scarce and a specialist when resources are abundant, because high abundance of a prey species will allow specialisation with decreased handling and searching time and net energy gain as the result (MacArthur & Pianka 1966).

The arctic fox is a small canid with a circumpolar distribution inhabiting coastal arctic habitats, flat tundra plains and alpine inland areas. Several studies have shown that the arctic fox is a highly opportunistic omnivore (e.g. Macpherson 1969, Fine 1980, Garrot et al. 1983, Prestrud 1992a, Hersteinsson & Macdonald 1996). It can be both a scavenger and a predator on a wide variety of prey. The summer food habits of arctic foxes have earlier been studied in two distinct habitats: coastal areas with seasonally high variation in food abundance and inland areas with large annual variation in the main prey of lemmings *Lemmus* spp. and *Dicrostonyx* spp. (Hersteinsson & Macdonald 1996, Angerbjörn et al. 1999, Strand et al. 1999, Dalerum & Angerbjörn 2000, Elmhagen et al. 2000). Both environments are dominated by dramatic intra- and inter-annual variation in food availability.

Few studies have been carried out on the summer diet of arctic foxes on Svalbard (but see Prestrud 1992a, Frafjord 1993, 2002). Except for a small population of accidentally introduced voles *Microtus rossiaemeridionalis* living in a restricted geographical area, no resident rodents are present on Svalbard (Ims & Yoccoz 1999). The central part of the high-arctic Svalbard archipelago is characterised by highly contrasting patterns in distribution and abundance of prey over a relatively short gradient. Seabirds appear every summer in large breeding colonies along the coast, geese breed in colonies restricted to a few river canyons close to the coast, whereas Svalbard reindeer *Rangifer tarandus platyrhynchus* and Svalbard rock ptarmigan *Lagopus mutus hyperboreus* are distributed throughout the landscape. These characteristic patterns of prey distribution cause large variation in the abundance and availability of prey across the landscape. The objective of this study was to find out to what extent arctic foxes change their diet as a response to varying abundance and availability of different prey species.

Material and methods

Study area

Our study was conducted on Svalbard, a high-arctic archipelago (74°-81°N, 10°-30°E). Except for four permanent settlements and a few scientific stations, the archipelago is uninhabited. Permanent snow and glaciers cover approximately 60% of the 62,700 km^2 archipelago. The study area covered 1,000 km^2 on the west coast of Spitsbergen Island (Fig. 1). Two major U-shaped valleys, Adventdalen and Sassendalen, cut through the study area. To the north and west the study area bordered the sea. The landscape is mountainous and moderately glaciated, with most summits below 1,000 m a.s.l. Central west Spitsbergen is classified as middle arctic tundra zone (Elvebakk 1989) with no shrubs or bushes. Vegetated, productive areas are found in the flat valley bottoms and on the slopes up to 400-500 m a.s.l.

Several large seabird colonies, dominated by fulmar *Fulmarus glacialis*, Brünnich's guillemot *Uria lomvia*, little auk *Alle alle* and puffin *Fratercula arctica*, are found along the coast of the study area (see Fig.1). Pink-footed geese *Anser brachyrhynchus* and barnacle geese *Branta leucopsis* breed in large numbers in inland river canyons in the eastern part of the study area (Sassendalen; see Fig. 1). The diversity of other birds is low, restricted to snow buntings *Plectrophenax nivalis*, purple sandpiper *Calidris maritima* and a few other waders *Calidris* spp. Svalbard reindeer and Svalbard rock ptarmigan, the

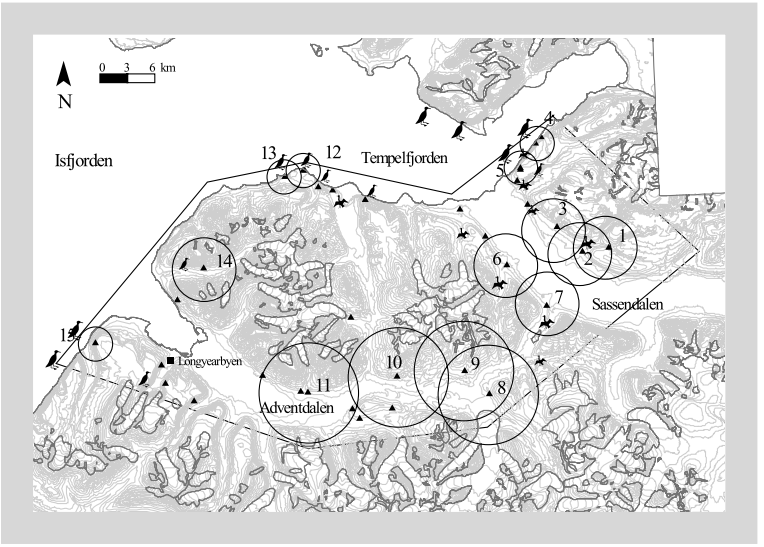

Figure 1. The study area on Svalbard showing the different arctic fox breeding dens surveyed in this study, numbered 1-15. Breeding dens are symbolised by triangles surrounded by circles indicating calculated home ranges, varying in size according to the resource area in which they are situated. Triangles without circles symbolise non-breeding dens. The abundance of geese colonies are indicated by long-necked birds, while the seabird colonies are indicated by short-necked birds. Glaciers are outlined on the map.

only residents together with the arctic fox, are distributed throughout the landscape. Apart from the fulmar, arriving in February/March and leaving in October/November, other migrating bird species arrive in late April/mid May, and most leave in August/September.

Den survey

All active natal den sites in the study area (N = 34) were visited annually during 1997-2000. Dens were watched continuously for at least 12 hours from mid-June to mid-July, using telescopes, to determine if pups were present. Fresh scats were collected from five dens in 1997, five dens in 1998 and from 15 dens in 1999 (see Fig. 1). The sampling of scats was complete for all breeding dens only in 1999. Arctic foxes sometimes use more than one den when raising a litter, often moving between two den sites (Prestrud 1992b). In our study four litters were moved between dens. When a litter used more than one den, the scats from these dens were combined in the analysis as one breeding den. Different dens used by the same foxes were all within the same general habitat, however, so that none of the breeding foxes alternated between coastal and inland habitats.

Scat analysis

All scats found at the dens were collected and removed at the beginning of the study. Scats analysed in our study were collected during June-September 1997, 1998 and 1999. Obviously old scats were discarded from the sampling. Scats from adult and juvenile foxes were not separated. As juvenile foxes only eat food brought to denning areas by their parents, we assumed that scats collected at the den sites reflected arctic fox dietary composition in general. This assumption can be questioned, since large prey species are more often brought to the den site than smaller prey species (see e.g. Lindström 1994). Concerning the main prey species this bias will be the same for all dens and it will not have effects on the relative results. After collection the scats were stored in freezers at -18°C. Before analysis the scats were heated to ≥ 90°C for three hours to prevent human exposure to eggs from the tapeworm *Echinococcus multilocilaris* (Bantle & Alisauskas 1998). Between 21 and 81 scats were analysed per breeding den, summing up to 132 scats from 1997, 136 scats from 1998 and 550 scats from 1999, in total 818 scats.

The individual scats were soaked in water for 2-3 hours and fragmented by hand under a magnifying glass. The volume proportion of fur, feathers, eggshells, vegetation and 'other' was estimated visually to the nearest 5% for each scat. Using known reference material, fur was identified as reindeer, arctic fox or seal. One seal claw and a few arctic fox claws were identified using reference material. Feather remains were identified by examining the downy barbules (Chandler 1916), using known reference material and the keys of Day (1966), Hersteinsson (1984) and Brom (1991). Feet and beaks were identified by comparison with study skins at the Zoological Museum at the University of Oslo. It was possible to identify feathers to the taxonomic groups *Alcidae*, Anserinae, Anatinae, Galliformes (only Svalbard rock ptarmigan), *Laridae*, Passeriformes (only snow bunting), *Procellariidae* (only fulmar) and *Scolopacidae*. No attempt was made to further classify eggshells or vegetation. We were not able to classify eggshells to species or taxonomic groups. Due to the lack of conversion factors for arctic foxes, we had to assume that the proportion of remains of a prey species in the scats gave a proper representation of its proportion in the diet. Since the general question of our paper is to compare relative occurrence of prey at different den sites, the lack of conversion factors was considered to have little influence on the results of the analysis.

Frequency of occurrence summing to 100% (Occ.) and the method of whole scat equivalent (WSE) were used to present arctic fox diet (see Angerbjörn et al. 1999). When using WSE all volume percentages of a food category found in the scats from the same den were summarised and expressed as whole scats. For example, a scat containing 20% reindeer fur and 80% fulmar feathers, and a scat containing 80% reindeer fur and 20% fulmar feather would add up to one scat with fulmar feathers and one with reindeer fur. The total number of scats analysed remained the same, i.e. the sample size was not changed. Based on spatial distribution of prey species we pooled the results for alcids, fulmar, ducks and gulls into the category 'seabirds' before testing for differences in the diet among areas and breeding dens.

The arctic fox dens were grouped based on the diet composition at each den. A cluster analyses based on the Morisita index of similarity was used to compute a cluster tree by the unweighted pair-group method using arithmetic averages of the breeding dens (Sneath & Sokal 1973, Romesburg 1984). The simplified Morisita index of similarity (Horn 1966) was calculated because it is designed for proportions, and because it was recommended by Wolda (1981) as the best overall measure of similarity in ecology. WSE data were used for the classification process as the relative volume of each prey group was considered rather than only their occurrence. To avoid potential differences between years, only data from scats collected in 1999 of the main prey groups of seabirds, reindeer, geese and ptarmigan were used to calculate the index. Other prey species, as well as eggs, were not included as they were of proportionally minor importance. The clustering process led to a division of the study area into three different resource landscapes, defined as areas where the arctic foxes showed relatively uniform food habits compared to the adjacent areas.

Available biomass within individual ranges

Based on the cluster analyses of arctic fox diet composition (described above) we estimated mean home range sizes for the foxes in the three prey resource landscapes, following Eide et al. (2004). Circles of three different sizes, corresponding to mean home range sizes, were assigned to each den site depending on which resource landscape the den site belonged to. The following home range sizes were used: dens > 10 km from the coast and without geese breeding colonies ≈ 60 km^2, dens close to geese breeding colonies or > 4.5 km from the coast ≈ 27 km^2, and dens in coastal areas dominated by seabird colonies ≈ 7 km^2 (after Eide et al. 2004, Eide 2002). In estimating available biomass, only the main prey species reindeer (carcass, slaughter and calves), geese (pink-footed geese and barnacle geese) and seabirds (alcids and fulmar) were considered. Although capable of killing healthy reindeer calves (Prestrud 1992a), arctic foxes primarily scavenge reindeer carcasses, and live reindeer were therefore not included. Other prey species, such as Svalbard ptarmigan, waders, snow bunting, ducks and gulls were excluded because they occurred in minor volumes in the arctic fox remains.

Abundance of the main prey species within the simulated home ranges for each individual den site in 1999 was sampled from a GIS prey database (N.E. Eide, unpubl. data). Distribution of reindeer was obtained and merged from two different surveys. In Adventdalen, systematic ground surveys have been conducted along contiguous transects separated by 1 km during seven days in mid-July every year since 1980 (N. Tyler, pers. comm.). All reindeer and reindeer carcasses were classified according to sex and age, and locations were recorded on maps with an accuracy of approximately 100 m. Systematic aerial surveys covered the rest of the study area along contiguous 2-km wide transects one day in mid-July in 1997, 1998, 1999 and 2000 (Governor of Svalbard, Environmental Protection Dept., unpubl. data). Animals were classified by age (calves and adults), and locations were recorded to 18 subareas, 5-40 km^2 large, allowing estimates of relative population distributions. Both these surveys were limited to areas below 400 m altitude. Abundance and position of reindeer carcasses within fox home ranges were determined by GPS during systematic ground surveys along 200-m wide transects. Reindeer slaughter remains, left over from the reindeer hunt in August-September, constitute a large temporary food resource for arctic foxes in parts of the study area (Note: Adventdalen is closed to hunting). All hunters were asked to report the location, sex and age of their kill. Reindeer calves eaten by foxes were counted as actual numbers determined from calf remains found at den sites.

All seabird colonies, except for the largest, were surveyed almost annually during 1988-2000, as part of a seabird-monitoring programme (SCRIB 1998). The surveys followed standard field methodology outlined in Walsh et al. (1995). Goose breeding colonies were located by searching systematically along transects separated by approximately 5 km in all areas below 400 m altitude. Vocalisation from adult non-breeding geese made these colonies easy to detect at great distance. Breeding geese (nests) were counted and mapped by GPS using systematic surveys with 20-m wide transects immediately after the geese had abandoned the breed-

ing colonies. Geese display large changes in distribution through the summer season, and were counted using spotting scopes during four separate periods (period 1 on breeding areas, period 2-4 on grazing areas) and located at maps with approximately 250 m accuracy during summer in 1998, 1999 and 2000 (Jepsen et al. 2002).

Estimates of available prey biomass (in kg) were based upon counts of prey present within each simulated home range. For reindeer the direct counts of carcasses, slaughter remains and calf remains were used. Since total numbers give a much distorted picture of what is actually accessible to the arctic fox, availability of avian prey species were calculated using total counts of seabirds and geese present in each home range, together with species-specific reproduction and natural mortality data (see Appendix I). Although not site specific, the mortality rates used also include predation from arctic foxes. The number of avian prey (adults, eggs and chicks) available to the predator community were calculated using the following equation:

Available numbers of an avian species =

$$(n_{adb} + n_{adnb})q_{adsm} + ((\frac{n_{adb}}{2})n_{juv})q_{juv} \qquad (1),$$

where (n_{adb}) is the number of breeding adults, (n_{adnb}) is the number of non-breeding adults, (q_{adsm}) is 'at site' adult mortality, (n_{juv}) is the number of eggs laid per breeding pair, and (q_{juv}) is the breeding mortality, or the mortality from egg until fledged chick (Appendix I). Due to similarity in life-history parameters, the small number of little auks and puffins were added to the Brünnich's guillemot data. Since life-history data on inland breeding geese in general are very limited (Mitchell et al. 1997), geese were treated as a group.

Crude numbers of available prey is an inadequate measure of resource availability, as biomass is not considered. Hence the values of the different prey resources were recalculated in relation to their average mass (kg). These biomasses are: reindeer carcass (20 kg), reindeer slaughter (10 kg), reindeer calves (4 kg), geese (1.5 kg), seabirds (0.5 kg) and eggs (0.1 kg) (Mehlum & Gabrielsen 1995, Tombre et al. 1996; N. Tyler, pers. comm.). Biomass equivalents were multiplied by the number of the different prey to give available biomass of each prey within each simulated home range.

Preference estimations

Preference for prey was evaluated using the forage ratio (Savage 1931, Williams & Marshall 1938). The ratio was estimated by pooling the diet data from the scat analyses and the availability data of seabirds, reindeer and geese for all the breeding dens. A similar preference index was also calculated for the coastal dens separately, as this was the only resource area with all the main prey species present, i.e. seabirds, reindeer and geese. The preference index was ranked, as we assumed that all the prey types were perfectly substitutable. To avoid errors caused by the estimation of available biomass, we also calculated the forage ratio as if the available biomass were sampled, and hence were subject to sampling errors (Krebs 1999).

Statistical analyses

Statistical analyses were performed using SigmaStat (version: Jandel 1992). Log-linear likelihood analyses (G-test) were used to test for differences among prey and breeding dens, and prey and resource landscapes (Sokal & Rohlf 1995). Chi-square goodness-of-fit tests were used when the G-test could not be performed, as some of the prey occurred relatively infrequently. As the proportions of different prey types in one scat are interdependent (Reynolds & Aebisher 1991), frequency of occurrence was used to test for differences between dens, resource landscapes and years and when calculating preference indices. Prey preference was calculated using frequency of occurrence and available biomass of the main prey: seabirds, reindeer and geese. The G-test was used to compare overall dietary preference, and 95% confidence intervals with Bonferroni corrections were computed for each selection index. To further test for differences among the selection indices, we perform-

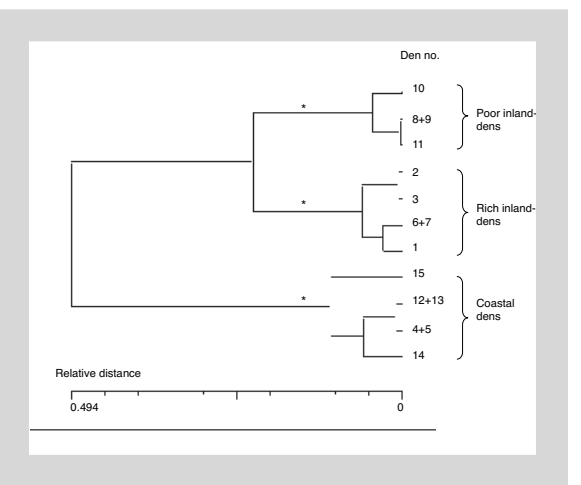

Figure 2. Clustering tree of the diet of arctic foxes breeding in different dens in the study area on Svalbard (1999), prepared by unweighted pair-group method using arithmetic averages (Sneath & Sokal 1973, Romesburg 1984). The main branches that define the resource areas are marked with *.

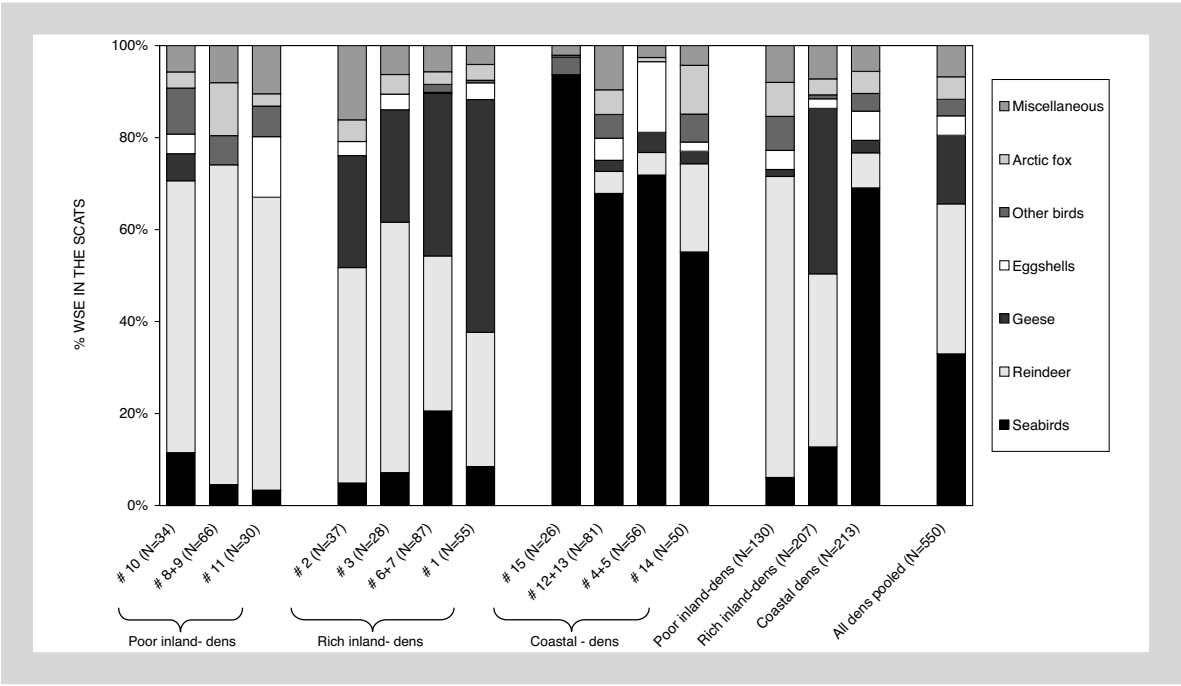

Figure 3. Summer diet of the arctic fox on Svalbard (1999), shown as percentage whole scat equivalents (WSE). Breeding dens are shown at the left and resource areas at the right, and at the far right the overall average diet in the study area is shown. The term 'other birds' refers to Svalbard rock ptarmigan, snow bunting and waders, and the term 'miscellaneous' refers to vegetation, sand, stone and other/unidentified matter.

ed a χ^2-test on the forage ratio of seabirds versus reindeer, seabirds versus geese, and reindeer versus geese, as recommended by Manly et al. (1993) and described in Krebs (1999). The relationship between available biomass and frequency of occurrence in the scats was evaluated using correlation and polynomial linear regression of second order, after standardising the percent frequency of occurrence data with an arcsine transformation to obtain normal distribution (Zar 1999). P = 0.05 was considered to be statistically significant.

Results

Arctic fox diet

Based on similarities in content of scats, three resource landscapes could be identified in the classification process (Fig. 2). One contained dens in the inland, with reindeer as the main prey occurring in the diet, termed poor inland dens. One contained dens with both geese and reindeer in the diet, termed rich inland dens, and one contained dens with mainly seabirds in the diet, termed coastal dens. Whole scat equivalents (WSE; in %) for the den sites is presented in Figure 3. We tested for statistical differences in the occurrence of the main prey types at two levels: among and within the resource areas. There were significant differences in diet among the resource landscapes (Table 1). Within the poor inland dens, there were no significant differences in the diet among the breeding dens, whereas for the rich inland dens and the coastal dens there were significant differences in the diet (Table 2). Within the rich inland dens, we found differences in the amount of seabirds at den number six (see Fig. 1), which contained significantly more seabirds than the other dens. Also the amount of reindeer varied among the rich inland dens. At the coastal dens we found differences among the dens for seabirds, reindeer and ptarmigan, but this was of minor importance as the amount of seabirds dominated in all the dens.

The dominant prey of arctic foxes based on WSE from 1999 were reindeer (33%), seabirds (33%) and geese (15%) for the summer period, defined as mid-June to

Table 1. Test for differences in frequency of occurrence for the main four arctic fox prey species/species groups among the three resource areas in the study area on Svalbard.

Model	df	χ^2	P
Seabirds	2	242.9	<0.01
Reindeer	2	150.9	<0.01
Geese	2	146.3	<0.01
Ptarmigan	2	10.9	<0.01

Table 2. Log-linear likelihood test for differences in frequency of occurrence of the main arctic fox prey species/species groups among the breeding dens within each resource area in the study area on Svalbard. Significant P-values indicating differences are in *italics.*

Resource area	Seabirds	Reindeer	Geese	Ptarmigan	Comments
Poor inland dens (df = 2)	G_{adj} = 2.10 P = 0.35	G_{adj} = 0.95 P = 0.62	χ^2 = 5.74 P = 0.06	G_{adj} = 0.10 P = 0.95	Marginal difference in the occurrence of geese.
Rich inland dens (df = 3)	G_{adj} = 9.64 *P = 0.02*	G_{adj} = 17.7 *P < 0.01*	G_{adj} = 7.42 P = 0.06	χ^2 = 1.08 P = 0.78	Differences in the occurrence of seabirds and reindeer.
Coastal dens (df = 3)	G_{adj} = 7.78 *P = 0.05*	χ^2 = 17.0 *P < 0.01*	χ^2 = 5.38 P = 0.15	χ^2 = 10.2 *P = 0.02*	Significant difference in the occurrence of seabirds, reindeer and ptarmigan.

mid-August (N = 550). Ptarmigan constituted only 3% (see Fig. 3). The pattern was the same for both frequencies of occurrence and WSE, except for vegetation, which occurred frequently but in small volumes.

Arctic fox diet composition at selected den sites was very similar in 1997, 1998 and 1999 (Fig. 4). Eggs comprised 4% WSE of the scats and were the fourth most abundant food category. The arctic fox summer diet also contained arctic fox fur, vegetation, snow buntings, waders, sand and stones. Arctic fox fur and claws comprised on average 5%, and never more than 12%. Vegetation constituted 2% WSE of the diet and snow buntings and waders contributed on average less than 1% of the diet, and never more than 5%. Sand and gravel constituted 1% of the arctic fox remains. On an annual basis, we found only small differences in arctic fox diet at the same dens.

Available biomass and diet

The correlation between diet and available biomass in the resource landscapes was positive and significant for each of the main prey species: seabirds (r = 0.936, df = 10, P < 0.01), reindeer (r = 0.914, df = 10, P < 0.01) and geese (r = 0.812, df = 10, P < 0.01). Pooling data reveals large differences in prey availability and diet between the resource landscapes (Fig. 5). The poor inland dens were dominated by reindeer in both the diet and available biomass, with no estimated available biomass of seabirds and almost none of geese. Despite this, seabirds comprised 6% WSE and geese about 2% of the diet. For the rich inland dens there was considerably more geese and reindeer biomass available than in the poor inland dens, and the amount of geese and reindeer in the diet was almost equal. The coastal dens were considerably different, with seabirds dominating both the

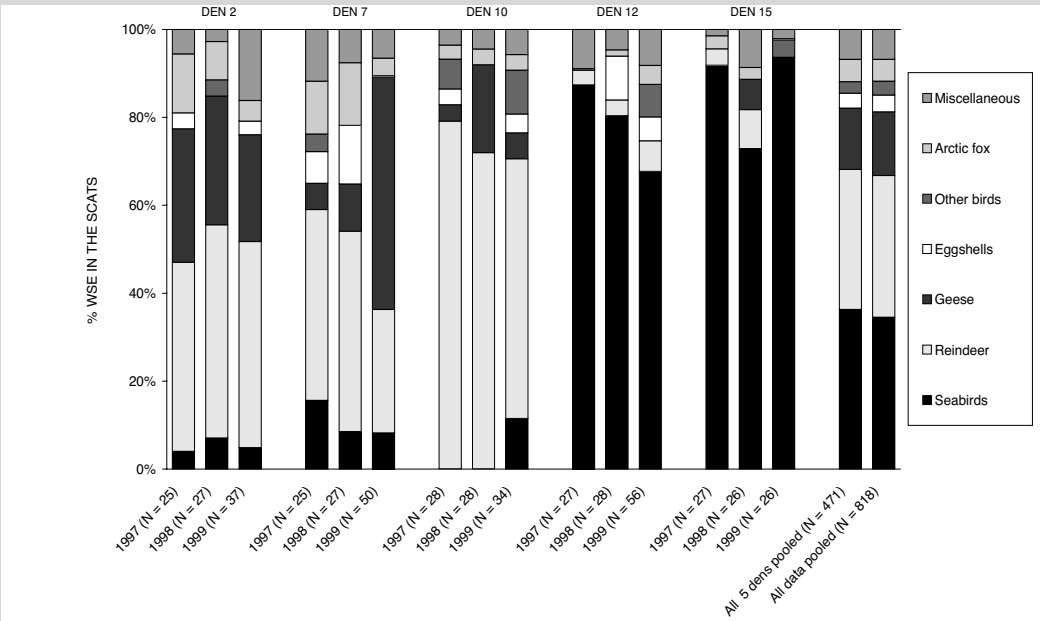

Figure 4. Summer diet of arctic fox at five breeding den sites during the summers of 1997-1999 on Svalbard. Data are shown as percentage whole scat equivalents (WSE). The term 'other birds' refers to Svalbard rock ptarmigan, snow bunting and waders, and the term 'miscellaneous' refers to vegetation, sand, stone and other/unidentified matter.

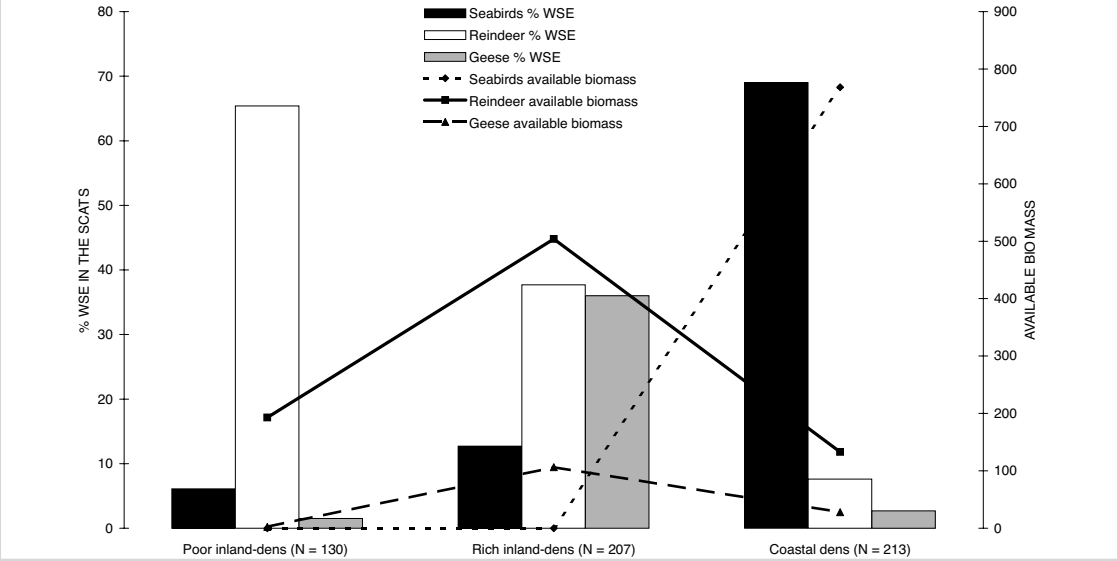

Figure 5. Summer diet (bars) of arctic foxes from different resource areas in relation to variations in available biomass (lines) of prey species (during 1999) within the home ranges of the foxes in each resource area. The diet of arctic fox in percentage whole scat equivalents (WSE) is listed at the top of each bar. The available biomass is given in relative units, based on the average normal biomass weight (in kg) of the different prey species.

available biomass and the diet. Reindeer and geese only comprised a small proportion of both available biomass and diet in the coastal dens. Thus, it becomes clear that arctic foxes change their prey preference with prey availability, following a functional response (after Solomon 1949). However, low sample size did not allow statistical power tests to distinguish between the different shapes of the functional response curves to different prey species presented in Figure 6.

Food preference

The arctic foxes showed a significant preference pattern for the three prey types seabirds, reindeer and geese ($\chi^2 = 1420.7$, df = 2, $P < 0.001$). Geese were the most preferred prey species (forage ratio: 1.15; 95% CL: 1.37-0.92), seabirds the second most preferred prey (forage ratio: 0.61; 95% CL: 0.73-0.48), and reindeer the least preferred prey species (forage ratio: 0.40; 95% CL: 0.51-0.28). The forage ratio for seabirds, reindeer and geese all differed significantly; arctic fox preference for seabirds differed significantly from preference for geese ($\chi^2 = 54.36$, df = 1, $P < 0.001$) and from reindeer ($\chi^2 = 817.80$, df = 1, $P < 0.001$). Preference for reindeer and geese also differed significantly ($\chi^2 = 29.50$, df = 1, $P < 0.001$). For the coastal dens the same preference pattern was found, with geese as the most preferred prey (forage ratio: 3.57; 95% CL: 3.96-3.19), followed by seabirds (forage ratio: 1.03; 95% CL: 1.14-0.92) and reindeer (forage ratio: 0.55; 95% CL: 0.85-0.26). The indices for preference all differed significantly ($P < 0.001$).

Discussion

Our study suggests that arctic foxes on Svalbard are true opportunistic feeders and hence their food habits vary according to the availability of different prey species. As predicted, arctic foxes fed on all available food items, whereas the most abundant and easily accessible prey constituted the main basis of the foxes' summer diet. The diet varied at a spatial scale, while no temporal variation (between years) could be detected during the three years of this study.

Based on the large spatial variation in the composition of arctic fox summer diet, our study area was clustered into three different prey resource landscapes, i.e. 1) inland areas with only reindeer present (Adventdalen), 2) inland areas with both geese and reindeer present (Sassendalen) and 3) coastal areas dominated by bird cliffs with reindeer and some geese present (see Fig. 1). In other areas arctic foxes have been considered to inhabit two different habitats, coastal and inland (see e.g. Fay & Stephenson 1989, Hersteinsson & Macdonald

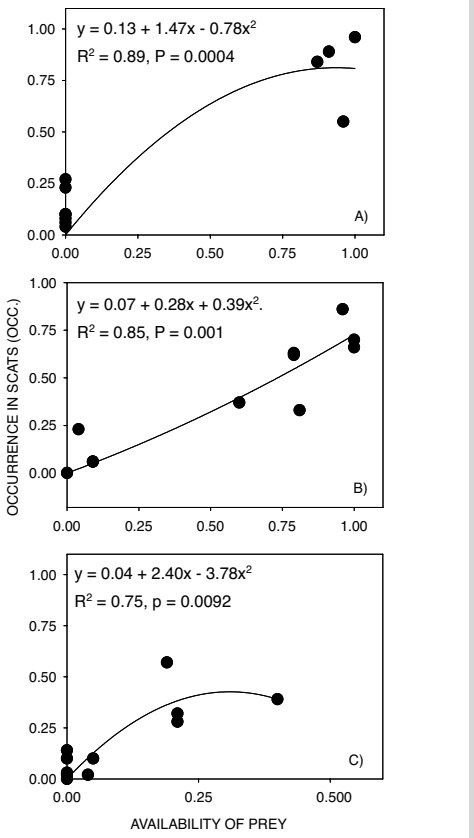

Figure 6. Relationship between availability of seabirds (A), reindeer (B) and geese (C) within the estimated home ranges of arctic fox den sites in 1999 (N = 11), and the occurrence of these prey species in arctic fox scats.

1996, Dalerum & Angerbjörn 2000). In our study the subdivision of inland areas into two different resource landscapes was necessary to distinguish between 'rich' and 'poor' inland areas. Thus the traditional dichotomy of arctic fox habitats as 'coastal' and 'inland' cannot be applied to Svalbard without accounting for the large differences in prey availability.

Reindeer and seabirds constituted approximately one third each of the total scat volume, but reindeer probably represented a larger biomass as meat and fat brought to the dens do not leave many remains in the faeces (Prestrud 1992a), whereas birds contain a large proportion of indigestible matter which later can be found in the scats. Due to the lack of conversion factors for arctic fox prey species, we had to assume that the proportion of remains of a prey species in the scats gave a proper representation of its proportion in the diet. Since we compare relative occurrence of prey at different den sites, this assumption was considered to have little influence on the results of the analysis. Lockie (1959) and Goszczynski (1974) both studied red fox and found that roe deer *Capreolus capreolus* are more digestible than birds, but that this difference decreases with the increasing size of the prey bird. The ratios presented by WSE would increase for reindeer, and decrease for birds, if the digestibility were accounted for. However, the fact that most prey birds, e.g. geese, fulmar and Brünnich's guillemot, are relatively large suggests that this could be of less importance in our study.

Geese were the most preferred prey on Svalbard. In the rich inland dens they constituted more than one third of the diet. Based on prey remains at den sites, Prestrud (1992a) also concluded that geese, whenever present, were an important food resource for foxes on Svalbard during summer. Studies from throughout the species' range have documented the presence of geese in arctic fox diet (Thompson & Raveling 1987, Stickney 1991, Syroechkovskiy et al. 1991, Bantle & Alisauskas 1998, Samelius & Alisauskas 2000). On several occasions, we have observed arctic foxes effectively killing adult geese (see detailed descriptions of foxes' attack behaviour in Prestrud 1992a). However, arctic foxes mostly prey on geese eggs and chicks (Stickney 1991, Frafjord 1992, Bantle & Alisauskas 1998, Samelius & Alisauskas 2000). Foxes living in the poor inland areas can and do kill adult geese only in the spring when these forage on the snow free slopes of the large valleys (G. Bangjord, pers. comm.). When foxes had access to geese breeding beneath the bird cliffs and in canyons close to the coast, remains of geese were also present in the diet of coastal foxes.

Reindeer constituted approximately one third of the total scat volume. Earlier investigations from Svalbard concluded that reindeer was the most important prey species both during summer and winter (Prestrud 1992a). As in our study, reindeer dominate the diet of inland foxes in West Greenland and on Iceland (Birks & Penford 1990, Hersteinsson & Macdonald 1996). Reindeer carcasses and cached meat from the previous hunting season might play a major role in supplying arctic foxes with reindeer meat far into the summer season. Natural mortality of newborn reindeer calves can also be high during summers of severe weather conditions (Tyler & Øritsland 1999, Solberg et al. 2001). At den site no 10, in Adventdalen (see Fig. 1), remains of as many as 11 young reindeer calves were found in 1998: all probably < 1 month old at death and three possibly < 1 day old (assessed for us by Nicholas Tyler). Although calf remains found at dens are mostly presumed to originate from scavenging, individual foxes in the poor

inland areas were capable of switching to hunting on several-week-old reindeer calves (see also Prestrud 1992a). As far as we know, such behaviour has not been reported from other areas. Hunting skills such as these were not observed in areas where geese and seabirds breed, probably because alternative and more profitable prey were available. This could, however, also indicate that foxes in poor inland areas have adopted special hunting skills.

Seabirds constituted the major part of the summer diet along the coast. All coastal dens were located near bird cliffs with easy access to eggs, chicks and injured and sick adults. Both Prestrud (1992a) and Frafjord (1993, 2002) found large proportions of seabirds in the diet of foxes living close to the coast on Svalbard. Throughout the arctic, seabirds tend to constitute a major component of the diet when the local abundance is high, as reported from Iceland (Angerbjörn et al. 1994, Hersteinsson & Macdonald 1996), Alaska (Fay & Cade 1959, Chesemore 1968) and Greenland (Birks & Penford 1990, Kapel 1999). Inland breeding foxes seldom left their territories during the reproductive summer season (N.E. Eide, unpubl. data), probably because they were restricted by their territorial behaviour (Strand et al. 2000, Eide et al. 2004). Hence the presence of seabirds in the diet of foxes in inland areas, though no seabirds appeared breeding there, probably reflected incidental availability of such prey. Occasionally injured birds could be observed sitting on the tundra far from bird cliffs or the sea.

Svalbard rock ptarmigan constituted a remarkably small proportion of the diet, and probably was of minor importance in the summer diet of arctic foxes in our study area. Ptarmigan have been found to be of minor importance as summer food also in other parts of Svalbard (Frafjord 1993, 2002), and similar results have been reported from Scandinavia and Greenland (Birks & Penford 1990, Kaikusalo & Angerbjörn 1995, Elmhagen et al. 2000). As winter food, however, Prestrud (1992a) found Svalbard rock ptarmigan to be of major importance, occurring in 30% of the stomachs of the foxes he analysed. Although abundant throughout the study area, the abundance of Svalbard rock ptarmigan was probably too low in the summer for the foxes to prey upon ptarmigan except when they encountered them incidentally. Other studies have indicated that Svalbard rock ptarmigan might also be more difficult for arctic foxes to catch during summer (Larson 1960, Birks & Penford 1990).

Eggs constituted only a minor part of the summer diet, although they were probably underestimated. Most parts of an egg are easily digested, and few remains are therefore found in the scats. The difference between WSE and percent occurrence for eggs in the diet was small, suggesting either that the diet of arctic foxes consisted of ca 4% eggs as indicated from WSE, or that they ate eggs without eating the eggshell. Foxes were observed on several occasions to crack eggs open, only eating what was inside the egg (N.E. Eide, pers. obs.). Eggs may also be cached rather than eaten immediately. In large goose colonies in Canada eggs were cached in large quantities when their availability was high (Bantle & Alisauskas 1998, Samelius & Alisauskas 2000). Stickney (1991) found that > 80% of the eggs taken were cached. These eggs may form an important part of winter diet, or supplement the diet of the pups close to large geese colonies (Samelius & Alisauskas 2000). The importance of eggs from seabirds is not well studied, but as seen from Figure 3, there were no large differences in the amount of eggs in the diet among the three resource landscapes. Vegetation occurred in most of the scats, but only in small amounts, and was probably ingested incidentally as no plant species on Svalbard are known to have any nutritional importance for arctic foxes (Frafjord 1993). Several other food items, such as waders, snow bunting, garbage, arctic fox fur and claws, sand and gravel, were found in small but varying amounts in the arctic fox remains. The low presence of food scavenged along the shore (e.g. fish, molluscs, crustaceans), largely contrasts what Hersteinsson & Macdonald (1996) found in coastal areas on Iceland. We have never seen fish or molluscs drifting ashore along the coast in our study area. However, we have observed adult arctic foxes combing the beaches, probably searching for small invertebrates like crustaceans (N.E. Eide, pers. obs.). Small invertebrates are likely eaten at once, rather than delivered to cubs at the den site, which could explain the low presence of invertebrates in the scats.

The lack of temporal variation in diet composition largely contrasts what has been found in other areas. In areas with fluctuating rodent populations, arctic fox diet composition shifts towards alternative prey species in years with low lemming abundance (Braestrup 1941, Angerbjörn et al. 1995, Hersteinsson & Macdonald 1996, Strand et al. 1999, Elmhagen et al. 2000). The reasons why such shifts were not found in our study could be several: on Svalbard the summer food resources are probably more stable between years than in areas with fluctuating populations of small rodents. The colonial breeding birds, both seabirds and geese, are present in large numbers every year (SCRIB 1998, Jepsen et al. 2002), although reindeer winter mortality range within 1-35% (Tyler & Øritsland 1999, Solberg et al. 2001). The strong caching behaviour of arctic foxes could, however, probably stabilise the food supply between sea-

sons, and maybe also between years (Macpherson 1969, Fay & Stephenson 1989, Prestrud 1992a, Birkhead 1993, Sklepkovych & Montevecchi 1996).

Arctic foxes preferred geese and seabirds to reindeer. Reindeer were mostly available as winter cached food stores that probably were used when nothing else was available. Reindeer calves are probably also harder to prey upon than eggs and birds, forcing the foxes to specialise on these only when nothing else is available. (Note: most of the remains of reindeer calves at den sites presumably originate from scavenging rather than predation). The difficulties of estimating the amount of eggs eaten leaves open the possibility that arctic foxes may prefer birds even more than indicated. The small differences in the amount of eggs eaten in the three resource landscapes, however, suggest that the order of preference would not be altered even if the amount of eggs could have been estimated better.

Arctic fox prey preferences changed with availability of prey following a functional response, which implies that foxes could have regulating effects on local prey populations. Arctic foxes preferred geese and seabirds whenever available, and they seemed to hunt reindeer calves only in areas where no other prey species were present. Thus, the absence of alternative prey apparently made arctic foxes adapt specialised hunting skills not normally observed. The capability of individuals to specialise on catching reindeer calves might be essential to the survival of the foxes in these poor inland areas during periods of food scarcity. Compared with mainland Scandinavia, where the arctic fox, at it's present distribution, mainly reproduces during peaks in rodent populations (Strand et al. 1999, Elmhagen et al. 2000), the arctic foxes on Svalbard must utilise a wider range of resources to ensure survival and reproduction. The arctic fox on Svalbard appears to specialise when necessary, but it is generally an opportunistic feeder utilising all available prey species, both as a scavenger and as a predator.

Acknowledgements - voluntary field assistance from numerous people was essential to complete this study. All participants deserve warm thanks for collecting scats at the den sites. Christian Aas at the Zoological Museum at the University of Oslo helped us identify the feather remains in the scats. Special thanks go to Georg Bangjord, Christian Nellemann, Anders Angerbjörn, Bodil Elmhagen and Karoline Bredland for their comments on early drafts of the manuscript. Rolf A. Ims, Pall Hersteinsson, John D.C. Linnell and two anonymous referees also supplied many improving comments. Funding for the project was provided by the Norwegian Polar Institute and the Agricultural University of Norway. The Governor of Svalbard and the logistic department at the Norwegian Polar Institute provided important logistic assistance.

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Appendix I

Life-history data used in the calculation (Equation 1) of output from seabird and geese colonies.

Species	Input in formula	Variable	Value	Reference
Fulmar	No. individuals counted	n	sampled within simulated home range	SCRIB 1998
	Breeders	n_{adb}	$n \bullet 0.70$	Hatch 1987, Falk & Møller 1997
	Non-breeders	n_{adnb}	$n \bullet 0.30$	Hatch 1987, Falk & Møller 1997
	Annual adult mortality	q_{adsm}	3%	Hatch 1987
	Residence at colony	S	8 months	N.E. Eide, pers. obs.
	At site adult mortality	q_{ads}	$s \bullet q_{ads} = 2\%$	calculated from data
	Clutch size	n_{juv}	1	Mehlum 1989
	Juvenile mortality [1]	q_{juv}	59%	Hatch 1987
Brünnich's guillemot	No. individuals counted	n	sampled within simulated home range	SCRIB 1998
	Breeders	n_{adb}	$n \bullet 0.6 \bullet 2$	Bakken & Mehlum 1988
	Non-breeders	n_{adnb}	vary variable	Vidar Bakken, pers. comm.
	Annual adult mortality	q_{adsm}	10 %	Nettleship & Birkhead 1988)
	Residence at colony	S	3 months	N.E. Eide, pers. obs.
	At site adult mortality	q_{ads}	$s \bullet q_{ads} = 2.5\%$	calculated from data
	Clutch size	n_{juv}	1	Mehlum 1989
	Juvenile mortality [1]	q_{juv}	28%	Gaston & Nettleship 1981
Geese[2]	No. individuals counted	n	sampled within simulated home range	(N.E. Eide, pers. obs)
	Breeders	n_{adb}	$n \bullet 2$	calculated from data
	Non-breeders	n_{adnb}	not counted	-
	At site adult mortality	q_{adsm}	2%	prey remains at den site
	Clutch size	n_{juv}	4	Mehlum 1989
	Juvenile mortality [1, 2]	q_{juv}	38%	Mitchell et al. 1997

[1] mortality until fledging from nest (hence a minimum estimate of juvenile seasonal mortality).
[2] barnacle geese and pink-footed geese were treated as one species.