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The arctic island group of Svalbard has no native species of voles or lemmings, but the vole *Microtus rossiaemeridionalis* has been accidentally introduced. Mainly found in the region of the abandoned Russian mining town of Grumant, the vole has not been able to colonise larger parts of Svalbard. The food habits of arctic foxes *Alopex lagopus* were studied by collecting and analysing samples of scats from various sites in the region in 1996, including fresh scats from three litters. Hairs of voles were found in scats from all sites, but the proportion of voles in the diet of arctic foxes varied considerably. Overall, voles made up 13% of the diet by occurrence, but were insignificant in the diet of the three litters. Birds were the most important (79%) and reindeer carcasses the second most important food item (22%). Other estimates used gave less importance to voles (10 and 4%). Birds most often constituted the major part of a scat, voles less often. Pups from three litters had consumed 97% birds, with the proportion of alcids and gulls varying largely according to availability near the respective litter. The population of voles at Grumant was very low in 1996, but in other years it may grow to much higher numbers. However, a large proportion of the scats collected were old and reflected arctic fox diet over many years. Although arctic foxes at Grumant have gained access to a new food source, voles appear to be of minor importance in their diet.

Key words: Alopex lagopus, arctic fox, predation, sibling vole, Svalbard

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Introductions of new mammals to tropical islands often have devastating effects on indigenous species and may upset whole ecosystems. Introductions to arctic islands are, on the other hand, rarely successful, because southern species have difficulties in surviving north of their natural distribution range (e.g. Gjertz & Lønø 1998). The sibling vole *Microtus rossiaemeridionalis* (= *epiroticus*) was accidentally introduced to Svalbard from Russia 30-70 years ago (Fredga, Jaarola, Steen, Ims & Yoccoz 1990, Yoccoz, Steen & Ims 1990, Yoccoz & Ims 1999), and established an isolated population. Adult body mass is larger compared to individuals in a population in Finland (Yoccoz, Ims & Steen 1993), so the species may have adapted somewhat to the arctic conditions or be exhibiting the 'island syndrome' (Adler & Levins 1994). The sibling vole appears to be more vulnerable to predation than the field vole *M. agrestis* (Hakkarainen, Korpimäki, Mappes & Palokangas 1992), perhaps because it lives in patches of higher density (Norrdahl & Korpimäki 1993). On Svalbard, finding both good shelter and food in the same patch could be difficult for the voles, which may explain why they have not spread away from the area to which they were introduced. Winter conditions are harsh. The snow conditions depend very much on the wind, and occasional thaws with freezing rain may cause ice formation on the ground.

The arctic fox *Alopex lagopus* is an opportunistic

hunter and scavenger (e.g. Garrott, Eberhardt & Hanson 1983, Fay & Stephenson 1989, Stickney 1991, Angerbjörn, Hersteinsson, Lidén & Nelson 1994, Kaikusalo & Angerbjörn 1995, Anthony 1997). Throughout most of its circumpolar distribution the arctic fox preys on small mammals, notably various species of lemmings (reviewed by Frafjord 1995). On some arctic islands there are no small mammals, and arctic foxes depend mostly on sea birds. Bræstrup (1941) suggested that there are two groups or ecotypes of the arctic fox; inland (or lemming) foxes and coastal foxes (feeding on marine animals). On Svalbard there are no native arvicolines (microtines); the recently introduced vole has a very limited distribution between the towns of Grumant and Longyearbyen (Yoccoz et al. 1990). The questions asked were: Do voles occur in the diet of arctic foxes at Grumant, and if so, do they form a significant part of their diet? Are voles an important food source for arctic foxes during the summer (breeding) season? Are there any indications that the vole population affects arctic fox density or the number of litters?

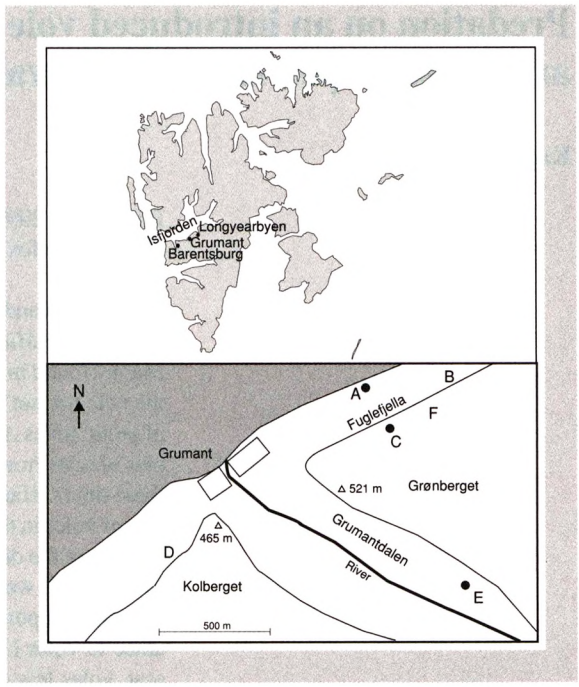

Figure 1. The study area at Grumant, Svalbard, with names of 'regions' and the positions of arctic fox litters (A-F) indicated.

Study area

Grumant is an abandoned Russian mining town, where some empty buildings are still standing. It is located on the southern shore of Isfjorden, between Longyearbyen and Barentsburg (78°11'N 15°09'E). Mining was discontinued in 1962. A population of the sibling vole is living in the region, mostly beneath the bird cliffs 'Fuglefjella' (Fig. 1). It is believed that the founders of the population were brought to Svalbard by Russian ships (Yoccoz et al. 1990, Ims & Yoccoz 1999). Beneath the bird cliffs there is a steep area with a thick bog and a very lush vegetation of grasses. The voles may find cover among stones, e.g. in the ridges along gullies with small streams in early summer, because the permafrost prevents much digging. Thousands of voles may live along a 10-km stretch of the coastline (Yoccoz et al. 1990). Earlier, voles have been found at a few other places on Svalbard, but Yoccoz et al. (1990) found no signs of voles outside Fuglefjella except at one site 10 km further south. They suggested that the vole may be the most abundant mammal on Svalbard, but in 1996 the population was low and fresh signs were few, perhaps following a hard winter.

Large colonies of sea birds exist in the region, mostly kittiwakes *Rissa tridactyla* and Brünnich's guillemot *Uria lomvia* on the cliffs Fuglefjella, and little auks *Alle alle* in the scree. Lush vegetation is also found in some areas in the colonies of little auks. Some reindeer *Rangifer tarandus platyrynchus* graze in the region during both summer and winter. In the winter of 1995/96, a thawing period resulted in much ice covering the ground, and many reindeer died. I found evidence of about 15 carcasses, which could make a significant contribution to the fox's winter diet. Ringed seals *Phoca hispida* and bearded seals *Erignathus barbatus* occur in the waters, but no haul-out place exists on the shore. Most likely there were six arctic fox litters in the region in 1996, as pups were observed at six different places (see A-F in Fig. 1), but few pups in each litter (Frafjord, Rofstad & Fuglei 1997). The only other predator in this area, the glaucous gull *Larus hyperboreus*, nests in considerable numbers.

Methods

Fox faeces (scats) were collected at various sites in the region surrounding Grumant during 19-30 July 1996 (see Fig. 1). Most scats were old (one to several years), and a few were even found embedded in the layer of moss covering the ground. Fresh scats of the season were collected from three litters (A, C and E). For litters A and C scats were collected at the natal den. Litter E had probably abandoned their natal den completely, and the scats were collected in a secondary

area where the pups were observed (Frafjord et al. 1997). Of the six litters (A-F) recorded in the region (see Fig. 1), two were out of reach (B and F). Scats were collected from the site were the sixth litter (D) was found, but few of them were fresh, and they were collected over a wider area. A large number of the scats at this site most likely were from the previous winter and spring, and were found along the ridge above the cliff. Consequently, they were assigned to the region 'Kolberget' (see Fig. 1). Other regions were 'Grumantdalen' (Grumant valley; excluding litter E), 'Beneath Fuglefjella' (beneath the cliffs of Fuglefjella; excluding litter A), and 'Grumant' (among the buildings of the 'city'). Samples collected in 1994 and 1995 by Rolf A. Ims and Nigel G. Yoccoz were also included, but with no specific region of collection given they were combined and classified as 'Unspecified'. Prey remains from the two dens A and C and the site of litter E were recorded, and a few observations of hunting foxes were included.

A total of 1,035 scats were analysed. Three methods were used: percent of occurrence, percent of volume and caloric value. All three methods give approximate results, but they may supplement each other. Food items were identified from hairs and feathers (Frafjord 1995), mostly to major groups only: vole, reindeer, birds, bird eggs, seal, arctic fox and invertebrates. Vegetable matter was ignored in this study. For each of the three litters A, C and E, a sample of 81 scats were analysed in more detail (i.e. 243 scats in total), identifying also the major groups of birds, alcids and gulls (Alcidae and Laridae), according to Frafjord (1993) and Hersteinsson (1984). Sample size was then determined by the size of the smallest sample (litter E). The results are given as percent of occurrence.

Furthermore, food items in each scat were arranged according to their significance, giving a simplified measure of their relative volume in the scat (major and minor items). The data were then recalculated using only the prey that made up the major part of each scat, giving the 'specific volume' as a simplified volume index. Including only the major prey item in each scat may give a simplified percent of volume, because this method does not pay attention to the more insignificant prey. This is in contrast to the frequency of occurrence method, which gives equal weight to every prey item in a scat.

The caloric value was calculated according to Hersteinsson (1984: 37), using the percent of occurrence and the specific volume as dry weight percentages. For birds, a wet weight conversion factor of 53 and a caloric value (calories/g wet weight) of 1.76 were used. For reindeer the values given for sheep were used (61 and 1.93), and the values for voles were 23 and 1.37, respectively (Hersteinsson 1984).

Results

Voles were found in all samples, but their proportion varied (Table 1). Voles were insignificant in the diet of the three litters A, C and E, but constituted about a third of the items in scats from 'Beneath Fuglefjella' and 'Grumant'. On average, the eight samples in Table 1 contained 13% voles, with a large standard deviation. Birds made up the largest proportion in all samples, and averaged nearly 80%. Reindeer also had a relatively large proportion which varied greatly between the samples. The pups of litters C and E had eaten small amounts of reindeer compared with the pups of litter A. The proportion of reindeer in the arctic fox diet was notably large in Grumant and on Kolberget (see Table 1). Most reindeer carcasses were found near Grumant. Other prey were insignificant.

The sum of the average percent of occurrence of the seven groups of prey was 120.5%; it exceeds 100% because one scat may contain remains of more than one prey. This also means that, in fact, most scats only contained one prey group (note that 'birds' may include several species). In most cases where more than one group

Table 1. Number and percent of occurrence of seven different prey types in scats from eight 'regions' at Grumant, Svalbard. At the bottom of the table mean and standard deviation are given.

	Prey type														No of
	Voles		Reindeer		Birds		Eggs		Seal		Fox		Invertebrates		scats
'Region'	N	%	N	%	N	%	N	%	N	%	N	%	N	%	analysed
Grumant	14	29.2	22	45.8	27	56.3	0		0		0		0		48
Beneath Fuglefjella	24	35.8	10	14.9	48	71.6	4	6.0	0		0		1	1.5	67
Grumantdalen	9	5.8	61	39.6	96	62.3	7	4.6	4	2.6	1	0.7	0		154
Kolberget	21	12.2	73	42.4	107	62.2	2	1.2	1	0.6	3	1.7	0		172
Litter A	8	3.7	35	16.4	207	96.7	16	7.5	2	0.9	3	1.4	0		214
Litter C	4	3.1	2	1.6	126	97.7	5	3.9	1	0.8	1	0.8	0		129
Litter E	2	2.5	4	4.9	79	97.5	3	3.7	3	3.7	0		0		81
Unspecified	24	14.1	16	9.4	154	90.6	7	4.1	1	0.6	0		0		170
Mean		13.3		21.9		79.4		3.9		1.2		0.6		0.2	
SD		12.7		17.9		18.0		2.4		1.3		0.7		0.5	

Table 2. Relative importance of voles, reindeer and birds in scats from the eight 'regions' at Grumant, Svalbard. The major and minor constituents sum to 100% in each type of prey.

	Major constituent						Minor constituent					
	Voles		Reindeer		Birds		Voles		Reindeer		Birds	
'Region'	N	%	N	%	N	%	N	%	N	%	N	%
Grumant	12	85.7	16	72.7	17	63.0	2	14.3	6	27.3	10	37.0
Beneath Fuglefjella	20	83.3	9	90.0	38	79.2	4	16.7	1	10.0	10	20.8
Grumantdalen	7	77.8	56	91.8	86	89.6	2	22.2	5	8.2	10	10.4
Kolberget	15	71.4	66	90.4	87	81.3	6	28.6	7	9.6	20	18.7
Litter A	5	62.5	9	25.7	198	95.7	3	37.5	26	74.3	9	4.3
Litter C	3	75.0	1	50.0	123	97.6	1	25.0	1	50.0	3	2.4
Litter E	0	0.0	1	25.0	79	100.0	2	100.0	3	75.0	0	0.0
Unspecified	14	58.3	14	87.5	142	92.2	10	41.7	2	12.5	12	7.8

was present, a single prey type made up the major part of the scat. The data were split into major and minor parts of the scat for the three main prey types: voles, reindeer and birds (Table 2). Birds formed a major part of the scat in all eight samples, voles in seven and reindeer in five. Thus, reindeer more often formed only a minor part of the scat than birds and voles, and notably so for the three litters. The average percentages for Table 2 are given in Figure 2. Birds more often formed the major prey type of scats than the two other prey types (Kruskal Wallis test: $\chi^2 = 6.3$, df = 2, $P = 0.04$), and consequently may be relatively more important than indicated by the frequency of occurrence in Table 1. Voles were on average least often the major prey type (see Fig. 2).

The relative significance of voles, reindeer and birds may be more correctly estimated using the percent of volume method (specific volume) than by the percent of occurrence. This method included on average 98% of the prey, with 10.1% voles, 17.0% reindeer and 70.9% birds. The results were significantly different from the percent of occurrence in Table 1 for voles, reindeer and birds, respectively (Wilcoxon Signed Rank tests: z = 2.4-2.5, $P < 0.05$), even though their proportions were about the same. The caloric value was calculated for voles, reindeer and birds using both the average percent of occurrence and the average specific volume. The percent of occurrence gave caloric percentages of 4.0%, 24.8% and 71.2%, respectively. The specific volume gave 3.6%, 22.4% and 74.0%.

Litter E was found in Grumantdalen (see Fig. 1), and although its natal den was not found, it was probably situated somewhere on the mountainside not far away. Large numbers of little auks were breeding there. The den of litter C was located on the ridge above the bird cliffs, and the den of litter A was beneath the bird cliffs close to the sea. Guillemots were generally breeding higher up in the cliffs, and were therefore more acces-

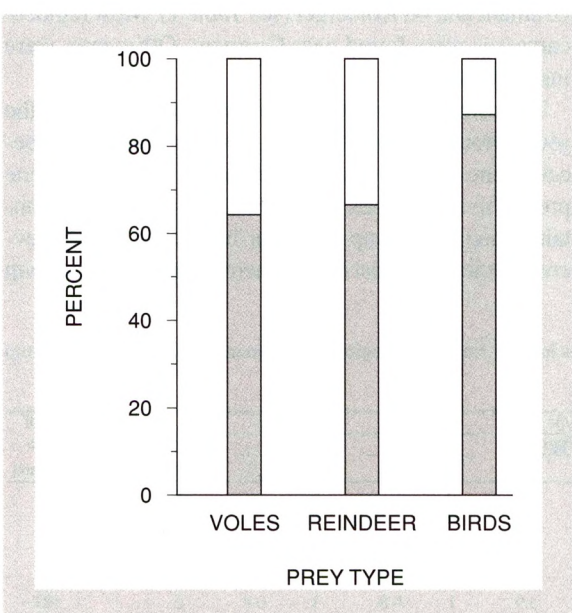

Figure 2. Relative importance of the prey types voles, reindeer and birds in scats expressed as major (■) or minor (□) contents. Calculated as the means of percentages given in Table 2.

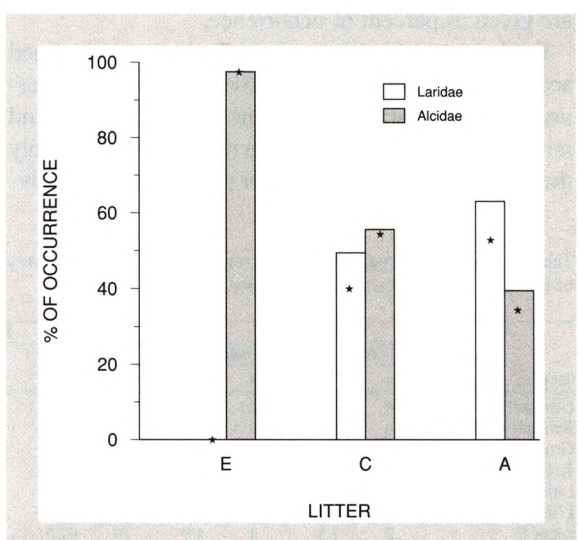

Figure 3. Percent of occurrence of Laridae (□) and Alcidae (■) in scats from the litters E, C and A with specific volumes indicated (*).

Table 3. Numbers of bird wings (of three bird species), bird eggs, and reindeer remains found at the dens or sites of the three litters A, B and C. The number of dead foxes found is also given (*sensu* Frafjord et al. 1997).

	Brünnich's guillemot	Little auk	Kittiwake	Bird eggs	Reindeer	Fox
Litter A	31	2	31	2	Some	3
Litter C	26	0	11	0	0	2
Litter E	0	Numerous	0	0	Some	0

sible from above than kittiwakes. The steep cliffs may have been difficult to climb for arctic foxes, but some kittiwakes were accessible from below. In addition, chicks and eggs falling off the ledge were a source of food beneath the bird cliffs. Litter E had only consumed alcids and no gulls (Fig. 3), litter C had consumed about equal amounts of alcids and gulls, and litter A had consumed more gulls than alcids ($\chi^2 = 81.5$, df = 2, $P < 0.001$). The results were about the same when calculating the specific volume (see Fig. 3). Litter A had the highest proportion of bird eggs in their diet (see Table 1).

These results were supported by the different prey remains found at den sites (Table 3) and by observations of hunting adults. Foxes beneath the bird cliffs were mainly patrolling below the bird colonies. The parents of litter E were observed giving pups little auks three times, and the adult female was once seen turning over a stone with her paw to capture an adult little auk. Adult foxes were observed on many occasions, but never seemed to search for voles, perhaps with one exception when a fox sniffed around a site possibly inhabited by voles.

Discussion

Several methods have been used to estimate prey types through scat analyses. The percent of occurrence estimate has been most frequently used, but the percent of volume or the caloric intake of prey may be better in some respects. My study gives all three estimates, although a very simplified percent of volume is used. The three different estimates gave comparable results for the relative proportion of voles, reindeer and birds, except that the significance of voles was reduced in the estimate of caloric value. Percent of occurrence may overestimate small prey because they have a greater ratio of indigestible/digestible matter. Percent of volume may underestimate large prey because they have a smaller indigestible/digestible ratio. Caloric intake additionally suffers from the use of a wet weight conversion factor and a caloric value (calories/g wet weight), which have not been estimated for all prey species, and which may also be affected by the digestive efficiency of the predator. Consequently, all estimates are approximate, and the true values for relative importance of prey probably lie somewhere between them. The frequency of occurrence of 13% voles may be somewhat too high, and the caloric intake of 4% voles may be too low. In fact, the simplest measure, specific volume (10% voles), may be the most useful.

The opportunistic nature of the arctic fox is reflected in its predation on the vole recently introduced to Svalbard. Arctic foxes may quickly have learned to exploit this new food source, but probably do not depend on it for reproduction or survival. Although it was the third most frequent prey type, its caloric value was relatively small compared to that of both birds and reindeer. The population of voles was very small in 1996 (Ims & Yoccoz 1999, Yoccoz & Ims 1999) and fresh signs were rare, which may explain the very low proportion of voles in the diet of the three litters from which fresh scats were collected. At other seasons or in other years, voles may form a more significant part of the arctic fox diet. Voles may possibly be found along a stretch of 10-15 km (*sensu* Yoccoz et al. 1990), but may not be evenly distributed. Their accessibility to foxes in summer or winter is not known.

Most studies on continental arctic foxes have confirmed the importance of small mammals, notably lemmings, in their diet (Frafjord 1995). Many arctic islands have one or more arvicoline species, which are hunted by arctic foxes (Hersteinsson & Macdonald 1996, Fay & Stephenson 1989). Where small mammals are absent, sea birds and other marine animals are the most common prey, and so are reindeer carcasses where they exist. Introduced rodents such as rats *Rattus norvegicus* in the Aleutians (West 1987) are hunted in small numbers. The wood mouse *Apodemus sylvaticus* in Iceland is also preyed upon by arctic foxes (Hersteinsson & Macdonald 1996). Rats and wood mice may be more wary and difficult to capture for arctic foxes than voles and lemmings. Arctic foxes living along the mountain Fuglefjella have recently gained access to a completely new type of prey, very different from any other prey that the arctic fox has been hunting on Svalbard during thousands of years. The arctic fox has a general, non-specialist hunting technique ('search, dash and capture') and is able to learn quickly and quickly adapt to new food types, so it is not surprising that the arctic fox

started to hunt voles. Arctic foxes in the Norwegian mountains seem to use the same general hunting technique, and probably rarely capture voles or lemmings by the 'mouse jump' common to red foxes *Vulpes vulpes*. In the summer of 1996, no fox was seen hunting voles at Fuglefjella, and their hunting technique is not known. However, playing arctic fox pups on Svalbard sometimes show the 'mouse jump' as they do in Norway (*sensu* Frafjord 1992).

The numbers of arctic foxes and litters at Fuglefjella were relatively high, although the mortality in 1996 was also particularly high (Frafjord et al. 1997). The number of scats found in the region was also high, and about the same as was found in a larger region during several seasons in northwestern Svalbard (Frafjord 1993). High concentrations of sea birds and possibly a larger population of reindeer may have supported more foxes, perhaps aided by the presence of voles. The proportion of reindeer in the diet of foxes at Fuglefjella was higher than in northwestern Svalbard (22 vs 0.4%), but less than in a study based on analyses of stomach contents (Prestrud 1992). The reindeer carcasses found had little or no edible matter left, and were probably largely consumed during the winter and spring by foxes and glaucous gulls. The larger proportion (about 40%) of reindeer in scats from some sites (Grumant, Kolberget and Grumantdalen) probably reflected this. This proportion is similar to the proportion found by Prestrud (1992) in arctic fox stomachs collected during the winter on Nordenskiöldland, of which the Grumant region is a part. However, seabirds were less significant in the study of Prestrud (1992); the proportions I found at Grumant were similar to those found along the northwestern coast of Svalbard (Frafjord 1993).

The different proportion of alcids and gulls in the diet of the three litters most likely reflected the availability of prey in their parents' ranges, assuming that most hunting took place close to the den. This may be due to the territoriality of adult foxes, or simply due to physical barriers between the ranges of several families. The linear distance between the dens of litter A and C was only about 200 m, but climbing up and down was most likely possible only by a detour around the cliffs. Despite this, several conflicts between adult foxes were witnessed beneath the cliffs between these two litters, which could indicate that the parents of litter C descended from the cliffs into the range of the other foxes.

Arctic foxes that depend on arvicolines for successful reproduction normally show cycles in the number of litters born, following the cycles of their major prey. On Svalbard, Prestrud (1992) found little or no overall fluctuation in the reproduction of arctic foxes. The Grumant region appeared to have a relatively dense population of foxes and many litters, which could be a result of the presence of introduced voles as additional prey. However, voles were unlikely to have had a significant impact on fox reproduction in 1996, both because the population of voles was very low and actually may have gone extinct in several areas, and because voles were insignificant in the diet of the three arctic fox litters. Nevertheless, some patches may still have held quite a large number of voles, which may have increased during the summer. Arctic foxes have been seen searching for and capturing voles in the fall (N.G. Yoccoz, pers. comm.), indicating that voles may be of significance in some seasons. The large number of sea birds (kittiwake, Brünnich's guillemot and little auk) is likely to influence the arctic fox population most, but if voles are available during the winter they may influence fox survival along with reindeer carcasses. The large mortality among fox pups in 1996 was more likely due to disease than to starvation (Frafjord et al. 1997). Evidence of cannibalism was found in scats from two litters, but this was not supported by the four dead pups that were recovered 'undamaged'. It appears that the population of voles at Grumant has only a marginal influence on the arctic fox population.

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